

Title	The impacts of past land-use on the ecology of an ancient woodland in south-west Ireland
Authors	Cudmore, Aileen V.
Publication date	2012-02
Original Citation	Cudmore, A.V., 2012. The impacts of past land-use on the ecology of an ancient woodland in south-west Ireland. PhD Thesis, University College Cork.
Type of publication	Doctoral thesis
Rights	© 2012, Aileen V. Cudmore. - http://creativecommons.org/licenses/by-nc-nd/3.0/
Download date	2025-07-06 16:49:54
Item downloaded from	https://hdl.handle.net/10468/520

The impacts of past land-use on the ecology of an ancient woodland in south-west Ireland

Aileen V. Cudmore, BSc. (Hons)



This thesis is presented to the National University of
Ireland, Cork, in fulfilment of the requirements for the
degree of Doctor of Philosophy

Research supervisors:
Dr. Simon Harrison
Prof. Peter Jones

Head of School: Prof. John O'Halloran

School of Biological, Earth and Environmental Sciences,
College of Science, Engineering and Food Science,
University College Cork

February 2012

TABLE OF CONTENTS

Declaration	vi
List of figures.....	vii
List of tables.....	xv
Abstract.....	1
Chapter 1: General introduction	3
1.1 The importance of history in ecology	4
1.2 Land-use change and woodlands.....	5
1.3 Woodland terms and definitions	7
1.4 Ancient woodland characteristics	8
1.5 Ancient woodland in Ireland	10
1.6 Study overview	12
1.7 References.....	15
Chapter 2: The evolution of the present-day landscape of the Gearagh woodland.....	21
2.1 Abstract	22
2.2. Introduction	22
2.3 Materials and methods	23
2.4 The Gearagh woodland	24
2.5 Woodland prior to AD 1650	29
2.5.1 Formation of the Lee Valley	30
2.5.2 Development of an anastomosing river channel	31
2.5.3 Early post-glacial period (11,000 – 7,000 BC).....	34
2.5.4 Mesolithic period (7,000 – 4,200 BC)	35

2.5.5 Neolithic period (4,200 – 2,000 BC).....	36
2.5.6 Bronze Age (2,000 – 500 BC)	36
2.5.7 Iron Age (500 BC – 500 AD)	37
2.5.8 Early Medieval period (500 – 1000 AD).....	39
2.5.9 Late Medieval period (1000 – 1650 AD).....	42
2.6 Woodland from AD 1650 to present.....	43
2.6.1 Landscape of the Gearagh AD 1650 - 1842	43
2.6.2 Landscape of the Gearagh AD 1842	48
2.6.3 Landscape of the Gearagh AD 1842 - 1904	51
2.6.4 Landscape of the Gearagh AD 1904 - 1938	55
2.6.5 Landscape of the Gearagh AD 1938 - present.....	57
2.7 Conclusions	59
2.8 References.....	60
Chapter 3: The impacts of land-use history on the soil properties in the	
Gearagh.....	68
3.1 Abstract	69
3.2 Introduction	69
3.3 Materials and methods	73
3.3.1 Study area and history.....	73
3.3.2 Site selection and sampling	75
3.3.3 Laboratory analyses.....	78
3.3.4 Data analyses.....	78
3.4 Results	79
3.4.1 Soil morphological characteristics.....	79
3.4.2 Soil chemical properties	87
3.5 Discussion.....	94

3.6 Conclusions	99
3.7 References.....	99
Chapter 4: The impacts of land-use history on vegetation composition in the Gearagh	105
4.1 Abstract	106
4.2 Introduction	106
4.3 Materials and methods	109
4.3.1 Vegetation sampling.....	109
4.3.2 Data analysis	111
4.4 Results	113
4.4.1 Tree stand composition and structure	113
4.4.2 Ground flora characteristics	117
4.4.3 Life-history characteristics.....	123
4.5 Discussion.....	126
4.5.1 Tree characteristics.....	126
4.5.2 Ground flora characteristics	129
4.5.3 Life-history traits.....	131
4.5.4 Ellenberg indicator values	133
4.6 Conclusions	135
4.7 References.....	135
Chapter 5: The impacts of land-use history on the seed bank and germination potential of woodland plants in the Gearagh	142
5.1 Abstract	143
5.2 Introduction	143
5.3 Materials and methods	148
5.3.1 Study site	148

5.3.2 Soil seed bank sampling.....	148
5.3.3 Seed germination and survival	150
5.3.4 Data analysis	152
5.4 Results	154
5.4.1 Seed bank composition	154
5.4.2 Seed germination and survival	159
5.5 Discussion	166
5.5.1 Seed bank composition	166
5.5.2 Seed germination and survival	170
5.6 Conclusions	173
5.7 References.....	174
Chapter 6: The impacts of land-use history on woodland decomposer populations and decomposition dynamics in the Gearagh	182
6.1 Abstract	183
6.2 Introduction	183
6.3 Materials and methods	187
6.3.1 Ground- and litter-dwelling invertebrates	187
6.3.2 Oligochaete communities.....	188
6.3.3 Bacterial community-level physiological profiling	188
6.3.4 Decomposition dynamics	190
6.3.5 Data analysis	191
6.4 Results	194
6.4.1 Ground- and litter-dwelling invertebrates	194
6.4.2 Carabid beetles	202
6.4.3 Oligochaete communities.....	207
6.4.4 Soil bacterial community-level physiological profile.....	209

6.4.5 Decomposition dynamics	213
6.5 Discussion	217
6.5.1 Community structure and functioning	217
6.5.2 Factors influencing community structure and functioning in response to land-use change	220
6.6 Conclusions	227
6.7 References.....	227
Chapter 7: General discussion.....	237
7.1 Importance of study	238
7.2 Indicators of ancient woodland	240
7.3 Survival of ancient woodland.....	244
7.4 Woodland management and restoration	247
7.5 Suggestions for further research	253
7.6 References.....	255
Acknowledgements	263
Appendix.....	265

DECLARATION

I hereby declare that the work presented in this thesis is to the best of my knowledge and belief original (except as acknowledged in the text) and is the result of my own independent work/investigation. This work has not previously been submitted in any form for another degree or diploma at any institution.

Signed _____

Aileen Cudmore

LIST OF FIGURES

Fig. 1.1 Diagram representing the different terms that are used to describe the land-use history of woodland sites. The terms ancient and secondary will be consistently used in this thesis. Adapted from Baeten (2010).	8
Fig. 1.2 Outline of the structure of the thesis and the main topics dealt with in each chapter. The chapter numbers are indicated by the numbers 2-6.....	13
Fig. 2.1 Map showing the location of the Gearagh in relation to features in the surrounding landscape.....	25
Fig. 2.2 First Ordnance Survey map (surveyed in the 1830s) showing the River Bandon, Co. Cork, flowing from north to south. The anastomosing channel pattern of the river can clearly be seen, although all the islands had been cleared of wooded vegetation. The town of Dunmanway lies directly west of the river.	33
Fig. 2.3 Location of national monuments in the area surrounding the Gearagh. Most of the pre-Christian monuments date from the Bronze Age. Many of the Early Christian monuments are ringforts and souterrains. Medieval monuments date from the 5 th to the 15 th century. Recent monuments date from the 15 th century to the present day.....	38
Fig. 2.4 The location of the Gearagh in relation to parish boundaries.....	41
Fig. 2.5 Civil Survey (1654-6) map of Macloneigh parish. The river Lee marks the northern and western extent of the parish. The tree symbols along the course of the river correspond with the present-day location of the Gearagh.....	45

- Fig. 2.6 Extract of the Taylor and Skinner map 1778 showing the roads around Macroom. A wooded area, indicated by tree symbols (circled in red), is marked along the river Lee in the same location as the Gearagh today..... 47
- Fig. 2.7 Extract of the first Ordnance Survey map from 1842 showing a section of the Gearagh, Co. Cork. The major channels and islands along the river Lee can be seen on the map. Many of the larger islands have been cleared of woodland (circled in red)..... 50
- Fig. 2.8 Extract from the first Ordnance Survey map (1842) showing the townland boundaries (thick red lines) and land ownership boundaries (fine red lines) in the area surrounding the Gearagh, as recorded in Griffith's Valuation of property in Ireland (1847-64). Islands that are clear of woodland evidently correspond to land ownership boundaries..... 52
- Fig. 2.9 Extract of the second Ordnance Survey map from 1904 showing a section of the Gearagh, Co. Cork. Islands in the northern section of the Gearagh that had previously been clear of woodland (Figs. 2.7 and 2.8) are now shown to have tree or scrub symbols (circled in red)..... 54
- Fig. 2.10 Extract of the third Ordnance Survey map from 1938 showing part of the Gearagh, Co. Cork. Most of the islands are now shown as woodland or scrub..... 56
- Fig. 2.11 Map showing the boundaries of the different woodland stands and grassland areas in a section of the Gearagh woodland used for this study..... 58
- Fig. 3.1 Locations of the habitat types within the Gearagh woodland that were used for investigation, including soil sampling. 75
- Fig. 3.2 Design of one sampling site, i.e. one of the replicate study sites, with the location of the soil sampling plots (grey plots) and soil pit outlined in black. The sampling designs used in other sections

of the thesis are outlined in grey; see Figs. 4.1, 5.2, and 6.1 for further details. Four of the nine 1 m × 1 m plots were randomly chosen for soil sampling, from which six subsamples were collected (dotted plots).....	77
Fig. 3.3 Soil profiles of the a) ancient woodland, b) old secondary woodland, c) recent secondary woodland, and d) grassland habitats in the Gearagh. Horizon notations for each of the profiles are also given. See Table 3.2 for description of soil horizon notation	80
Fig. 3.4 Principal components analysis of soil properties. The upper panel shows axis 1 and axis 2 plots for the soil property data collected from the four habitat types of the Gearagh. The lower panel shows the soil properties based on their eigenvectors (coefficients in the linear combinations of variables making up the first two principal components). Axis 1 = 28%, Axis 2 = 22 %, cumulative = 50 %.....	88
Fig. 3.5 Variation in soil properties at different depths (0-10 cm, 10-20 cm, 20-40 cm and 40-80 cm below the soil surface) for the four different habitat types of the Gearagh: Ancient woodland; Old secondary woodland; Recent secondary woodland; and Grassland. Mean values with standard error are shown	92
Fig. 4.1 Design of one sampling site, i.e. one of the replicate study sites, with the location of the nine ground flora sampling plots (grey plots) and the transect for sampling tree communities outlined in black. The sampling designs used in other sections of the thesis are outlined in grey; see Figs. 3.2, 5.2, and 6.1 for further details.	110
Fig. 4.2 Tree size distributions of the three historical woodland types in the Gearagh (dbh ≥ 5 cm; ten trees with dbh > 80 cm are not shown).	114
Fig. 4.3 Total number of multi-stemmed trees (possessing more than one primary stem) in the ancient, old secondary, and recent	

secondary woodland areas of the Gearagh; the main tree species are indicated. *B. pubescens*, *C. monogyna*, *I. aquifolium*, and *S. cinerea* spp. *oleifolia* are combined under Other. 117

Fig. 4.4 NMS ordination of woodland ground flora vegetation. The upper panel shows axis 1 and 2 plots for the three woodland sites in the Gearagh. The lower panel shows axis 1 and 2 plots of the 36 taxa used in the analysis. Cumulative variation in the original dataset explained by the ordination is 47 %: Axis 1 = 39 %, Axis 2 = 8 %, Final Stress = 5.8; Final Instability = 0.00001..... 119

Fig. 4.5 Mean (\pm standard error) Ellenberg indicator values for a) light, b) moisture, c) soil reaction, and d) nitrogen of indicator species for each of the four habitat types of the Gearagh. Any bars with a common letter within a figure are not significantly different using Tukey's honestly significant difference test ($P < 0.05$)..... 124

Fig. 5.1 A conceptual diagram showing the bottle-neck model of plant colonisation in ancient and secondary woodland. After dispersal from the parent plant, seeds are incorporated into a seed bank, which may be persistent or transient. From that, seed may germinate and develop into juvenile and then adult plants. The decreasing number of individuals through the various life stages due to mortality and predation is represented by the funnel-shaped lines for both the ancient and secondary woodland. Dispersal limitation (arrow A) causes lower seed availability in the secondary woodland. Establishment limitation, caused by altered environmental conditions, may cause further loss of individuals in the secondary woodland (arrow B). The strength of the environmental effect may vary between species and is highly dependent on the nature of the former land-use (adapted from Hermy & Verheyen, 2007) 146

Fig. 5.2 Design of one sampling site, i.e. one of the replicate study sites, with the location of the seed bank sampling plots (grey plots) and

the seed sowing experiment outlined in black. The sampling designs used in other sections of the thesis are outlined in grey; see Figs. 3.2, 4.1, and 6.1 for further details. Three of the nine 1 m × 1 m plots were randomly chosen for seed bank sampling, from which eight soil cores were collected (dotted plots).	149
Fig. 5.3 Design of one experimental block, i.e. woodland site. The three species were introduced into the three subplots (Sp. 1-3) as seeds.....	151
Fig. 5.4 Characteristics of the seed bank data for the four habitat types in the Gearagh per depth layer, showing (a) species richness, (b) total seed density, and (c) density of <i>Juncus effusus</i> seeds. Mean values ± standard error are shown. Significant differences between the treatments are indicated with different letters above the bars; any bars with a common letter are not significantly different using Tukey's honestly significant difference test ($P > 0.05$).	156
Fig. 5.5 Mean (± standard error) Ellenberg indicator values for (a) light, (b) moisture, (c) soil pH, and (d) nitrogen of seed bank species for each of the four habitat types of the Gearagh per soil layer. Significant differences between the treatments are indicated with different letters above the bars; any bars with a common letter are not significantly different using Tukey's honestly significant difference test ($P > 0.05$).....	157
Fig. 5.6 Mean (± standard error) Sørensen's similarity index between seed bank and vegetation composition for the total sample depth (0-20 cm) per habitat type in the Gearagh. Letters above each bar signify Tukey's honestly significant differences between the habitat types ($P > 0.05$) after testing with ANOVA; any two bars with a common letter are not significantly different.....	163

- Fig. 5.7 Mean (\pm standard error) numbers of (a) *Anemone nemorosa*, (b) *Hyacinthoides non-scripta*, and (c) *Primula vulgaris* seedlings recorded per 150 seeds sown over the sampling period in each of the three woodland habitats of the Gearagh..... 164
- Fig. 6.1 Design of one sampling site, i.e. one of the replicate study sites, with the location of the pitfall traps (grey circles), earthworm sampling plots (grey plots), and soil cores for the bacterial community-level physiological profiling (black dots) outlined in black. The sampling designs used in other sections of the thesis are outlined in grey; see Figs. 3.2, 4.1, and 5.2 for further details. Six of the twelve 0.25 m \times 0.25 m plots were randomly selected for earthworm sampling (hatched plots) 189
- Fig. 6.2 NMS ordination of ground- and litter-dwelling invertebrates captured in pitfall traps. The upper panel shows axis 1 and axis 2 plots for all sites in the four habitat types of the Gearagh. The lower panel shows axis 1 and axis 2 plots of the 35 taxa selected by the analysis as the most important (score greater than ± 0.2). Cumulative variation in the original dataset explained by the ordination is 51 %: Axis 1 = 43 %, Axis 2 = 8 %, Final Stress = 9.2; Final Instability = 0.00001..... 198
- Fig. 6.3 Total number of mobile surface-dwelling individuals according to feeding preference group in each of the four habitat types from the total sampling effort. The three most abundant Collembolan groups (Dicyrtominae, Hypogastrurinae, and Sminthuridinae) were excluded in order to aid interpretation. 202
- Fig. 6.4 Percentage of individuals in each total habitat catch that belong to each carabid beetle class for (a) habitat preference and (b) microhabitat preference 205
- Fig. 6.5 NMS ordination of carabid beetle assemblages captured in pitfall traps. The upper panel shows axis 1 and axis 2 plots for all sites in

the four habitat types of the Gearagh. The lower panel shows axis 1 and axis 2 plots for the carabid species. Cumulative variation in the original dataset explained by the ordination is 93 %: Axis 1 = 63 %; Axis 2 = 30 %; Final stress = 10.21; Final Instability = 0.00001. 206

Fig. 6.6 Mean (\pm standard error) abundance (individuals m^{-2}) of (a) earthworms and (b) enchytraeids in the four habitat types of the Gearagh. Letters above each bar signify Tukey's honestly significant differences between the habitat types after testing with ANOVA; any two bars with a common letter are not significantly different ($P \geq 0.05$). 208

Fig. 6.7 Mean (\pm standard error) abundance (individuals m^{-2}) of earthworms divided into ecological categories in the four habitat sites (excluding juveniles). Letters above each bar signify Tukey's honestly significant differences between the habitat types ($P < 0.05$) after testing with ANOVA; any two bars with a common letter are not significantly different. 210

Fig. 6.8 Average well colour development (AWCD) (a), substrate diversity (b), substrate evenness (c), and substrate richness (d) of the microbial community in the four habitat types of the Gearagh after incubation with Biolog EcoPlatesTM. All show significant differences after Kruskal-Wallis test ($P < 0.05$). Significant differences between habitat types are indicated with different letters; any two bars with a common letter are not significantly different using the Tukey test ($P > 0.05$). 211

Fig. 6.9 Principal components analysis (PCA) of individual carbon resource utilisation in soils incubated over 72 hours in Biolog EcoPlatesTM. The upper panel shows axis 1 and axis 2 plots for the four habitat types of the Gearagh. The lower panel shows the carbon sources based on their eigenvectors (coefficients in the linear combinations of variables making up the first two principal

components). The first two axes of the PCA plot account for 37.2 % of the cumulative total variation in carbon source utilisation	212
Fig. 6.10 Interaction between habitat (ancient, secondary or grassland), mesh size (coarse (10 mm), medium (2 mm) or fine (0.5 mm)), and position (surface, buried at 5 cm depth, or buried at 20 cm depth). Bars represent mass loss (mean \pm standard error) after 120 days in the field	215
Fig. 6.11 Mean (\pm standard error) quantity (black bars) and depth (white bars) of litter on the woodland floor in each of the four habitat types of the Gearagh. Letters above each bar signify Tukey's honestly significant differences between the habitat types ($P <$ 0.05) after testing with ANOVA; any two bars with a common letter are not significantly different.	216
Fig. 6.12 Mean (\pm standard error) annual litterfall biomass in each of the four habitat types of the Gearagh; the main components of the litterfall are also indicated. There is no significant difference in litterfall biomass between the sites after testing with ANOVA	216
Fig. 7.1 Diagram illustrating the main changes and processes that occurred in the Gearagh during conversion of ancient woodland to grassland and the subsequent regrowth and development of woodland from recent secondary to old secondary.	249
Fig. A.1 Species area curve of ground flora collected using nested quadrats, which was used to determine the minimal sampling area required to sample the plant communities in the Gearagh (Chapter 4). The point on the curve that represents the area which contains 95 % of the total number of species is indicated with a dashed line. Each point represents the mean of 14 samples (\pm standard error)	266

LIST OF TABLES

Table 2.1 Historical overview of Irish woodland development to the present-day.....	25
Table 3.1 (a) Soil profile description of the ancient woodland. See Table 3.2 for description of soil horizon notation.....	81
Table 3.1 (b) Soil profile description of the old secondary woodland. See Table 3.2 for description of soil horizon notation.....	82
Table 3.1 (c) Soil profile description of the recent secondary woodland. See Table 3.2 for description of soil horizon notation.....	83
Table 3.1 (d) Soil profile description of the grassland. See Table 3.2 for description of soil horizon notation	84
Table 3.2 Description of selected soil horizon notation (adapted from Avery, 1980).....	85
Table 3.3 Physical properties of the mineral soil profiles from the four habitat types of the Gearagh. The bulk density and coarse fragment contents from the C horizon in the ancient woodland and old secondary woodland could not be measured due to inadequate samples.....	86
Table 3.4 Pearson's Product Moment correlation coefficient matrix of PCA axis 1, 2 and 3 scores of soil properties in the Gearagh. Significance levels of Pearson's Product Moment correlation coefficient shown where applicable: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$	89
Table 3.5 Results from two-way ANOVA on (a) pH(H ₂ O), (b) pH(CaCl ₂), (c) loss-on-ignition, (d) moisture, (e) phosphorus, (f) calcium, (g) magnesium, (h) manganese, and (i) iron with Habitat (Ancient, Old secondary, Recent secondary, or Grassland) and Depth (0-10	

cm, 10-20 cm, 20-40 cm, or 40-80 cm) as treatments. Data that were ln-transformed prior to analysis are indicated with *	91
Table 4.1 Mean values (\pm standard error) of the structural characteristics in the three woodland types in the Gearagh. Results of ANOVA test are shown	114
Table 4.2 Characteristics of the most frequent tree and shrub species in the three historical woodland types of the Gearagh (stems \geq 5 cm dbh). Mean values and results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different superscript letters; any two with a common letter within a row are not significantly different ($P \geq 0.05$)	115
Table 4.3 Main types of coarse woody debris as a percentage of total dead stems in each of the three historical woodland types of the Gearagh. Mean values and results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different letters; any two with a common letter within a row are not significantly different ($P \geq 0.05$).....	116
Table 4.4 Differences in average number of ground flora species, total cover, Shannon-Wiener diversity index, and Pielou's evenness between the four habitat types in the Gearagh. Median values and results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different letters; any two with a common letter within a row are not significantly different ($P \geq 0.05$).	118
Table 4.5 Summary of the multi-response permutation procedures analysis comparing all habitat types of the Gearagh.....	120
Table 4.6 Indicator species and their indicator values of ground flora vegetation for each of the four habitat types in the Gearagh. Species with a significant indicator value ($P \leq 0.05$) are shown in	

bold. Significance of 1000 permutations in a Monte-Carlo test: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$	121
Table 4.7 Differences in Ellenberg indicator values between the four habitat types in the Gearagh. Median values and results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different letters; any two with a common letter within a row are not significantly different ($P \geq 0.05$).	123
Table 4.8 Differences in the relative contribution of the life-forms expressed as species and cover values between the habitat types of the Gearagh. Mean values and results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different letters; any two with a common letter within a row are not significantly different ($P \geq 0.05$).	125
Table 4.9 Differences in the dispersal modes expressed as species and cover values between the habitat types of the Gearagh. Mean values and results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different letters; any two with a common letter within a row are not significantly different ($P \geq 0.05$).	126
Table 5.1 Woodland plant species included in the study. For each species, the mean seed mass (mg), life-form, seed production, dispersal mode, and leaf phenology are indicated.....	150
Table 5.2 Characterisation of the experimental sites in the ancient, old secondary, and recent secondary woodland stands. Percent cover (mean of 30 subplots \pm standard error) of four ground cover types in the three woodland stands is given. The total ground cover may be over 100 % due to overlap of ground cover types	152
Table 5.3 Results from two-way ANOVA on seed data with Habitat (Ancient, Old secondary, Recent secondary, or Grassland) and Depth (0-10	

cm or 10-20 cm) as factors. Data that were log transformed prior to analysis are indicated with *	155
Table 5.4 Results of two-way PERMANOVA testing the effects of Habitat and Depth on Sørensen (Bray-Curtis) distances for the composition and relative abundance of soil seed banks collected in the Gearagh	158
Table 5.5 Species occurring in the seed bank in each habitat type of the Gearagh. Species are listed according to Indicator Value (IV). Species with a significant indicator value ($P \leq 0.05$) are shown in bold. Significance of Monte-Carlo tests: * $0.01 < P \leq 0.05$; ** $0.001 < P \leq 0.01$; *** $P \leq 0.001$. The percentage frequency of occurrence of each species in the seed bank, the ground flora vegetation, and the canopy layer in the four different habitat types of the Gearagh is also given.....	160
Table 5.6. Results of a two-way ANOVA on the effect of woodland habitat and year on the maximum number of seedlings that emerged in each year of the three study species. Values with significant differences are shown in bold ($P \leq 0.05$). Data that were log transformed are indicted with *	165
Table 6.1 Total number of individuals and relative abundance of each macrofaunal taxon group from the four habitat types of the Gearagh (excluding microfauna: Acarina and Collembola) from the total pitfall sampling effort. Significance of a one-way chi-squared test on the frequency of individuals per habitat type in each taxon group is given.....	195
Table 6.2 Mean (\pm standard error) values of total ground-dwelling invertebrate and carabid species diversity indices per sampling site in the four different habitat types of the Gearagh. Results of a one-way ANOVA are given. Significant differences between habitat types are indicated with different superscript letters; any	

two within a row with a common letter are not significantly different ($P \geq 0.05$).....	196
Table 6.3 Average number of microfauna (Acarina and Collembola) per trap site in the four habitat types of the Gearagh. Results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different superscript letters; any two within a row with a common letter are not significantly different ($P > 0.05$).....	197
Table 6.4 Ground- and litter-dwelling invertebrates identified in each habitat type of the Gearagh by Indicator Species Analysis and their feeding preference. Taxa with a significant indicator value ($P \leq 0.05$) are shown in bold. Significance of Monte-Carlo tests: $*P \leq 0.05$; $**P \leq 0.01$; $***P \leq 0.001$. See text (section 5.3.1) for a list of keys used to obtain information on feeding preference	200
Table 6.5 Abundance (%) of carabid species trapped in the four different habitats of the Gearagh that makes up $> 1\%$ of the catch of at least one habitat during sampling. Results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different superscript letters; any two within a row with a common letter are not significantly different ($P \geq 0.05$). Habitat and micro-habitat preference based on information from Luff (2007)	204
Table 6.6 Mean abundance (individuals/m ²) of common earthworm taxa (those occurring in at least 5 % of all samples) in the four habitat types of the Gearagh. Results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different superscript letters; any two within a row with a common letter are not significantly different ($P \geq 0.05$).....	209
Table 6.7 ANOVA summary of log transformed earthworm abundances comparing the ecological categories (epigenic, endogenic, or	

anecic) in the four habitat types of the Gearagh (ancient woodland, old secondary woodland, recent secondary woodland, or grassland).	210
Table 6.8 ANOVA results for the litter decomposition experiment after log transformation of the data. The factorial design consisted of three factors for the evaluation of mass loss: habitat (ancient, secondary or grassland), mesh size (coarse, medium or fine), and position (surface, buried at 5 cm or buried at 20 cm). There were five replicates for each treatment.....	214
Table 7.1 Summary of main findings indicating differences between the ancient woodland and the other habitats of the Gearagh. Some markers are only suggestive of woodland history (vegetation, carabid beetles), while others are stronger indicators of ancient woodland (soil type, oligochaetes, seed bank density).	241

ABSTRACT

A multi-disciplinary study was conducted to compare stands of ancient and secondary origin within a single wood, the Gearagh woodland, County Cork. These sites were compared with adjacent areas of grassland, which provided a reference for the former land-use (pasture) of the secondary woodland.

A historical study confirmed that while the core of the Gearagh has been subject to minimal human interference, other sections have been cleared in the past for agricultural purposes. Investigations into soil structure and composition showed that soil properties in these secondary woodland areas were significantly altered by this past woodland clearance and conversion to agriculture, while the soil of the ancient woodland showed little signs of disturbance. The vegetation community also differed between the two woodland areas, partly due to altered environmental conditions. Many of the ancient woodland plant species were unable to form a persistent seed bank, while there was increased representation of species associated with more open-habitat conditions in the seed bank of the secondary woodland. While germination of woodland species was low in all sites, overall, seeds tended to germinate more successfully in the ancient woodland. The ancient woodland also provided a suitable habitat for many soil and ground detritivores, most notably enchytraeids, although earthworms were not abundant. Past agricultural use, however, changed the decomposer community considerably, with increased representation of earthworm species and a decline in the abundance of enchytraeids in the secondary stands.

In conclusion, the legacies of historical agricultural activities can continue to significantly affect the structure and composition of present-day woodlands so that they may differ considerably from undisturbed ancient woodland stands, even within the same woodland. A greater understanding of the origin, development and ecological functioning of ancient woodlands should aid in determining future conservation and management requirements.

CHAPTER 1

GENERAL INTRODUCTION

1.1 The importance of history in ecology

In recent years, there has been an increasing awareness about the important role that past disturbances can play in shaping the structure and functioning of present-day ecosystems (Christensen, 1989; Foster *et al.*, 2003; Rhemtulla and Mladenoff, 2007). Often, the legacies of historical events, both natural and anthropogenic, can persist for several hundreds and even thousands of years (Dupouey *et al.*, 2002; Foster *et al.*, 2003). A greater understanding of these historical patterns can therefore provide useful information on the development, functioning, and composition of contemporary ecosystems, and also contribute to future management and restoration decisions (Swetnam *et al.*, 1999; Foster, 2000; Bürgi and Gimmi, 2007; Jackson and Hobbs, 2009). Failure to include a historical perspective when assessing modern landscape patterns can potentially lead to the development of inappropriate management strategies (Foster, 2000).

The history of an ecosystem includes any changes in the patterns and processes of that system that have occurred in the past (Rhemtulla and Mladenoff, 2007). Often these changes are due to natural disturbance events such as pathogen outbreaks, climate change, and fire (Hotchkiss *et al.*, 2007). However, more often than not, they are due to human-induced modifications of the landscape (Bowman, 1998; Goudie, 2006). Indeed, few ecosystems have managed to avoid the effects of some form of human activity over time. Although the impact of man on the landscape has long been recognised (Marsh, 1865), it is only in recent decades that the true extent and consequences of these impacts have begun to be appreciated (Birks, 1988; Turner, 1990; Goudie, 2006). Certainly, human activities have helped to shape landscapes and ecosystems for thousands of years. A growing body of evidence suggests that even prehistoric human activity had substantial impacts on the environment (Butzer, 1996; Redman, 1999; McIntosh *et al.*, 2000; Briggs *et al.*, 2006). These past actions can affect ecosystems in numerous ways. For instance, they can lead to changes in community composition, successional dynamics, soil structure, hydrology, and nutrient cycling. Investigations into the range and extent of these historical human impacts can provide a greater understanding of the ability of an ecosystem to recover from past disturbances (Foster, 2000). Such research is

also crucial for understanding the potential legacies of present-day land-uses, and for developing suitable management strategies in the future, particularly with regard to ecosystem restoration.

1.2 Land-use change and woodlands

The most significant impact of man on the temperate landscape has undoubtedly been the deliberate removal of woodland to create agricultural land (Rackham, 1980; Peterken, 1993; Foster *et al.*, 1998; Kirby and Watkins, 1998). The creation of agricultural land can modify the landscape in two ways: (i) through the removal of existing vegetation (including canopy-forming trees and understorey plants), and (ii) by altering environmental conditions (such as nutrient availability, hydrology, and soil structure). Consequently, the composition of plant and animal communities can be influenced by past agricultural activity both directly, through disturbance, and indirectly, through its impact on the abiotic and biotic environment (Hermy *et al.*, 1999; Honnay *et al.*, 2004; Flinn and Vellend, 2005; Hermy and Verheyen, 2007). Although stands of trees are apparently capable of re-establishing quite rapidly following agricultural abandonment, these woodlands are in fact quite vulnerable to past human impacts (Magnuson, 1990). It has been widely observed that woodland recovery from past disturbances is a very slow process that may take tens to hundreds of years, particularly with regard to the soil properties and ground flora vegetation (Honnay *et al.*, 2004). In some cases, it seems that systems may never be able to return to their pre-disturbance state (Dupouey *et al.*, 2002).

The extensive deforestation of temperate woodlands and subsequent recovery after agricultural abandonment has been well documented in both Europe and North America. In eastern North America, the majority of woodland clearances for agriculture only began with the arrival of European colonists during the 17th and 18th centuries (Foster *et al.*, 1998; Flinn and Vellend, 2005). The relatively short period since European settlement means that land-use history in North America is relatively straightforward; usually, it involves a single deforestation phase followed by a single phase of recovery. For instance, in most regions, exploitation of woodlands reached a peak during the 19th century. This area of woodland then

gradually increased again during the early 20th century (Foster *et al.*, 1998), in part due to the shift of agriculture to the mid-west of North America. Those areas that remained unaltered by human activity are often referred to as ‘old-growth forests’.

In north-western Europe, however, historical human impacts on the landscape are often far more complicated. Pollen analyses have revealed that the first woodland clearances for agriculture occurred over 5,000 years ago during the Neolithic period (Bradshaw, 2004). Grazing of livestock was probably the principal factor in reducing woodland area, as this would have restricted tree regeneration (Bradshaw and Mitchell, 1999). However, the first phase of large-scale woodland removal in most of Europe occurred during the Roman period, as intensive settlements spread throughout the continent. Indeed, evidence of Roman agriculture from nearly 2,000 years ago still exists in present-day woodlands in northern and central France (Dupouey *et al.*, 2002; Dambrine *et al.*, 2007; Plue *et al.*, 2008). The long history of human activity in Europe also means that the current wooded areas are often the result of several periods of woodland clearance and re-colonisation. For instance, following the collapse of the Roman Empire, certain agricultural areas went into decline and woodlands began to recover. This was followed by another great phase of deforestation in central and western Europe from 1050 onwards, which lasted for about 200 years (Goudie, 2006), although the timing and extent of these land-use changes varied considerably from one region to another. In most European countries, the area of woodland cover reached its lowest level during the 18th and 19th centuries (Kirby and Watkins, 1998). These subsequent patterns of agricultural expansion and contraction frequently occurred in different locations to those from earlier periods. Consequently, modern surviving woodlands often consist of a mixture of stands with different land-use histories (Verheyen *et al.*, 1999). This variation is likely to have an effect on current woodland structure, function and biodiversity, and will continue to do so in the future. In recent decades, the pattern of woodland development in Europe has mainly been one of spatial expansion, due to commercial planting of coniferous species and because of the widespread collapse of traditional forms of land-use, particularly extensive grazing (Forest Europe *et al.*, 2011).

1.3 Woodland terms and definitions

The term 'forest' is now used to describe an area with a high density of trees, including artificial plantations and natural habitats. However, the original word in English simply referred to an area of land legally set aside for hunting of deer, which did not necessarily contain many trees (Rackham, 2000). In this thesis, to avoid confusion between the different meanings of 'forest', the words 'wood' and 'woodland' will be used instead to describe land on which trees have arisen naturally.

Woodland in its natural state which has never been altered by man is referred to as 'virgin woodland'. However, it is unlikely that any virgin woodland still remains in north-west Europe due to the pervasive impact of humans on the landscape. Instead, an alternative method of classifying woodlands based on their historical continuity is used (Rackham, 1980; Peterken, 1993). Under this classification scheme, 'primary woodland' is defined as woodland that has existed continuously since the end of the last glacial period when the original Holocene woodlands first developed. However, because agricultural use often pre-dates historical records in Europe, it is difficult to define conclusively the status of primary woodland. Instead, woodlands are generally classified as 'ancient woodland', that is, woodlands that have been continuously wooded since at least the oldest available historical data. In contrast, 'secondary woodlands' are those woodlands that have established since that date on sites that had previously been used for agriculture. The terms ancient and secondary will be consistently used in this thesis. Although strictly both terms refer only to woodland continuity, in this instance they will be used to indicate important differences in land-use history.

Many secondary woodlands in Europe have developed due to active policies of site restoration wherein one or two particular tree species have been planted after agricultural abandonment (Forest Europe *et al.*, 2011). Natural secondary woodlands are comparatively rare in the contemporary landscape. As a result, few studies investigate ecological processes in woodlands that have regenerated naturally. In this thesis, secondary woodland refers to those woodlands that have

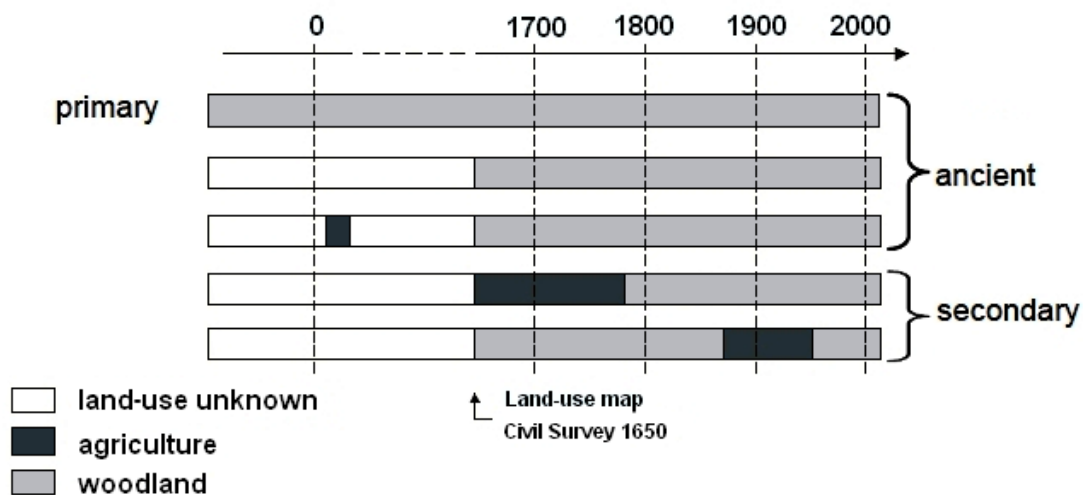


Fig. 1.1 Diagram representing the different terms that are used to describe the land-use history of woodland sites. The terms ancient and secondary will be consistently used in this thesis. Adapted from Baeten (2010).

established naturally within the past 200 years (Fig. 1.1). Ancient woodland refers to sites that have not been used for agriculture since the threshold date of 1650, which is when the first comprehensive survey (the ‘Civil’ survey) of Irish land took place (Fig. 1.1). Although previous clearances or traditional forms of agriculture at some point in the history of these ancient woodlands cannot be ruled out (Dupouey *et al.*, 2002; Dambrine *et al.*, 2007; Plue *et al.*, 2008), those practices would have occurred long before the development of intensive agriculture. Accordingly, the potential legacies of past agriculture are much smaller in ancient compared to secondary sites.

1.4 Ancient woodland characteristics

The term ‘ancient woodland’ originated in England, where it was originally defined to be an area of land that had been wooded continuously since at least the year 1600 (Rackham, 1980; Peterken, 1993). In recent years, inventories in several countries have confirmed the scarcity of this habitat (Kirby and Watkins, 1998; Forest Europe *et al.*, 2011), and it is now widely regarded as a priority for conservation (Thomas *et al.*, 1997), particularly woods that were never greatly

modified by human activities. Moreover, ancient woodlands provide an opportunity to investigate long-term ecosystem dynamics, and can provide valuable baselines against which to measure the effects of human disturbance on woodland structure and function.

Ancient woodlands, because of their long continuity on a site, have important cultural values, and can provide useful insights into past land-use and woodland management (Goldberg *et al.*, 2007). In north-western Europe, they are associated with the tradition of coppicing, whereby understorey trees are cut periodically (generally every 10 to 30 years) to provide timber for tools, construction and firewood (Peterken, 1993; Rackham, 2000). Ancient woodlands are also associated with the preservation of undisturbed soils and watercourses, which would otherwise have been altered in the modern landscape. They often contain important archaeological features such as old historical boundaries, charcoal-pits, limekilns and ancient coppiced and pollarded trees, which often live for much longer than natural, unmanaged trees (Rackham, 1980).

Ancient woodlands also often contain communities of plants and animals that are rarely found in more disturbed, secondary woodland or plantations (Hermy *et al.*, 1999). Extant areas of ancient woodland are therefore important sites for the conservation of these species both as refugia and as a source of colonists for new habitats (Goldberg *et al.*, 2007).

Although ancient woodlands have a history of continuous tree cover, many have been subject to a range of management practices in the past. Indeed, exploitation is an integral part of the history of most woodlands, and so present-day ancient woods are often highly varied in structure and composition (Rackham, 1980). Historically, woodlands have been managed for a wide variety of purposes, including traditional coppicing, charcoal production, fruit-picking, game hunting, livestock grazing, and the removal of leaf litter. Not only do these activities frequently change woodland structure and composition (Rackham, 1980), but they can also affect the plant and animal communities of present-day woodlands (Kirby and Watkins, 1998). For instance, intensive deer grazing has been found to affect

the relative cover of different species of ground flora in a woodland (Kirby, 2004), while woods that were used as pastures to graze livestock often developed impoverished ground flora. In addition, the widespread practice of coppicing is known to favour certain tree species (e.g. hazel, elm) over others (e.g. pine, beech). Regular coppicing also maintains the presence of more light-demanding, long-lived species in the ground vegetation that would otherwise be rare or absent (Peterken, 1996). Traditional woodland uses such as the collection of leaf litter can result in considerable biomass removal and lower nutrient availability over time (Bürgi and Gimmi, 2007). Even Białowieża Forest in Poland, which is often regarded as being one of the last remnants of primary woodland in Europe, has a extensive history of human exploitation and much of it is now being managed for commercial timber (Peterken, 1996). In Britain, many woodlands have undergone complex ecological modifications since 1900 due to several changes in woodland policies and management that have occurred over the course of the century (Spencer and Kirby, 1992; Hopkins and Kirby, 2007). Because of the overall impact of human activities, studies on woodlands that have experienced low intensity and frequency of human disturbance are particularly valuable; they can provide useful insights into natural disturbance regimes, woodland dynamics, soil development, biogeochemical cycling, and species-site relationships (Foster *et al.*, 1996). However, few ecological studies have investigated the dynamics of ancient woodlands with low disturbance regimes (Emborg *et al.*, 2000).

1.5 Ancient woodland in Ireland

In Ireland, ancient woodland is defined as an area that has been continuously wooded since at least 1650, the date of the first comprehensive historical land survey. Only 123 such stands still remain in the Republic (Perrin and Daly, 2010), and 1,033 hectares in Northern Ireland (Anon., 2007); this corresponds to approximately 10 % of all native woodland sites across the whole island or just 0.1 % of the total land cover. In contrast, commercial conifer plantations cover over 8 % of the country. The majority of native broadleaved woodlands are quite small (less than 10 ha), with just ten woods in the entire country reaching over 100 ha in size (Perrin *et al.*, 2008). In general, ancient woodland stands, which average 13.5 ha in

size, tend to be slightly larger than more recent native woodlands, which are often only 7.8 ha in size (Perrin and Daly, 2010). Most ancient woods are located in counties Wicklow, Kerry, Galway, and Waterford, and often occur along parish boundaries.

Unlike the rest of Europe, where the conservation importance of ancient woodlands has long been recognised, the value of these remaining stands is only now being acknowledged. Many of these woods are located on inaccessible sites or on marginal agricultural land. For instance, the survival of a small wood at Knockagh in County Antrim has been largely attributed to the steepness and inaccessibility of the site (Cooper, 1984). Consequently, many of these woodlands may be unusual with respect to environmental conditions and species composition, structure, and productivity.

Many of those woods that have been designated as ancient actually have a history of significant human disturbance (Bohan, 1998). For instance, Derrycunihy wood in County Kerry has a history of repeated human exploitation, even though woodland is thought to have been maintained on the site for several thousand years (Mitchell, 1988). These past disturbances, including timber extraction, grazing and planting, have led to a reduction in the ecological and structural diversity of the wood. Another example is St. John's Wood in Roscommon, which has a history of many centuries of coppice; this was last coppiced in the 1920s (Rackham, 1995). Some ancient woods, such as Brackloon Wood in County Mayo, have evidence of human occupation dating back to the Bronze Age c. 3,000 years ago (Little, 2004). Continuous human impact in this woodland has led to a considerable alteration in biodiversity and to the impoverishment of the soil. Other ancient woods, for example Derryclare Wood in County Galway (Fahy and Gormally, 1998), have been planted with non-native conifers within the last 100 years.

Ancient woodlands in Ireland also face a number of problems. The majority of woodlands are small, with most sites being less than 15 hectares in size (Perrin and Daly, 2010). This makes them particularly vulnerable to clearance and neglect. Many woods are also under threat from invasive alien species such as

Rhododendron ponticum, *Prunus laurocerasus* and *Impatiens glandulifera*, many of which can outcompete native species. Increased browsing by sheep, feral goats, deer, and cattle may also lead to the loss of the understorey vegetation, leading to a decline in the shrub layer and increase in grass species and bracken (Kelly, 2005). Overgrazing may even suppress tree regeneration and threaten the continued existence of the wood (O'Sullivan and Kelly, 2006).

1.6 Study overview

The study area chosen for this research was the Gearagh woodland (N 51°52'09", W 9°01'00"), County Cork in south-west Ireland. This site was chosen because, unlike most other ancient Irish woodlands, it is not located on a steep slope and has no evidence of planting with non-native species. In addition, the site is one of the largest remaining areas of native deciduous woodland in the country, covering just over 100 ha once all water bodies and grassland areas are excluded (Perrin *et al.*, 2008). It also has a mixture of both ancient and secondary stands. Although it has long been recognised as being of high ecological importance (Braun-Blanquet and Tüxen, 1952; O'Reilly, 1955; White, 1985), it is still relatively understudied. Four categories of historical land-use within the Gearagh are the subject of this study, namely areas of ancient woodland (these have been continuously wooded since at least 1650 and cover approximately 33 ha), old secondary woodland (established between 1842 and 1904, covering approximately 22 ha), recent secondary woodland (established between 1904 and 1936, covering approximately 45 ha), and unimproved grassland that borders the woodland (occupying approximately 67 ha); these habitats are located in close proximity to one another and are defined further in Chapter 3. Both the old secondary and recent secondary sites have regenerated naturally on abandoned agricultural land.

The aim of this research is to enhance the understanding of the origin, development, and current structure and composition of ancient and secondary woodland in the Gearagh. By comparing woodland stands that differ in well-defined historical features, the key factors that contribute to the distribution of species and other ecological features may be discerned. Ultimately, this may help to improve

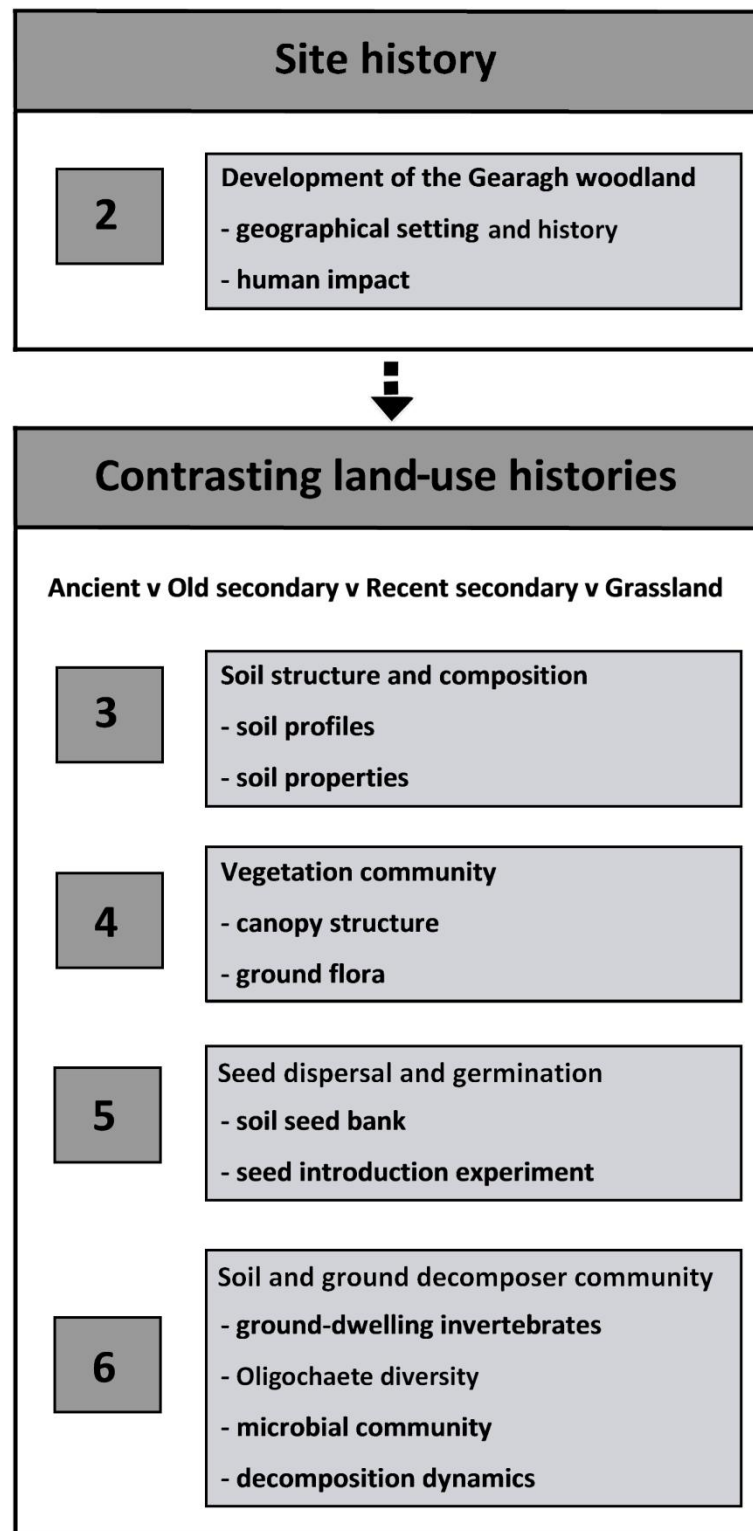


Fig. 1.2 Outline of the structure of the thesis and the main topics dealt with in each chapter. The chapter numbers are indicated by the numbers 2-6.

our understanding of the factors that drive woodland biodiversity, and thereby contribute to the formation of guidelines for managers and policy-makers. To achieve these aims, it was necessary to employ a multi-disciplinary approach, including history and archaeology, pedology and edaphology, plant and animal ecology, and biogeochemistry. The main research topics raised in each chapter are summarised in Fig. 1.2.

Chapter 2 describes the historical development of the landscape of the Gearagh since the beginning of the Holocene. The prehistoric and historic development of the woodland and surrounding landscape was reconstructed from a detailed analysis of published archaeological and palaeoecological studies, historical maps and documents. This provided a clearer perspective of how the wooded landscape developed over time, and how it has been influenced by past human activities. This study helps to explain the likely origin, development, and recent changes that have occurred within ancient and secondary stands of the Gearagh.

Following the historical study (Chapter 2), many questions remained regarding the development of the ancient and secondary stands in the Gearagh. The central issues that required clarification concerned the effects of past agricultural use on the environmental conditions within the secondary woodland, in particular, the ability of these land-use legacies to persist in woodland soils. These topics are addressed further in Chapter 3 by analysing the soil structure and composition of the ancient woodland and comparing it with that of the secondary woodland and adjacent grassland stands.

The vascular plant communities of the Gearagh have long been of scientific interest. However, the results of both Chapter 2 and 3 confirmed that land-use and environmental conditions had changed in certain parts of the woodland, such that the site now contains areas of ancient woodland and also secondary woodland of varying ages, dating back to phases of agricultural abandonment. Chapter 4 describes a study examining the effect of these changes on the structure and composition of the vegetation of the woodland.

An investigation into the ability of woodland plant species to establish in both ancient and secondary woodlands is the subject of Chapter 5. The ability of species to disperse through time is assessed through an examination of the persistent seed bank of the ancient and secondary woodland. The results of a seed introduction experiment are also presented; this was carried out with three woodland herbs in order to determine the germination ability of these species in the various woodland habitats.

Few studies have been carried out on the decomposer communities of native deciduous woodlands in Ireland. In Chapter 6, the diversity of soil- and surface-dwelling invertebrate and microbial populations in the ancient and secondary woodlands is described. The importance of these communities in relation to the decomposition of leaf litter is also assessed. The effects of past disturbance events on the structure and functioning of the decomposer community is highlighted. Finally, Chapter 7 integrates the main results reported in the preceding chapters and places them in the broader context of ancient woodlands generally. The implications of the various findings for woodland management are discussed.

1.7 References

- Anon. (2007) *Back on the Map: An Inventory of Ancient and Long-Established Woodland for Northern Ireland*. Preliminary report, The Woodland Trust, Bangor, UK, pp. 20.
- Baeten, L. (2010) *Recruitment and Performance of Forest Understorey Plants in Post-Agricultural Forests*. PhD thesis, Ghent University, Ghent, Belgium.
- Birks, H.H. (1988) *The Cultural Landscape: Past, Present, and Future*. Cambridge University Press, Cambridge, UK, pp. 544.
- Bohan, R. (1998) *The Historical Ecology of the Woodlands of Ireland, Western Scotland and the Isle of Mann*. PhD thesis, Trinity College Dublin, Dublin, Ireland.
- Bowman, D.M.J.S. (1998) The impact of Aboriginal landscape burning on the Australian biota. *New Phytologist*, **140**, 385-410.

- Bradshaw, R.H.W. (2004) Past anthropogenic influence on European forests and some possible genetic consequences. *Forest Ecology and Management*, **197**, 203-212.
- Bradshaw, R.H.W. & Mitchell, F.J.G. (1999) The palaeoecological approach to reconstructing former grazing-vegetation interactions. *Forest Ecology and Management*, **120**, 3-12.
- Braun-Blanquet, J. & Tüxen, R. (1952) Irische Pflanzengesellschaften. In: *Die Pflanzenwelt Irlands* (ed. W. Ludi), pp. 224-421. Hans Huber, Bern, Switzerland.
- Briggs, J.M., Spielmann, K.A., Schaafsma, H., Kintigh, K.W., Kruse, M., Morehouse, K. & Schollmeyer, K. (2006) Why ecology needs archaeologists and archaeology needs ecologists. *Frontiers in Ecology and the Environment*, **4**, 180-188.
- Bürgi, M. & Gimmi, U. (2007) Three objectives of historical ecology: the case of litter collecting in Central European forests. *Landscape Ecology*, **22**, 77-87.
- Butzer, K.W. (1996) Ecology in the long view: settlement histories, agrosystemic strategies, and ecological performance. *Journal of Field Archaeology*, **23**, 141-150.
- Christensen, N.L. (1989) Landscape history and ecological change. *Journal of Forest History*, **33**, 116-124.
- Cooper, A. (1984) Application of multivariate methods to a study of community composition and structure in an escarpment woodland in northeast Ireland. *Plant Ecology*, **55**, 93-104.
- Dambrine, E., Dupouey, J.L., Laut, L., Humbert, L., Thinon, M., Beaufils, T. & Richard, H. (2007) Present forest biodiversity patterns in France related to former Roman agriculture. *Ecology*, **88**, 1430-1439.
- Dupouey, J.L., Dambrine, E., Laffite, J.D. & Moares, C. (2002) Irreversible impact of past land use on forest soils and biodiversity. *Ecology*, **83**, 2978-2984.
- Emborg, J., Christensen, M. & Heilmann-Clausen, J. (2000) The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. *Forest Ecology and Management*, **126**, 173-189.

- Fahy, O. & Gormally, M. (1998) A comparison of plant and carabid beetle communities in an Irish oak woodland with a nearby conifer plantation and clearfelled site. *Forest Ecology and Management*, **110**, 263-273.
- Flinn, K.M. & Vellend, M. (2005) Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and the Environment*, **3**, 243-250.
- Forest Europe, UNECE & FAO (2011) *State of Europe's Forests 2011: Status and Trends in Sustainable Forest Management in Europe*. Ministerial Conference on the Protection of Forests in Europe, Oslo, Norway, pp. 339.
- Foster, D.R. (2000) From bobolinks to bears: interjecting geographical history into ecological studies, environmental interpretation, and conservation planning. *Journal of Biogeography*, **27**, 27-30.
- Foster, D.R., Motzkin, G. & Slater, B. (1998) Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. *Ecosystems*, **1**, 96-119.
- Foster, D.R., Orwig, D.A. & McLachlan, J.S. (1996) Ecological and conservation insights from reconstructive studies of temperate old-growth forests. *Trends in Ecology & Evolution*, **11**, 419-424.
- Foster, D.R., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D. & Knapp, A. (2003) The importance of land-use legacies to ecology and conservation. *BioScience*, **53**, 77-88.
- Goldberg, E., Kirby, K., Hall, J. & Latham, J. (2007) The ancient woodland concept as a practical conservation tool in Great Britain. *Journal for Nature Conservation*, **15**, 109-119.
- Goudie, A. (2006) *The Human Impact on the Natural Environment: Past, Present, and Future*. Blackwell, Oxford, UK, pp. 376.
- Hermý, M., Honnay, O., Firbank, L., Grashof-Bokdam, C. & Lawesson, J.E. (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation*, **91**, 9-22.

- Hermý, M. & Verheyen, K. (2007) Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. *Ecological Research*, **22**, 361-371.
- Honnay, O., Verheyen, K., Bossuyt, B. & Hermý, M. (2004) *Forest Biodiversity: Lessons From History For Conservation*. CABI Publishing, Wallingford, UK, pp. 320.
- Hopkins, J.J. & Kirby, K.J. (2007) Ecological change in British broadleaved woodland since 1947. *Ibis*, **149**, 29-40.
- Hotchkiss, S., Calcote, R. & Lynch, E. (2007) Response of vegetation and fire to Little Ice Age climate change: regional continuity and landscape heterogeneity. *Landscape Ecology*, **22**, 25-41.
- Jackson, S.T. & Hobbs, R.J. (2009) Ecological restoration in the light of ecological history. *Science*, **325**, 567-569.
- Kelly, D.L. (2005) Woodland on the western fringe: Irish oakwood diversity and the challenges of conservation. *Botanical Journal of Scotland*, **57**, 21-40.
- Kirby, K.J. (2004) Changes in the composition of Wytham woods (southern England) 1974-2002, in stands of different origins and past treatment. In: *Forest Biodiversity: Lessons From History For Conservation* (eds O. Honnay, K. Verheyen, B. Bossuyt & M. Hermý), pp. 193-204. CABI Publishing, Wallingford, UK.
- Kirby, K.J. & Watkins, C. (1998) *The Ecological History of European Forests*. CAB International, Wallingford, UK, pp. 384.
- Little, D. (2004) A new dawn for native woodlands: Brackloon wood, Co. Mayo - pilot site for the native woodland scheme. In: *Ireland's Native Woodlands* (eds C. Doyle & D. Little), pp. 176-183. Woodlands of Ireland, Galway, Ireland.
- Magnuson, J.J. (1990) Long-term ecological research and the invisible present. *BioScience*, **40**, 495-501.
- Marsh, G.P. (1865) *Man and Nature: Or, Physical Geography as Modified by Human Action*. Scribner, New York, USA, pp. 602.

- McIntosh, R.J., Tainter, J.A. & McIntosh, S.K. (2000) *The Way the Wind Blows: Climate, History, and Human Action*. Columbia University Press, New York, USA, pp.413.
- Mitchell, F.J.G. (1988) The vegetational history of the Killarney oakwoods, SW Ireland: evidence from fine spatial resolution pollen analysis. *Journal of Ecology*, **76**, 415-436.
- O'Reilly, H. (1955) Survey of the Gearagh, an area of wet woodland on the River Lee, near Macroom, Co. Cork. *The Irish Naturalists' Journal*, **11**, 279-286.
- O'Sullivan, A. & Kelly, D. (2006) A recent history of sessile oak (*Quercus petraea* L.)–dominated woodland in Killarney, S.W. Ireland, based on tree–ring analysis. *Biology & Environment: Proceedings of the Royal Irish Academy*, **106**, 355-370.
- Perrin, P., Martin, M., Barron, S., O'Neill, F., McNutt, K. & Delaney, A. (2008) *National Survey of Native Woodlands 2003-2008: Volume I: Main Report*. Unpublished report to the National Parks & Wildlife Service, Dublin, Ireland, pp. 187.
- Perrin, P.M. & Daly, O.H. (2010) *A Provisional Inventory of Ancient and Long-Established Woodland in Ireland*, Irish Wildlife Manuals, No. 46. National Parks and Wildlife Service, Department of the Environment, Heritage and Local Government, Dublin, Ireland, pp. 71.
- Peterken, G.F. (1993) *Woodland Conservation and Management*. Chapman & Hall, London, UK, pp. 374.
- Peterken, G.F. (1996) *Natural Woodland: Ecology and Conservation in Northern Temperate Regions*. Cambridge University Press, Cambridge, UK, pp. 522.
- Plue, J., Hermy, M., Verheyen, K., Thuillier, P., Saguez, R. & Decocq, G. (2008) Persistent changes in forest vegetation and seed bank 1,600 years after human occupation. *Landscape Ecology*, **23**, 673-688.
- Rackham, O. (1980) *Ancient Woodland: Its History, Vegetation and Uses in England*. Edward Arnold, London, UK, pp. 624.
- Rackham, O. (1995) Looking for ancient woodland in Ireland. In: *Wood, Trees and Forests in Ireland* (eds J.R. Pilcher & S. Mac an tSaoir), pp. 1-12. Royal Irish Academy, Dublin, Ireland.

- Rackham, O. (2000) *The History of the Countryside: The Classic History of Britain's Landscape, Flora and Fauna*. Phoenix Giant, London, UK, pp. 445.
- Redman, C.L. (1999) *Human Impact on Ancient Environments*. University of Arizona Press Tucson, USA, pp. 288.
- Rhemtulla, J. & Mladenoff, D. (2007) Why history matters in landscape ecology. *Landscape Ecology*, **22**, 1-3.
- Spencer, J.W. & Kirby, K.J. (1992) An inventory of ancient woodland for England and Wales. *Biological Conservation*, **62**, 77-93.
- Swetnam, T.W., Allen, C.D. & Betancourt, J.L. (1999) Applied historical ecology: using the past to manage for the future. *Ecological Applications*, **9**, 1189-1206.
- Thomas, R.C., Kirby, K.J. & Reid, C.M. (1997) The conservation of a fragmented ecosystem within a cultural landscape - the case of ancient woodland in England. *Biological Conservation*, **82**, 243-252.
- Turner, B.L. (1990) *The Earth as Transformed by Human Action: Global and Regional Changes in the Biosphere Over the Past 300 Years*. Cambridge University Press, Cambridge, UK, pp. 729.
- Verheyen, K., Bossuyt, B., Hermy, M. & Tack, G. (1999) The land use history (1278-1990) of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. *Journal of Biogeography*, **26**, 1115-1128.
- White, J. (1985) The Gearagh Woodland, Co. Cork. *The Irish Naturalists' Journal*, **21**, 391-396.

CHAPTER 2

THE EVOLUTION OF THE PRESENT-DAY LANDSCAPE OF THE GEARAGH WOODLAND

2.1 Abstract

Ancient woodland, i.e. woodland which has been in continuous existence for at least 400 years, is extremely rare in Ireland. Details of remaining ancient woods have recently been collated; however, little is known about the circumstances that have contributed to the survival of these particular sites. This chapter examines the development of one such woodland, the Gearagh in County Cork, with a view to assessing how a woodland might avoid historical felling. A combination of historical maps and documents were used to chart the survival of the woodland over time. The woodland initially developed along a fluvial-glacial outwash plain, which became part of an anastomosing channel of the River Lee. This protected it from significant human disturbance, until about 200 years ago when large parts were cleared for agriculture. Today, only part of the original woodland remains, due to felling that was carried out in the 1950s as part of the construction of a hydroelectric dam. The remaining ancient woodland has survived due to a combination of natural geographical features and historical management practices, which protected the core of the site from significant exploitation. This research highlights the importance of including detailed historical investigations in the assessment of ancient woodlands in Ireland.

2.2 Introduction

In recent decades, ecologists have increasingly begun to recognise the importance of long-term human disturbances in woodlands (Rackham, 1980; Peterken, 1993; Kirby and Watkins, 1998). Historical land-use is now widely acknowledged to have enduring impacts on the present-day ecology of woodlands. To assess the effects of former land-use on contemporary woodland ecosystems, it is extremely important to reconstruct land-use history in as detailed a manner as possible. In this way, historical land-use changes can be related to present-day ecological data. Generally, research assessing the impact of historical land-use only covers relatively short time periods within the past 100-200 years or so. However, most woodlands in Europe and Ireland have been subject to complex human disturbances over thousands of years. To fully understand the present-day ecology of a woodland, it is necessary therefore to gather information on the development of that woodland since the

commencement of the Holocene to the present-day. This chapter reviews the history of the Gearagh woodland in south-west Ireland, showing how the woodland landscape developed and then changed as a result of anthropogenic influences. This study should help to inform conservation objectives and future management requirements for the woodland.

2.3 Materials and methods

Since there is little published information available on the history of the Gearagh, it was necessary to conduct detailed historical analysis on the woodland in order to assess how the present-day landscape evolved and changed as a result of past human impacts. An extensive literature review was conducted on the history of Irish woodlands so as to provide a historical setting for the Gearagh in the Irish landscape. This information was derived from various sources, including published accounts and reviews of Irish woodland history, archaeological records, and regional palaeoecological and stratigraphical studies. Much of the early history of the site is based on regional descriptions from other studies, as a detailed pollen study of the area has yet to be carried out. However, when combined with archaeological evidence, this information can help to provide a description of much of the early history of the surrounding landscape. The main source of recent historical information is from documented historical accounts and detailed topographical maps produced since the 19th century. Historical maps of the landscape surrounding the Gearagh were obtained from library archives for five points in time between 1654 and 1938. Three of these were Ordnance Survey maps; the first of these, completed in 1842, was the world's first large-scale precise mapping of an entire country. Evaluation of these maps was aided by fieldwork to confirm their accuracy. Primary sources of information pertaining to the Gearagh were also obtained, including contemporary traveller's accounts, deeds and tax valuation lists, and estate papers. The validity and relevance of all these various sources of information were carefully interpreted and synthesised to provide a comprehensive review of the historical development of the Gearagh.

2.4 The Gearagh woodland

The climax vegetation of Ireland, like much of western Europe, is deciduous woodland (Cross, 2006). Although native woodlands once dominated the Irish landscape, at present, Ireland is one of the least wooded countries in Europe. Only 10% of the country is currently under woodland cover (Forest Service, 2008); in contrast, forest covers 36% of western Europe, although most of this consists of commercial plantations on former agricultural land (FAO, 2011). Indeed, much of Europe's original woodland cover has been removed at some point in the last 5,000 years (Rackham, 1980). While the first major phase of widespread European woodland clearance was closely associated with the spread of agriculture during the Neolithic period (Bradshaw, 2004), woodland cover continued to decrease well into the Roman era (Dupouey *et al.*, 2002). Subsequent phases of woodland expansion and decline have generally coincided with population cycles, leading to demand for fuel and food (Hermy and Verheyen, 2007). Even those woodlands which survived major clearance, mostly in remote districts of central and eastern Europe, have still been partly modified by local communities for fuel, pasture, charcoal, and hunting purposes (Peterken, 1993).

Woodlands in Ireland have also undergone many changes over the past few thousand years (Table 2.1). Today, the majority of Irish forests are composed of commercial conifer plantations, with just 1-2% consisting of semi-natural woodland (Perrin *et al.*, 2008). Most native woods are small and fragmented, and are also under severe pressure from grazing, invasive species and agricultural development (Cross, 2006). One of the few relatively large tracts of low-lying, native woodland remaining in Ireland is the Gearagh in County Cork. Despite its size, this woodland is relatively understudied, although it is acknowledged to contain a remnant of ancient woodland (Perrin and Daly, 2010).

The Gearagh lies along a broad, flat valley of the River Lee 2 km south of Macroom (51°52'31" N, 8°58'44" W). It is composed of a series of islands along a network of river channels, and extends for about 7 km along the river south-westwards of the

Table 2.1 Historical overview of Irish woodland development to the present-day.

Historical period	Timescale	Woodland cover
Midlandian Cold Stage	33,000-11,000 BC	Extensive ice cover over most of Ireland. Outside of ice-covered areas, there was limited plant life, most of which comprised herbaceous plants ⁽ⁱ⁾ .
Woodgrange Interstadial	11,000-9,000 BC	Some open grassland, tundra and low alpine scrub.
Nahanagan Stadial	9,000-8,000 BC	Tundra and low alpine scrub
Littletonian Warm Stage	8,000 BC-present	Postglacial period
Boreal phase	8,000-7,000 BC	<i>Juniperus</i> scrub replaces meadows. Arrival of <i>Salix</i> and <i>Betula</i> , leading to open woodland.
Mesolithic Period	7,000-4,200 BC	Woodland development throughout Ireland.
Sandelian phase	7,000-6,000 BC	Establishment of <i>Corylus</i> and <i>Pinus</i> . Extensive forest. No significant forest clearance.
Larnian phase	6,000-5,000 BC	Arrival of <i>Quercus</i> and <i>Ulmus</i> . Small clearances of woodlands.
Climax phase of woodland	5,000-3,000 BC	Spread of <i>Alnus</i> . Dense woodland.
Neolithic Period	4,200-2,000 BC	<i>Ulmus</i> declines and <i>Alnus</i> increases.
Early Neolithic	4,200-3,000 BC	Limited woodland clearances for agriculture, development of grasslands, followed by secondary woodland regeneration.
Late Neolithic	3,000-2,000 BC	Secondary woodland of <i>Ulmus</i> and <i>Fraxinus</i> .
Bronze Age	2,000-500 BC	Bog expansion. Increase in arable farming. General decline in woodland.
Iron Age	500 BC-300 AD	Lull in agricultural activity. Some contraction of grasslands and woodland regeneration, particularly of <i>Corylus</i> and <i>Fraxinus</i> .
Late Iron Age	300-400 AD	Increase in arable farming and establishment of permanent agricultural areas. Removal of major woodlands.
Early Christian Period	400-800 AD	Disappearance of <i>Pinus</i> . Continued agricultural expansion. Widespread woodland exploitation and clearance, leading to increased management.
The Viking Period	800-1150 AD	Significant coastal settlements.
The Anglo-Norman Period	1150-1550 AD	Intensive farming in eastern part of Ireland. Economic deterioration in 1300s leading to population decline and increase in scrub woodlands. Estimated 12% of Ireland still forested in 1400s ⁽ⁱⁱⁱ⁾ .

Table 2.1 continued.

Historical period	Timescale	Woodland cover
Stuart and Cromwellian colonisation	1550-1700 AD	Commercial exploitation of woodlands for shipbuilding, staves and charcoal. Deforested land occupied by livestock. Estimates of woodland cover range from 12.5% ⁽ⁱⁱⁱ⁾ to as little as 2.1% ^(iv) , although 3% ^(v) is more likely.
Economic growth and development	1700-1785 AD	Population doubles to 4 million by 1785. Woodland scarce as land needed to support growing population. Planting of exotic trees in demesnes. Estimated woodland cover of 0.5% ⁽ⁱⁱ⁾ .
Population peak	1785-1850 AD	Population rises to 8 million. Fuel scarce, bogs heavily cut for turf. Few woodlands outside of demesnes. Potato Famine (1845-51).
Post-Famine Period	1850-1900 AD	Transfer of land from landlord to tenant. Reduction in new plantations. Timber sold by proprietors for cash.
Modern Ireland	1900-present	Establishment of first forestry centre in 1903 ^(vi) , by which time woodlands cover around 1.5% of country ⁽ⁱⁱ⁾ . Woodlands cleared for fuel during World War I. Woodlands cover less than 0.5% of country in 1920s ^(vi) . 1928 Forestry Act to control felling and increase planting. Woodlands felled during World War II for fuel. Long-term afforestation plan subsequently adopted, in which mostly conifers are planted. 10% of country under woodland in 2006, mostly conifer plantations. Only 2% of total land cover is now composed of native woodland ^(vii) .

Note: Woodland history is summarised from Mitchell and Ryan (2007), except for ⁽ⁱ⁾ Mitchell (2006), ⁽ⁱⁱ⁾ Feehan (2005), ⁽ⁱⁱⁱ⁾ McCracken (1971), ^(iv) Rackham (1995), ^(v) Rackham (2005), ^(vi) Fitzpatrick (1966), and ^(vii) Forest Service (2008).

Lee Bridge to Dromcarra Bridge (Fig 2.1). The name of the Gearagh derives from the old Irish *An Gaoire*, meaning 'the wooded river' (Joyce, 1887). Most old Irish placenames refer to prominent topological features that were present during the Early Medieval Period (Fuller, 1990). *An Gaoire* then indicates that woodland has been present in this area since at least the 5th to 12th centuries (Perrin and Daly, 2010). It has been regarded as a prominent botanical site since the late 19th century (Praeger, 1907; Braun-Blanquet and Tüxen, 1952; O'Reilly, 1955), and is now protected by a number of national and international designations. It received the status of a Statutory Nature Reserve in 1987, and it qualifies as a Ramsar Convention site and a Council of Europe Biogenetic Reserve. It is also listed, with priority status, on Annex I of the European Union Habitats Directive.

The Gearagh has previously been described as a riparian or an alluvial woodland (Cross and Kelly, 2003; Kelly, 2005a). These habitats are often regarded as a type of wetland where the soil is saturated with moisture, either on a permanent or a seasonal basis (Brinson and Verhoeven, 1999). It is also frequently assumed that riparian vegetation is dominated by flood-tolerant species, and that the location of this zone is largely determined by the proximity of the river and the frequency and magnitude of flooding events (Naiman and Decamps, 1997; Toner and Keddy, 1997). However, the riparian zone merely refers to vegetation that is found along the banks of the river; the extent of this zone actually varies considerably between different streams and rivers, and is only partially influenced by the river (Mac Nally *et al.*, 2008). Rather, the hydrology of the riparian vegetation is more strongly influenced by the surrounding landscape hydrology (Vidon and Hill, 2004). It is particularly affected by factors relating to overland and subsurface flows from upland slopes, precipitation, and groundwater discharge from the bedrock below (Burt, 1996). In the case of the Gearagh, the areas outside the main channel section are influenced by all of these factors. The soil here is frequently saturated and the vegetation is dominated by moisture-tolerant plants such as rushes, reeds and sedges. However, the wooded islands that are located amongst the river channels are not affected by surface or subsurface runoff from upland slopes, and the groundwater level is low. While the Gearagh is certainly subject to overbank

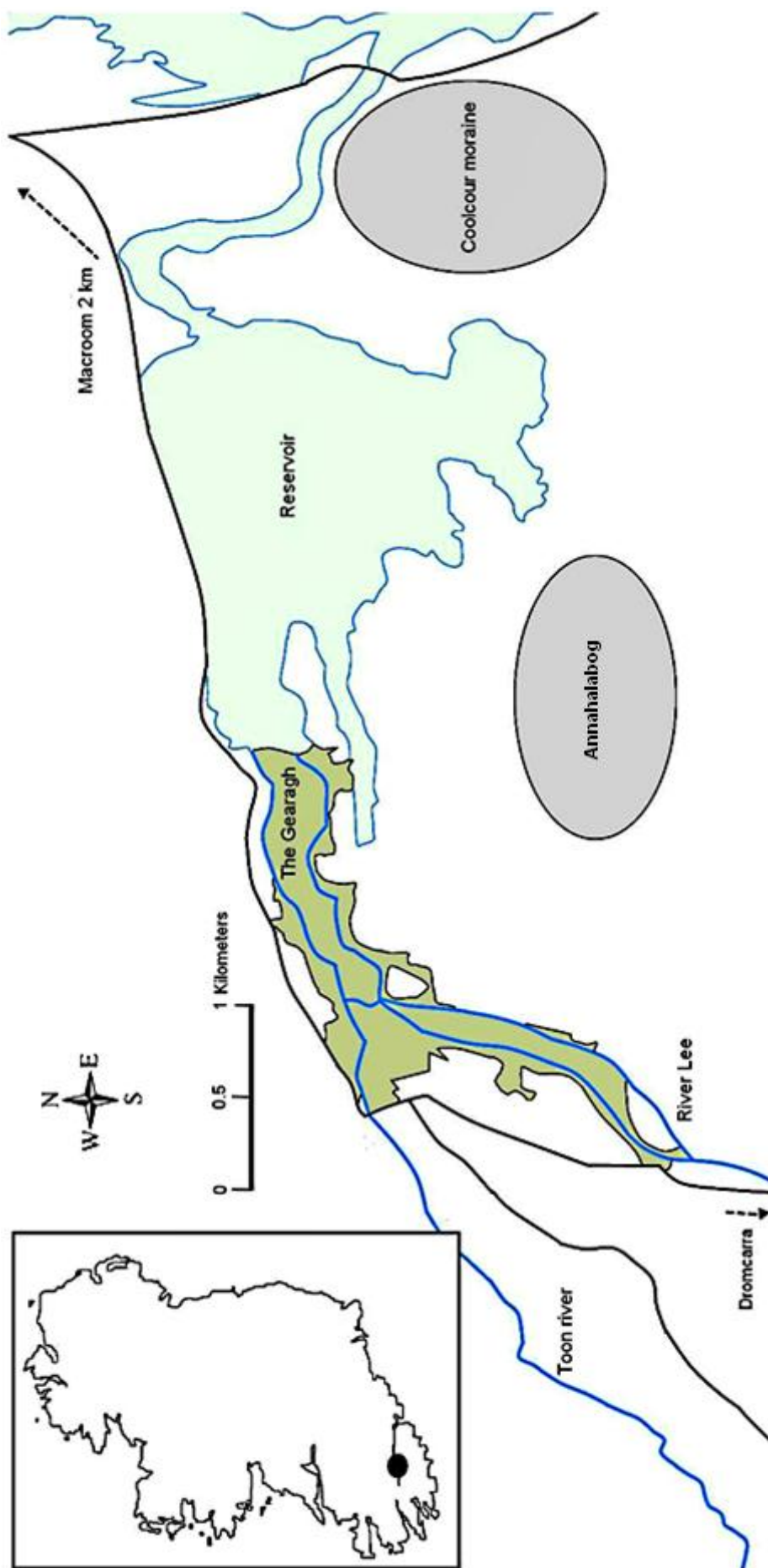


Fig. 2.1 Map showing the location of the Gearagh in relation to features in the surrounding landscape.

inundation, these are typically short-term flood events due to excessively heavy or prolonged rainfall. Floods usually last a few days at most before quickly draining away. Most native tree species are tolerant of these small flood events; flood-tolerant vegetation typically only develops in larger river systems that experience seasonal, long-term inundations due to snow or glacial melt (Brinson and Verhoeven, 1999). In addition, the islands in the centre of the Gearagh are extremely well-drained by the multiple channels that flow through the system. The islands therefore have fewer hydrological inputs in comparison with those areas on the outer edges of the river channel and are particularly well-drained. Therefore, although it is apparently a riparian woodland, the soils of the Gearagh are actually quite dry and may more closely resemble those of non-riparian woodlands.

The wooded part of the Gearagh is now relatively undisturbed, due mostly to the protection afforded by the conservation frameworks. However, certain areas of the site have been greatly affected by human activities in the past, and the surrounding landscape has also undergone numerous changes. An understanding of these past activities can help explain the current structure and diversity of the woodland, and demonstrate why this particular woodland survived when so many other native woodlands have been destroyed. The remainder of this chapter reviews the history of the Gearagh and the surrounding area, showing how the woodland developed and changed as a result of human activities. This study should provide useful information on the impact of past management on the current ecological status of Irish native woodlands.

2.5 Woodland prior to AD 1650

There are few reliable documentary records of the Irish landscape over the last two thousand years (Hall, 1997). Rather, a combination of palaeoecology and archaeology provides the best approach for acquiring information on the pre-historic landscape of Ireland. The following are accounts of how the landscape developed through pre-historic times within the Gearagh and the surrounding Lee Valley area.

2.5.1 Formation of the Lee Valley

The Gearagh is situated in the valley of the River Lee, which flows from its headwaters in the Shehy and Derrynasaggart mountains in west Cork to where it enters the sea at Cork Harbour. This valley has a distinct east-west orientation as a result of American folding. Carboniferous limestone occupies the valley floor and the more resistant Old Red Sandstone is exposed on the ridges. The current course of the river Lee, and consequently, the development of the Gearagh, owes much to the land-form changes that were made during the last glaciation, known as the Midlandian Cold Stage (Mitchell and Ryan, 2007).

Recent studies suggest that the Midlandian glaciation, instead of covering just part of Ireland, actually covered the entire island (Chiverrell and Thomas, 2010). The Killumney moraine just outside of Cork city, which previously was thought to mark the eastern limit of the south Munster ice cap, may actually have been one of the first deposits of moraine left by the retreating glacier. Approximately 15,000 years ago, the ice began to retreat, slowly at first, but without any significant re-advancement at any stage. There was, however, a considerable halt in the area around Macroom. This led to the build-up of several large moraines, including one at Coolcour (Farrington, 1959); see Fig. 2.1. The subsequent retreat of the glaciers from the Coolcour moraine was particularly rapid in the Lee valley; only at Dromcarra hill is there evidence that the ice stood for a period of time. This rapid retreat was due to a relatively abrupt increase in temperature, which resulted in an enormous flow of meltwater being released from the receding glaciers. However, the moraine at Coolcour acted like a dam to these glacial outwash rivers, causing a lake to form behind it. The gravel that the meltwater was carrying was deposited here to form a level outwash plain. By 13,000 years ago, all of the ice had disappeared and a young River Lee traced its course along the broad glacial-fluvial outwash plain left by the glaciers.

The outwash plain upstream of Coolcour occupies a wide, flat valley that extends back towards the gorge at Dromcarra. The River Lee flows north through the valley until it joins the Toon River and it then turns to flow eastwards, following the direction of the Toon. In cross-section, the valley bottom is particularly wide,

extending from 1.2 km to nearly 2.5 km in width (Farrington, 1959). The gradient is gentle, falling as little as 3 m in eight kilometres. The only prominent feature in the valley is a low rise of limestone at Annahala. Other than that, the terrain seldom rises to more than a few meters above the level of the river. The walls of the valley then rise steeply from the sides of the flood plain.

It is in this valley that the River Lee develops an anastomosing channel pattern (Harwood and Brown, 1993). Before it meets the River Toon, it divides into seven or eight channels across nearly 200 m. After joining the River Toon, it expands to 300 m in width, while the number of channels varies from three to twelve. It reaches its maximum extent at Annahala Bridge where it formerly extended to over 400 m, with a network of up to fifteen channels. After the Lee Bridge, the valley begins to close in and at Coolcour the river returns to a more well-defined course.

2.5.2 Development of an anastomosing river channel

Anastomosing rivers were relatively common in Europe during the early Holocene (Brown, 2002). However, few now remain; most have since been channelised or otherwise altered by man. In the early post-glacial period, the River Lee formed a braided system over the gravel beds left in the glacial outwash plain upstream of Coolcour (Brown *et al.*, 1995); it consisted of a network of small channels separated by small temporary islands. Over time, these beds became more stable as sediment continued to accumulate. Vegetation began to develop on the islands, making them less susceptible to erosion. Gradually, the islands became larger and an anastomosing channel pattern developed between them (Harwood and Brown, 1993).

The term anastomosing is used to describe rivers with multiple, interconnected, coexisting channel belts on alluvial plains with stable river banks (Makaske, 2001). Unlike the sand and gravel bars that are found in braided systems, islands in anastomosing channels are always vegetated, often with trees and shrubs. Although the formation of an anastomosing pattern may result from various processes, long-term anastomosing pattern is maintained by avulsions (flow diversions) and slow abandonment of channels. The low gradient in the Lee valley

at the Gearagh favours both of these processes; the stream power of the Lee is low at this point and the river has little erosive power. Vegetation also plays an important role by stabilising islands with their roots and also by enhancing ecological processes, particularly tree-throw and the formation of debris dams (Brown *et al.*, 1995). All of this amounts to a stable system where channel change only occurs gradually (Harwood and Brown, 1993).

The gravels in the channels of the Gearagh are coated, and in some cases cemented, with a manganese layer (Brown *et al.*, 1995). This adds to the stability of the gravel beds and reduces movement. A wavy iron and manganese pan can also be observed on exposed banks of the islands. This pan is cemented and is extremely resistant to erosion, and helps to further stabilise the islands. The soils of west Cork have unusually high levels of manganese and similar manganese pans can be seen on other rivers in the region (Conry and Ryan, 1965). Freshwater sponges, particularly *Ephydatia fluviatilis*, can be found in many of the gravel-bedded channels, indicating that the gravel beds on which they are found are quite stable, even in relatively high magnitude floods (Brown *et al.*, 1995).

The main channels in the Gearagh vary in width from 1 to 7 m. The system is made up of a few large islands, which are surrounded by hundreds of smaller islands. During low flows, many of the channels in the Gearagh are often dry (Brown *et al.*, 1995). These are flood channels, which only fill up during large floods. They act to reduce the frequency of overbank flow, thereby adding to the stability of the system. To the south of the Gearagh, beyond a low hill, lies an area of fen-peat, now known as Annahalabog (Fig. 2.1). The soil here is waterlogged due to large amounts of run-off from the valley sides and restricted drainage to the Lee.

Anastomosing channels containing vegetated islands are a notable characteristic of rivers in this part of south-west Ireland. Similar features to those found in the River Lee also occur along the River Bandon near the town of Dunmanway (Fig. 2.2), and along the River Bride by Aherla, both in County Cork. The Lee, Bandon, and Bride all flow from high gradient areas into wide flat valleys with a low gradients; such conditions are conducive to the development of anastomosing channel patterns

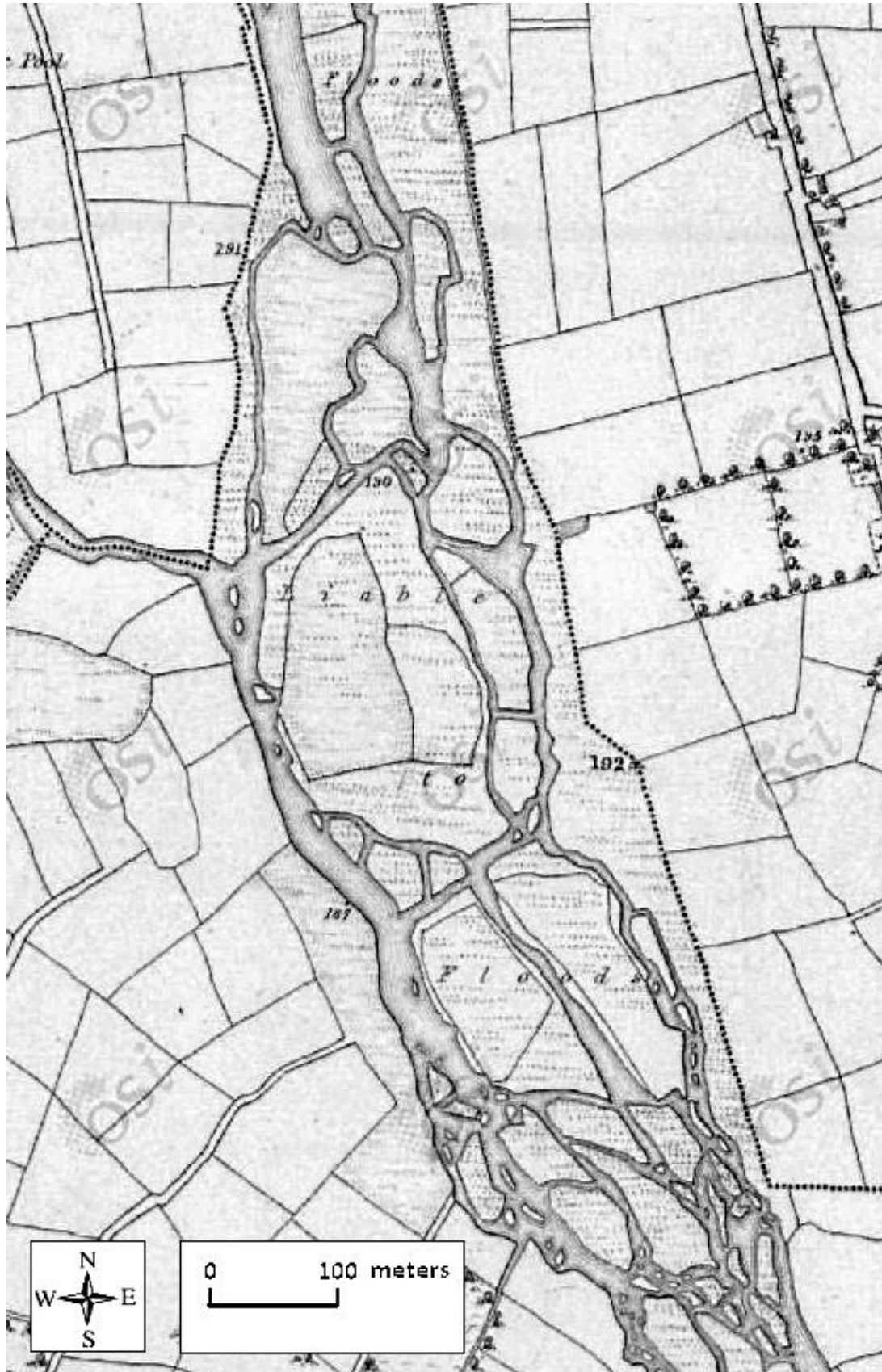


Fig. 2.2 First Ordnance Survey map (surveyed in the 1830s) showing the River Bandon, Co. Cork, flowing from north to south. The anastomosing channel pattern of the river can clearly be seen, although all the islands had been cleared of wooded vegetation. The town of Dunmanway lies directly west of the river.

(Makaske, 2001). Both the Rivers Lee and the Bride are also associated with peaty areas which developed on poorly-drained, waterlogged soils subject to high amounts of run-off from adjacent hillslopes. Kilcrea Bog along the River Bride was located in an area known in Irish as *Geary*, which also translates as 'a wooded area along a river' (Joyce, 1887). The lateral wetlands rendered these areas relatively inaccessible and would have made exploitation of the woodlands along the rivers difficult. However, an account by Smith (1774) describes how the area along the River Bride was cleared and drained in the early 1700s. The river was converted from a series of anastomosing channels into a single straight channel, thereby removing a system that would have otherwise been similar to the present-day Gearagh on the River Lee.

2.5.3 Early post-glacial period (11,000 – 7,000 BC)

About 13,000 years ago, the Irish climate improved rapidly and the glaciers finally retreated. However, the climate continued to fluctuate for a further 3,000 years, and this delayed the colonisation of Ireland by forest. A cold period known as the Nahanagan Stadial began about 10,600 years ago and lasted for approximately 600 years (Mitchell and Ryan, 2007). During this period, minor glaciers reappeared and permafrost covered the lowlands. Vegetation cover was limited and mostly composed of arctic species. Then, about 10,000 years ago, temperatures began to increase, marking the beginning of the Littletonian or Postglacial Warm Stage. Over the next 5,000 years, the landscape gradually transformed from open tundra to deciduous woodland (Mitchell, 2006). This coincided with the development of brown forest soils; these formed along the Lee valley, where the glacial drift and bedrock was overlain with river alluvium.

The pattern of woodland evolution at the Gearagh in the early Holocene would have largely reflected that of the rest of south-west Ireland, although these vegetation changes remain poorly understood (Mighall *et al.*, 2008). Early Holocene pollen records show how *Juniperus* was the first colonist, but this was rapidly replaced by *Betula*, which is a typical pioneer tree species (Mitchell, 2006). As the climate continued to improve, other woodland trees, including *Salix* and *Corylus* became established (Coxon, 1986). Although these early woodlands remained

relatively open, the more shade-tolerant *Corylus* rapidly replaced *Betula* as the dominant species in south-west Ireland (Mighall *et al.*, 2008). *Pinus* was next to arrive in Ireland, leading to a reduction in *Corylus*, which only survived as an understorey species (Lynch, 1981). Approximately 1,000 years later, *Quercus* and *Ulmus* became established on the well-drained lowland soils where they were able to out-compete *Pinus*. Gradually, the forests were enhanced with other species, including *Alnus*, *Ilex*, *Hedera*, *Fraxinus*, and *Prunus*. Despite these changes, it is the influence of man that was to have the most significant effect on Irish woodlands, including the Gearagh (Table 2.1). These impacts on the landscape were not always straightforward, and included various waves of clearances and woodland re-establishment.

2.5.4 Mesolithic period (7,000 - 4,200 BC)

Ireland was first settled 9,000 years ago by Mesolithic hunters, fishers and gatherers. Pollen records indicate that the landscape was heavily wooded at that time; Ireland had few large animals and no *Fagus sylvatica* or *Tilia cordata* (Caulfield, 2005; Rackham, 2005). Archaeological evidence suggests that people mostly relied on plants and fish for food; most Mesolithic sites are located along river banks, lake margins, islands and in coastal areas. Although most settlements have been discovered in the north-east of the country, evidence of Mesolithic activity has also been found in Cork along the Blackwater valley (Stout and Stout, 1997) and on the Mizen Peninsula (Mighall *et al.*, 2008). However, archaeological and palaeoecological evidence suggests that Mesolithic society had relatively little impact on the landscape or on woodlands (Lynch, 1981; Chiverrell *et al.*, 2004).

Alnus arrived late to the south-west of Ireland, approximately 5,000 BC (Mighall *et al.*, 2008). This tree is tolerant of moist soils and so was able to out-compete *Pinus* on poorly-drained sites. However, *Pinus* would have still been found on the more acidic soils, amidst a canopy of *Ulmus*, *Quercus* and *Corylus*. Woodland is estimated to have covered 80% of Ireland at this time (Mitchell, 1995). Consequently, this period is known as the Climax Phase of woodland, which lasted for over 2,000 years (Mitchell and Ryan, 2007).

2.5.5 Neolithic period (4,200 - 2,000 BC)

During the Neolithic period, the first farmers arrived in Ireland and domestic cattle were introduced. Almost all Irish pollen records dating from the Neolithic show a decline in *Ulmus* (O'Connell and Molloy, 2001), although this was most likely due to a pandemic elm disease, possibly exacerbated or initiated by man (Mitchell and Ryan, 2007). In many parts of the country, this was followed by woodland clearances and a period of sustained farming activity over several centuries (O'Connell and Molloy, 2001); this represents the first significant impact of Neolithic people on the pollen record. While evidence of agricultural activity has been found on the Beara and Mizen Peninsulas in south-west Ireland, there is little indication that farming spread farther inland (Lynch, 1981; Chiverrell *et al.*, 2004). The lack of significant Neolithic archaeological sites in the Gearagh landscape suggests that human activity in this area was limited. Neolithic clearances for agriculture were small and transient. Pollen studies show that woodland continued to dominate the south-west of Ireland from the Neolithic until well into the Bronze Age (Overland and O'Connell, 2009). Nonetheless, these clearances altered the composition of woodlands. Pollen evidence indicates that secondary woodlands contained little *Ulmus* and more *Fraxinus* and *Taxus* than the primary woodlands (O'Connell and Molloy, 2001). Towards the end of the Neolithic period, *Pinus* began to gradually disappear altogether from the woodlands (Lynch, 1981). *Quercus*, *Betula* and *Ilex* then formed dense climax woodland.

2.5.6 Bronze Age (2,000 - 500 BC)

During the Bronze Age, human activity began to intensify. Changes in the pollen record reflect the expansion of grassland and arable land that occurred in many parts of the country from around 1400 BC to 800 BC (Mitchell and Ryan, 2007). By 1,000 BC, *Pinus* had disappeared from most of the country and was rapidly replaced by *Quercus*, as well as *Alnus*, *Corylus*, *Ilex*, and *Hedera* (Lynch, 1981). Palaeoecological evidence also charts the expansion of raised and blanket bogs during the Bronze Age, most likely due to a combination of a deteriorating climate and the continued clearance of woodlands (Barnosky, 1988; Mitchell and Ryan, 2007).

There is archaeological evidence of continuous human settlement in the landscape around the Gearagh dating from the Bronze Age (Fig. 2.3). A wedge tomb can be found to the south of the Gearagh in Cooldaniel. Similar tombs are concentrated around the headwaters of the Lee and the Bandon rivers and around the south-west coast (Lynch, 1981). These date from the late Neolithic to early Bronze Age and signify the first permanent settlers to arrive in the west Cork area (O'Brien, 2009). The wedge tomb therefore represents the first significant impact of man on the landscape surrounding the Gearagh.

The late Bronze Age was a period of intense activity and population growth in south-west Ireland, as indicated by the abundance of stone circles in the region (Lynch, 1981; O'Brien, 2009), several of which occur near the Gearagh. It is suggested that the mining of copper may have provided much of the stimulus for these monuments (Stout and Stout, 1997). Indeed, pollen and archaeological records indicate that sophisticated metalworking industries developed as farming activity expanded (Plunkett, 2009). Certainly, evidence suggests that woodland clearance was widespread in this region, although most cleared land eventually reverted to scrub and woodland (Overland and O'Connell, 2009). This ultimately resulted in a mixture of woodlands in various stages of regeneration. Other Bronze Age sites that are found around the Gearagh include a stone row at Gortyleahy, as well as a number of cooking sites or *fulachta fiadh*. All are located near streams, drains or at the edge of wet areas, which provided water to fill the trough (Lynch, 1981). These Bronze Age sites in the Gearagh landscape are a reflection of the general expansion of farmland that was taking place in this period (O'Brien, 2009).

2.5.7 Iron Age (500 BC - 500 AD)

There was a general decline in agriculture towards the end of the Bronze Age and in the early Iron Age. This is thought to be linked to a deteriorating climate, possibly due to a volcanic episode, and a subsequent drop in population numbers (Mitchell and Ryan, 2007). From approximately 300-400 BC, woodland recovered throughout much of Ireland. *Corylus*, *Betula* and *Fraxinus* invaded abandoned clearings and their occurrence increased in the pollen record (Lynch, 1981).

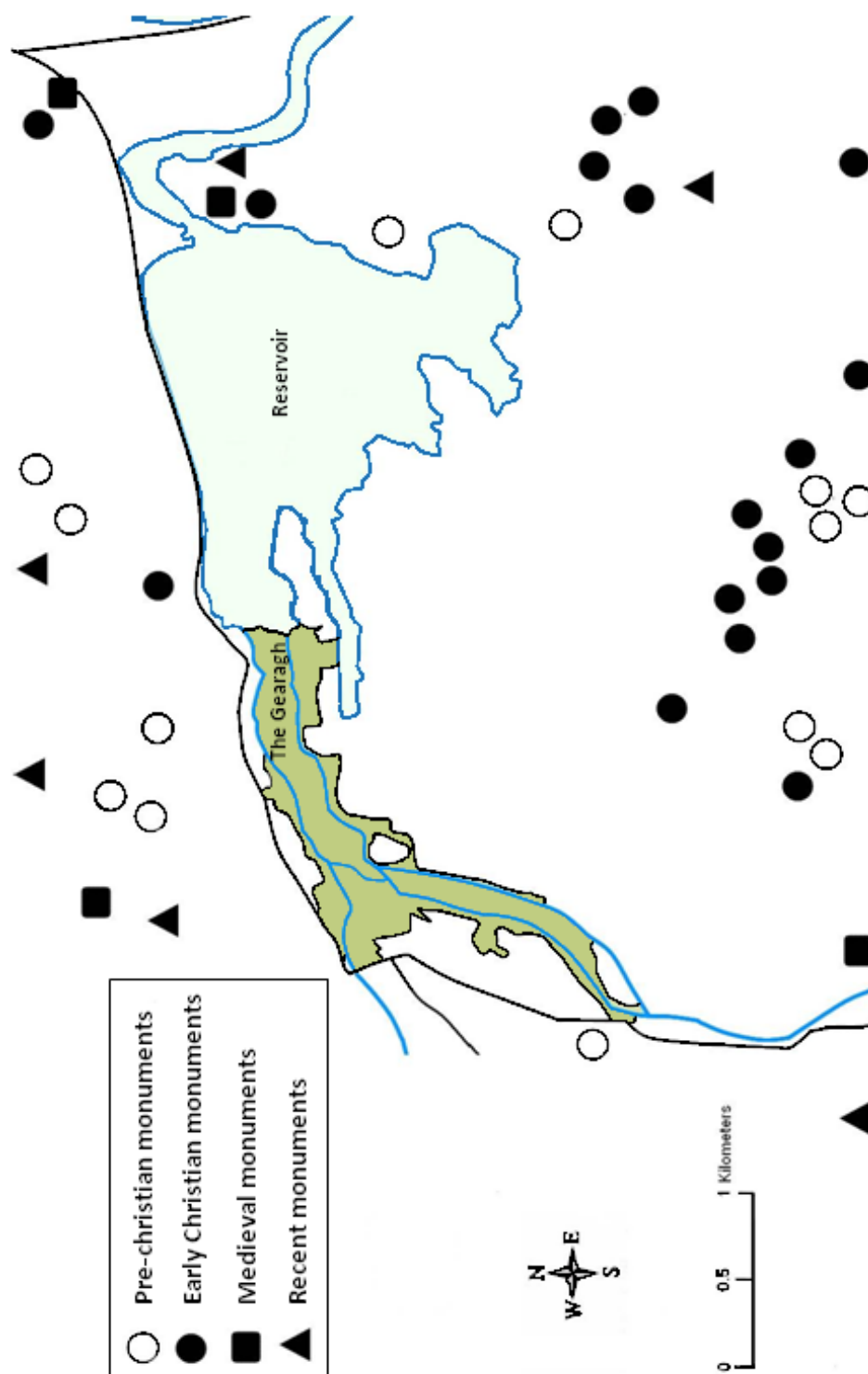


Fig. 2.3 Location of national monuments in the area surrounding the Gearagh. Most of the pre-Christian monuments date from the Bronze Age. Many of the Early Christian monuments are ringforts and souterrains. Medieval monuments date from the 5th to the 15th century. Recent monuments date from the 15th century to the present day.

The late Iron Age, however, saw the emergence of a highly organised society that adopted iron for the use of tools and weapons. Agriculture expanded once again and woodland cover in much of the country was cleared permanently for tillage and pasture (Mitchell and Ryan, 2007). Most of these were already secondary woodlands; very little primary woodland remained undisturbed at this point. Cattle dairying was practiced for the first time and pasture land became increasingly important (O'Brien, 2009). However, despite this overall increase in activity, there is limited archaeological evidence of a significant Iron Age society in south-west Ireland (Lynch, 1981; O'Brien, 2009). The only evidence of Iron Age activity near the Gearagh is a series of standing stones, which lie on the hillside to the north at Raleigh South and Dromreague. These are thought to be indicators of routeways or boundaries, but may also have been used as burial markers or commemorative monuments. The lack of significant monuments in the region is believed to be a consequence of a more fragmented local population (Overland and O'Connell, 2009).

2.5.8 Early Medieval period (500 - 1000 AD)

The Early Medieval Period witnessed an intensification of agriculture, particularly in central Ireland, although this was more moderate in the south-west (Lynch, 1981; O'Brien, 2009). This was due to a combination of factors, including the arrival of Christianity, the influence of the Vikings, and the spread of the Anglo-Normans. Pollen records indicate that this led to the creation of a largely open landscape throughout much of the country, which was dominated by mixed farming (Overland and O'Connell, 2009). However, there was considerable local variation in vegetation and land-use at this time.

There was an increase in population during the Early Medieval Period, leading to the construction of ringforts throughout the country, mostly during the 7th-9th centuries (Stout and Stout, 1997). Several ringforts can be found in the Lee Valley overlooking the Gearagh (Fig. 2.3); two lie to the south in Dromkeen and Gortacurragh. These structures functioned as residences or farmsteads for the larger farmers, while the smaller farmers lived in unenclosed structures in the surrounding fields (Lynch, 1981). The presence of these ringforts suggests that cattle may have

grazed on the surrounding lands and near the woodland margins. Several souterrains have also been found near the ringforts around the Gearagh. These were underground structures consisting of chambers connected by narrow passages. They were often built by the ringfort inhabitants as a defensive feature and for storage, particularly for dairy products (Stout and Stout, 1997).

In the major agricultural areas of the country, woodland resources were limited and needed careful protection by law (Kelly, 1997). Generally, each parish had just enough wood to supply communities that were largely self-sufficient (Tierney, 1998). Trees were classified on the basis of their economic importance under the Brehon Law tracts, and fines were imposed for damage to them (Neeson, 1997; Kelly, 1999). As in England, it was common practice to coppice the underwood every decade or so (Rackham, 1995). A few large *Pinus*, *Quercus*, and *Taxus* trees could then be kept to provide timber once mature. The timber trade became so sophisticated that specialised woodsmen and carpenters were employed in the felling and transport of timber (O'Sullivan, 1994). Although woods were usually protected by walls or banks and ditches, they were also often used for pasturing cattle (Feehan, 2005). Such regular grazing would have restricted the amount of natural regeneration in these woods.

Large woods were unusual and typically restricted to marginal land. Such woodlands were usually regarded as common land and lacked enclosures. These unenclosed woods were worth half the value of those that were enclosed (Tierney, 1998), but all the people of the locality would have the right to pick fruit, cut wood, and graze their livestock there during the summer months (Kelly, 2005b). In the Gearagh, the river formed the main part of the boundary and the anastomosing channel pattern of the River Lee would have made access difficult; this would have decreased the value of the woodland (Kelly, 2005b). The land immediately around the Gearagh would also have had a low value as the poor drainage and peaty soils would have made it unsuitable for cultivation. Turf was not widely used as a fuel, and peaty wetland areas such as Annahalabog were regarded as one of the least valuable types of land (Kelly, 1997).

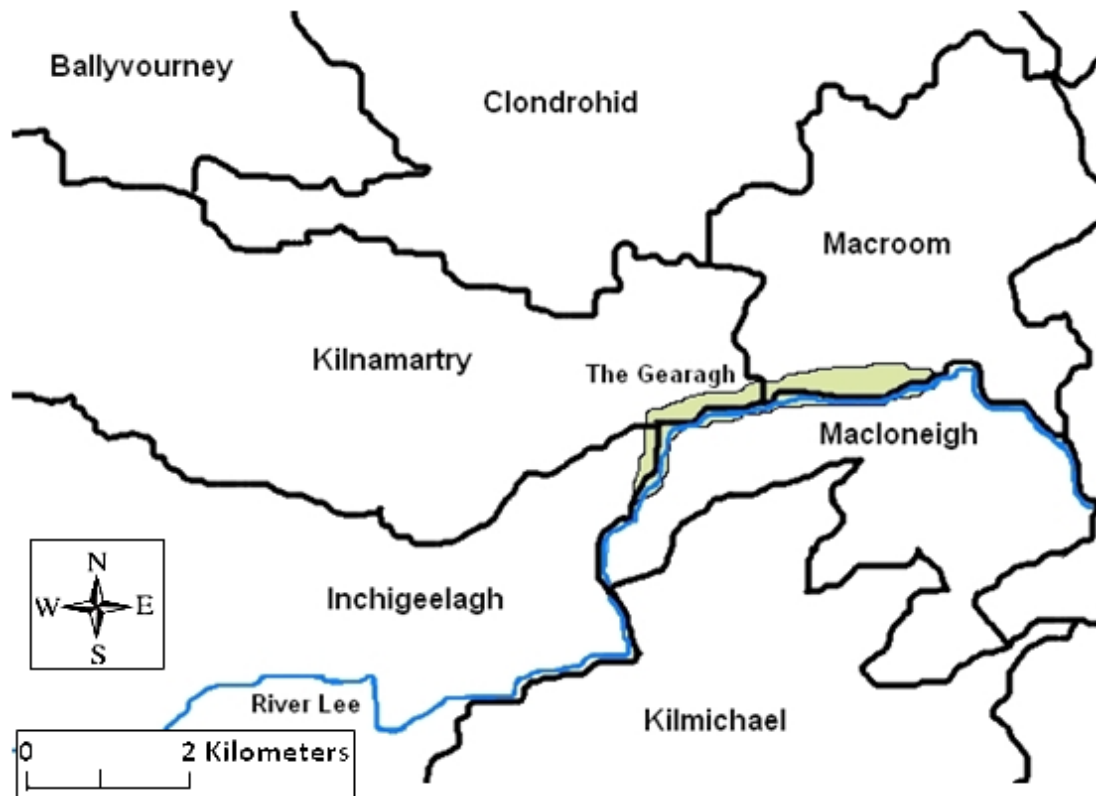


Fig. 2.4 The location of the Gearagh in relation to parish boundaries.

The River Lee around the Gearagh currently acts as a boundary between the parishes of Macloneigh to the south, Macroom and Kilnamartry to the north, and Inchigeelagh to the west (Fig. 2.4). Such boundaries most likely date from at least the Early Medieval Period, when streams and rivers were commonly used as boundary indicators between townlands or *tuatha* (Stout and Stout, 1997). Rivers were normally crossed at a ford where the riverbed was firm and the water shallow (Kelly, 1997). The crossing was made easier by building up the riverbed with stones. There are several such fording points with stepping stones in the Gearagh (see Fig. 2.9); it is likely that similar fords were in use during the Early Medieval Period.

A medieval stone church and graveyard is located at the eastern extent of the Gearagh at Farranavarrigane. This is known as Macloneigh church and it is associated with a ballaun stone, indicating that the church was most likely erected sometime between 800 and 1100 AD. Such ecclesiastical sites were often located in areas that had relatively low agricultural potential, usually in poorly-drained, low-lying areas; this land was only given with the permission of the whole kin-group

(Stout and Stout, 1997). Nonetheless, church farms were often responsible for the introduction of a number of agricultural innovations to an area and frequently helped to develop new land (Lynch, 1981). They were often the only places to produce vegetables and many became market centres for the dispersed rural population (O'Brien, 2009).

2.5.9 Late Medieval period (1000 - 1650 AD)

The arrival of the Vikings in the 9th century led Irish rulers to adopt new ideas of fortification. A series of castles were constructed, including Macroom castle, which was built in the 12th century (Ring, 1991). At the same time, the Anglo-Normans began to replace subsistence farming with a more intensive form of agriculture, as reflected in the pollen record (Hall, 2003). Anglo-Norman lords also began to use Irish woodlands as a source of timber for the English market. However, they did not expand much beyond east Munster, and so woodland in west Cork was still protected under old Irish law. The growth of market towns in Cork during the 13th century was generally confined to the coast and eastern parts of the county (O'Brien, 1993).

In the late 14th and early 15th centuries, a combination of a deteriorating climate, invasions, famine, and the Black Death resulted in economic decline and an overall decrease in the population of Ireland (Yeloff and Van Geel, 2007). Cereal cultivation declined and, in Munster, much of this was replaced with pasture land (O'Brien, 1993). The collapse of tillage and the abandonment of farms is indicated in pollen diagrams across Ireland (Cole and Mitchell, 2003; Overland and O'Connell, 2009). Rackham (2005) suggests that many Irish woodlands became denser during this period due to lack of exploitation; the same is almost certainly true of the Gearagh. Spore analysis from a site near the Gearagh indicates that a high abundance of bracken (*Pteridium aquilinum*) was present in the landscape at this time, reflecting a decline in agriculture in the region (Brown, 1999). Irish lords who had remained independent of Anglo-Norman rule regained much of their power during this period. This is demonstrated by an increase in the construction of towerhouses, including one to the north of the Gearagh in Dundareirke. A further three castles

were built in Inchigeelagh parish along the River Lee as far as the Gearagh between 1515 and 1615 (O'Brien, 1993).

The second half of the 1500s saw the beginning of the Tudor plantations in Ireland, which signalled a period of increasing human impacts on the landscape (Mitchell and Ryan, 2007). Many of the accounts of woodland by English settlers at this time give the impression that Ireland was a well-wooded country, although it appears from the pollen record that there were actually distinct regional differences in woodland cover (Cole and Mitchell, 2003). Certainly, woodlands were not as uniformly dense as described in the historical record (Hall, 2003). Nonetheless, to the English speculators, who were primarily interested in harvesting timber wherever it existed (Rackham, 2000), the country might have appeared reasonably well-wooded, particularly with respect to much of lowland England at the time. In Cork, they settled in towns on the coast and along the Bandon and Blackwater Rivers, and exploited many of the nearby woodlands. Macroom, however, remained a relatively isolated area (Ó Murchadha, 1993). The Plantation of Munster, which was part of the policy of English settlement in Ireland, began in 1585 (O'Brien, 1993). The MacCarthy family, under the rule of the Earl of Clancarty, managed to retain their lands, which included areas of the upper Lee Valley (Ó Murchadha, 1993). Much of this area was considered unimportant and remote. The woodlands on MacCarthy land, including the Gearagh, therefore escaped exploitation by the new English settlers. This relative lack of disturbance is reflected in pollen diagrams from the west of Ireland during this period (Hall, 2000; Cole and Mitchell, 2003).

2.6 Woodland from AD 1650 to present

2.6.1 Landscape of the Gearagh AD 1650 – 1842

During the Stuart and Cromwellian plantations, part of the policy of resettlement was to introduce the English system of land tenure. However, in the early 1600s, there was no proper survey of the confiscated areas, so land was granted on the basis of the pre-existing townlands or *tuatha* (Tierney, 1998). The Down Survey of

1655-7 undertook to create a list of townland names and define their boundaries so that they then came to be the established land unit.

Previous estimations of woodland cover in Ireland based on the Civil Survey in 1654-6 range from 2.1% (Rackham, 1995) to 12% (McCracken, 1971). However, it is now thought that overall woodland cover was unlikely to have exceeded 3% (Rackham, 2005). Cork was one of the most heavily wooded counties, with nearly 6 % woodland (Tierney, 1998), although pollen diagrams indicate that woodland cover varied considerably between counties (Hall, 2003). The majority of woodlands were dominated by a mixture of *Betula*, *Corylus*, *Alnus*, and *Quercus* (Cole and Mitchell, 2003). The Civil Survey classified most woods as 'shrubby', which suggests they were no longer managed for coppice. However, the woodlands to the west of Macroom along the River Lee were valued at nearly £4,000 in the mid-17th century (McCracken, 1959). This figure reflects a general trend for increasing woodland cover westwards through county Cork, where land was poorer and the population lower (Tierney, 1998).

The Civil Survey map clearly shows the presence of an extensive area of woodland along the River Lee to the north-west of Annahalabog (Fig. 2.5). Like many woodlands in the upper Lee Valley, the Gearagh was situated in an inaccessible and difficult location. Trees were not immediately felled because of the difficulty in transporting timber overland (Smyth, 2006). Roads were primitive and poorly maintained over rough terrain, while the River Lee was largely unsuitable for navigation. However, many of the more accessible woods in the lowlands and along the coast of Cork were rapidly exploited. Many of these were used to supply timber for pipe and barrel-staves, and to cask provisions for the American plantations (McCracken, 1971; Whelan, 1997). By the end of the 1600s, however, most of the timber to supply these industries was being imported from the Baltics and America (McCracken, 1971). Some woodlands were also associated with ironworks, and were managed as coppice to produce charcoal as fuel for iron smelting (Rackham, 1995). Areas without significant ironworks, such as the upper Lee Valley, received little investment in infrastructure. The only significant threat to the Gearagh thus came from agriculture.

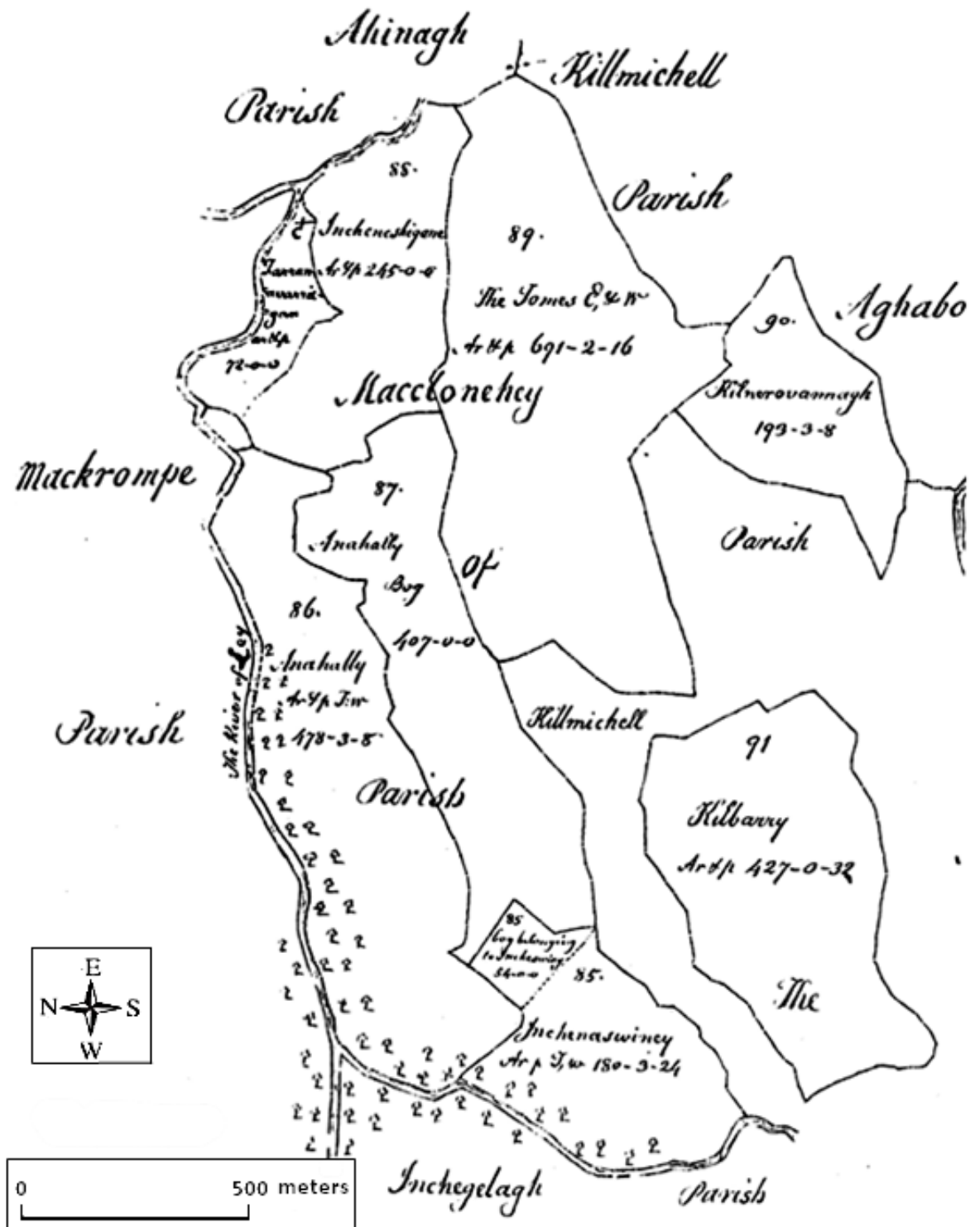


Fig. 2.5 Civil Survey (1654-6) map of Macloneigh parish. The River Lee marks the northern and western extent of the parish. The tree symbols along the course of the river correspond with the present-day location of the Gearagh.

Prior to the 18th century, the landscape of south-west Ireland consisted mainly of open grassland and woodland (Cole and Mitchell, 2003); this was primarily farmed by small partnership tenants (Dickson, 2005). In 1694, however, the fourth Earl of Clancarty forfeited his lands (Ó Murchadha, 1993), and the new owners immediately felled any standing timber for additional funds (Dickson, 2005). Once woodland was cleared, the land was then usually used as unenclosed sheep and cattle runs (Aalen, 1978). This prevented saplings from emerging and woodlands regenerating as they had previously done (Hall, 2000). Eventually, much of the wooded areas along the Lee Valley was severely reduced, although this reduction was probably not as extensive as portrayed in the historical record; many coppices and scrub were still to be found (Hall, 1995). It is likely that the Gearagh survived as one of these scrub woodlands, although the margins were undoubtedly altered by exploitation and agricultural encroachment. Crucially, the River Lee continued to act as a natural barrier to unrestricted cattle grazing, thereby preserving the core of the woodland.

Significant declines in woodland pollen from 1750 onwards are recorded in south-west Ireland (Little *et al.*, 1996; Cole and Mitchell, 2003). This coincides with population growth and the clearance of more marginal land for additional grazing areas (Whelan, 1997). Dairying replaced small subsistence farms in the Lee and Blackwater Valleys, and led to an increase in liming, draining, and enclosure across the landscape. Unregulated felling of timber increased (Feehan, 2005), and turf began to be used as an alternative source of fuel. Bogs such as Kilcrea Bog on the River Bride were drained and reclaimed for agriculture.

Although the population continued to expand, the road system remained in poor condition. Most goods were transported on the navigable rivers, particularly the Blackwater (Dickson, 2005). By 1785, the population had doubled again, trade had increased, and new roads were being built to cope with wheeled traffic. A map of the roads of Ireland by Taylor and Skinner in 1778 (Fig. 2.6) shows the road network of Macroom and the approach roads (Taylor, 1778). This map shows that the area around the Gearagh was not well serviced by roads at this time. The Inchigeelagh road, which now runs parallel to the north side of the Gearagh, is not yet mapped.

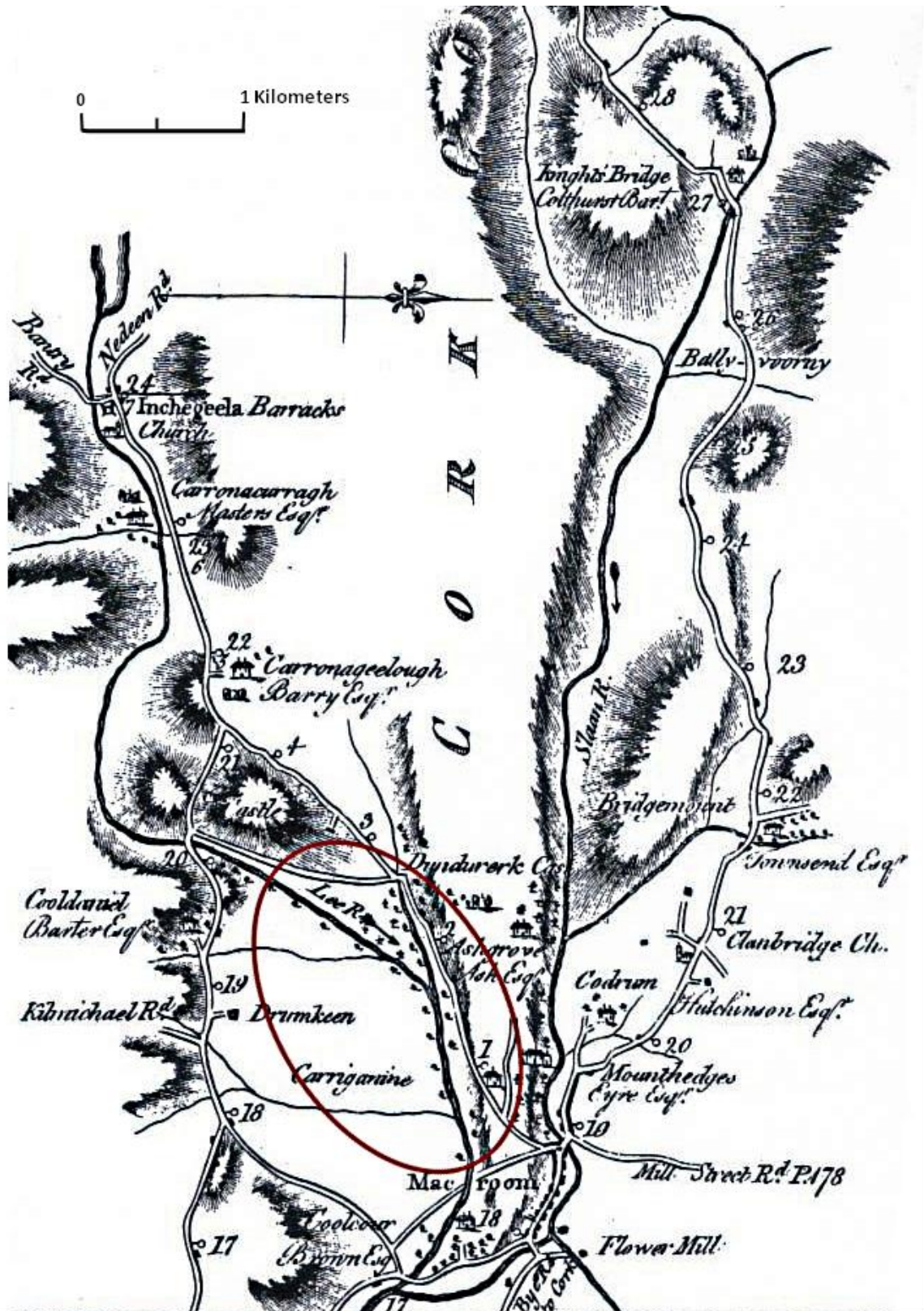


Fig. 2.6 Extract of the Taylor and Skinner map 1778 showing the roads around Macroom. A wooded area, indicated by tree symbols (circled in red), is marked along the River Lee in the same location as the Gearagh today.

Many of the minor roads are also missing; most of these were built in the early 19th century during a period of intense road construction (O'Flanagan, 1993).

Despite all the change in the Irish landscape, the Gearagh appears to have remained more or less wooded throughout this period. One of the first descriptions of the Gearagh comes from an account by Charles Smith (1774) in the late 18th century. He describes how the River Lee was occupied with wooded islands along its course from Carrignacurra as far as the bridge at Bealahaglashin, just beyond the Coolcour moraine (Smith, 1774):

These islands are covered, mostly, with oak, ash, hazel, and birch; at the feet of which grow fern, polypodium, and water dropworth. Here are great quantities of several kinds of water fowl, in their seasons, as bitterns, cranes, duck and mallard, teal, etc.

The river was noted as being hazardous to navigate under high flows, which rendered all fording sites impassable. This suggests that the area was still quite isolated and poorly developed. Smith (1774) also indicates that attempts were made to drain the land surrounding the river, much as Kilcrea Bog was drained and the River Bride channelised in the early 18th century. However, because the Lee is a larger river than the Bride, these drainage systems proved to be more difficult to maintain and were subsequently abandoned. This unsuccessful attempt to drain and channelise the River Lee meant that the Gearagh remained relatively unaltered during this period of increased exploitation and land improvement. However, Smith (1774) does note that an outcrop of limestone at Annahala just to the south of the Gearagh was used to supply farmers in Macroom and the surrounding area with lime.

2.6.2 Landscape of the Gearagh AD 1842

By the time of the first Ordnance Survey in 1837-42, only about one tenth of the woodland that was present in Ireland in the 1650s still remained (Rackham, 1995). In comparison, 80% of woods in England survived from the 1650s to the 1850s (Rackham, 2005). However, there were still significant wooded areas throughout the country; many new woodlands had been planted during the late 1700s, mostly on demesnes (O'Carroll, 2004). The extensive clearance of woodland that occurred outside of the demesnes during this period was driven primarily by the need to

produce more food and fuel for the rapidly expanding population. However, after several years of famine during the 1840s, population pressure was reduced, leading to abandonment of marginal fields and farms (Whelan, 1997).

It is with the Ordnance Survey map of 1842 (scale 1:10,560) that key morphological features of the Gearagh can be seen for the first time (Fig. 2.7). It shows that the southern part of the Gearagh, which was still mostly wooded, was divided into the townlands of Gearagh West and Gearagh East, both of which belonged in the parish of Macloneigh. The parish boundaries clearly followed the path of the largest channels of the River Lee as it flowed through the Gearagh. In almost all cases, the location of the larger islands and channels on the map remain the same today (Brown *et al.*, 1995). This indicates that the channel pattern has altered very little in the last 170 years, and the islands are quite stable systems. Many abandoned channels can be seen to the south of the Gearagh in the area of Annahala East and Annahala West, denoting the former extent of the system. These areas were marked 'Liable to Floods' and indicate that flooding was a significant problem in the area. Many of the islands had also been cleared of woodland, probably to create additional pasture for grazing cattle. Several fording sites can be seen as access points to these islands (Fig. 2.7).

Access to Annahala from the Inchigeelagh road was over the Port Road which crossed through the Gearagh. Both the Port Road and the Inchigeelagh road had been constructed during a period of road building between the late 1700s and early 1800s (O'Flanagan, 1993). These, like many of the roads constructed at this time, were remarkably straight, despite crossing difficult terrain such as the Gearagh (Aalen, 1978). The Ordnance Survey map also depicts a network of small roads and lanes (*bóthríní*) throughout Macloneigh. Such roads were frequently constructed as a result of changes in agriculture and the need to create additional access points to carry out land drainage, liming, and reclamation schemes (Killen, 1997). The growing small road network also reflected the increasing number of scattered farmsteads in the area.

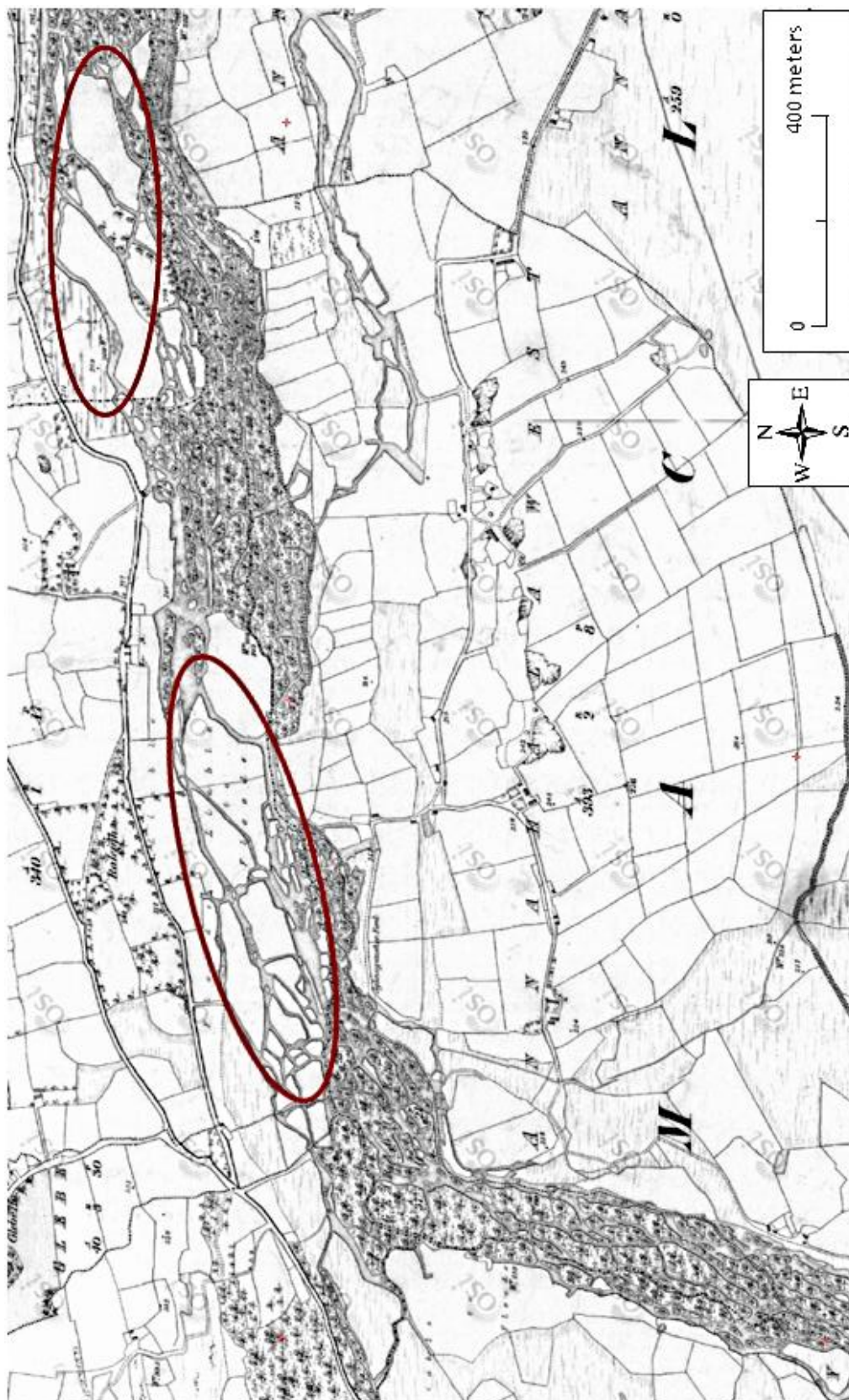


Fig. 2.7 Extract of the first Ordnance Survey map from 1842 showing a section of the Gearagh, Co. Cork. The major channels and islands along the River Lee can be seen on the map. Many of the larger islands have been cleared of woodland (circled in red).

Descriptions of property ownership were recorded in the Griffith Valuation of 1852 (General Valuation and Boundary Survey Ireland, 1852). The owner of Gearagh East and Gearagh West is recorded as William V. Stewart (otherwise known as William Villiers-Stuart), who also leased land in several other townlands in Macloneigh. These lands once formed part of the Cox estate, which passed to the Villiers-Stuart family in 1833 through the marriage of Catherine Cox to William Villiers-Stuart (PRONI, 2007). By the 1870s, William Villiers-Stuart, who resided in County Waterford, owned approximately 1,404 acres in County Cork. The lots relating to the Gearagh are described as woodland pasture, so cattle evidently grazed here. All of the other lots belonging to William Villiers-Stuart in the area were sublet to local individuals. The north of the Gearagh fell into the townlands of Raleigh South, Tullatreada, and Sleveen West. None of these lands are ascribed any value, but they correspond to areas of the Gearagh that had been cleared of woodland (Fig 2.8). Most of the landlords north of the Gearagh almost certainly belonged to the important local families who had greater interest in developing and maintaining their lands (Smyth, 1993). For instance, areas of tree-planting for shelter belts can be seen on several townlands to the north of the Gearagh, particularly in Raleigh South; no planting is apparent in William Villiers-Stuart's lands in Macloneigh. Indeed, much of the land in Macloneigh during the 1840s is described as being underdeveloped, and agriculture remained in quite a primitive state. Old wooden ploughs and spades were the main tools used for cultivation (Mac Suibhne, 1997).

The Macroom area was badly affected by the 1845-50 potato famine. The parish of Macloneigh lost a quarter of its population in the ten years from 1841 (Mac Suibhne, 1997). After the famine, many of the landowners in the parishes around Macroom became bankrupt and their properties were sold. It is likely that some of the islands in the Gearagh that had previously been used as marginal land for grazing cattle were gradually abandoned during this period.

2.6.3 Landscape of the Gearagh AD 1842 - 1904

At the beginning of the 20th century, it is estimated that less than 1% of the country was covered in woodland (Neeson, 1991). However, the second Ordnance Survey map of 1904 shows that the Gearagh woodland was still present, although it

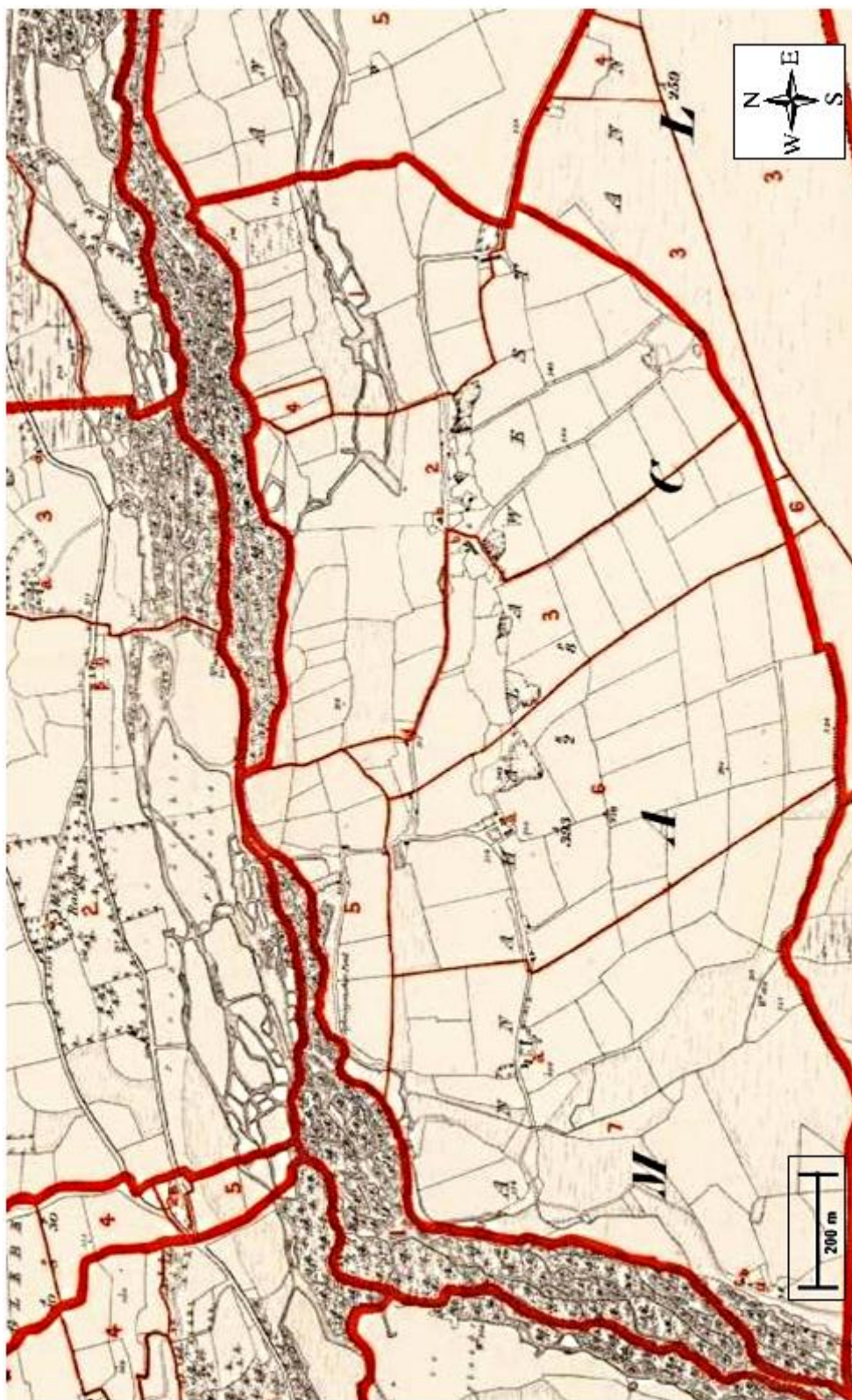


Fig. 2.8 Extract from the first Ordnance Survey map (1842) showing the townland boundaries (thick red lines) and land ownership boundaries (fine red lines) in the area surrounding the Gearagh, as recorded in Griffith's Valuation of property in Ireland (1847-64). Islands that are clear of woodland evidently correspond to land ownership boundaries.

differed in a number of ways from the 1842 map (Fig. 2.9). The most significant change was the increase in wooded areas along the Lee. Some of the areas of land that had been cleared in the 1842 map were by 1904 covered in scrub. This indicates that the land had been abandoned sometime in the preceding 50 years, thereby allowing woodland to naturally regenerate in these areas. An island called Illaunmore ('large island') and the surrounding islands, situated west of Annahalla Bridge, were free of woodland in the 1842 map. By 1904, only the three largest islands remained as grassland. The smaller islands had already reverted to scrub and woodland.

Fording sites through the Gearagh were important enough to be named on the 1904 map: Bealahy Ford or *Beal Lathaighe* ('miry passage') and Aughnagaushie Ford or *Áth na Gaisidhe* ('ford of the bog dealings'). However, consistent accounts of a bandit eluding the authorities in the Gearagh indicate that the woodland was not frequented by many people, even locals (O'Donoghue, 1996). An old ford on the river Lee was located at the eastern extent of the Gearagh; this was called *Áth an Teampuill* ('ford of the church'). The ford was still present on the 1842 Ordnance Survey map when a ferry was used to cross the river. At the time of the 1904 survey, however, a new bridge known as Ahteampaill Bridge had been built to replace the old fording point. This would have further increased accessibility to the Gearagh area. The establishment of a quarry in Annahala West, just to the south of the Gearagh, reflects the great demand for lime during this period (Walsh *et al.*, 1957). This particular quarry was used to supply Macroom and the surrounding area with lime for manure and building. It led to the construction of new roads in the area and, subsequently, increased trade and development (O'Donoghue, 1996). However, by the time the second Ordnance Survey was published, these quarries were no longer in use. The roadside grouping of buildings in Annahalabog labelled as the 'Gearagh Cottages' were built by the Poor Law Unions as public provision of housing for the rural poor (Whelan, 1997). This had the effect of retaining people on small farms, so that they did not need to migrate to the towns and cities.

Much of the land around the Gearagh that was still liable to flooding from the river was marked on the 1904 map. At some point in the past, an earthen embankment

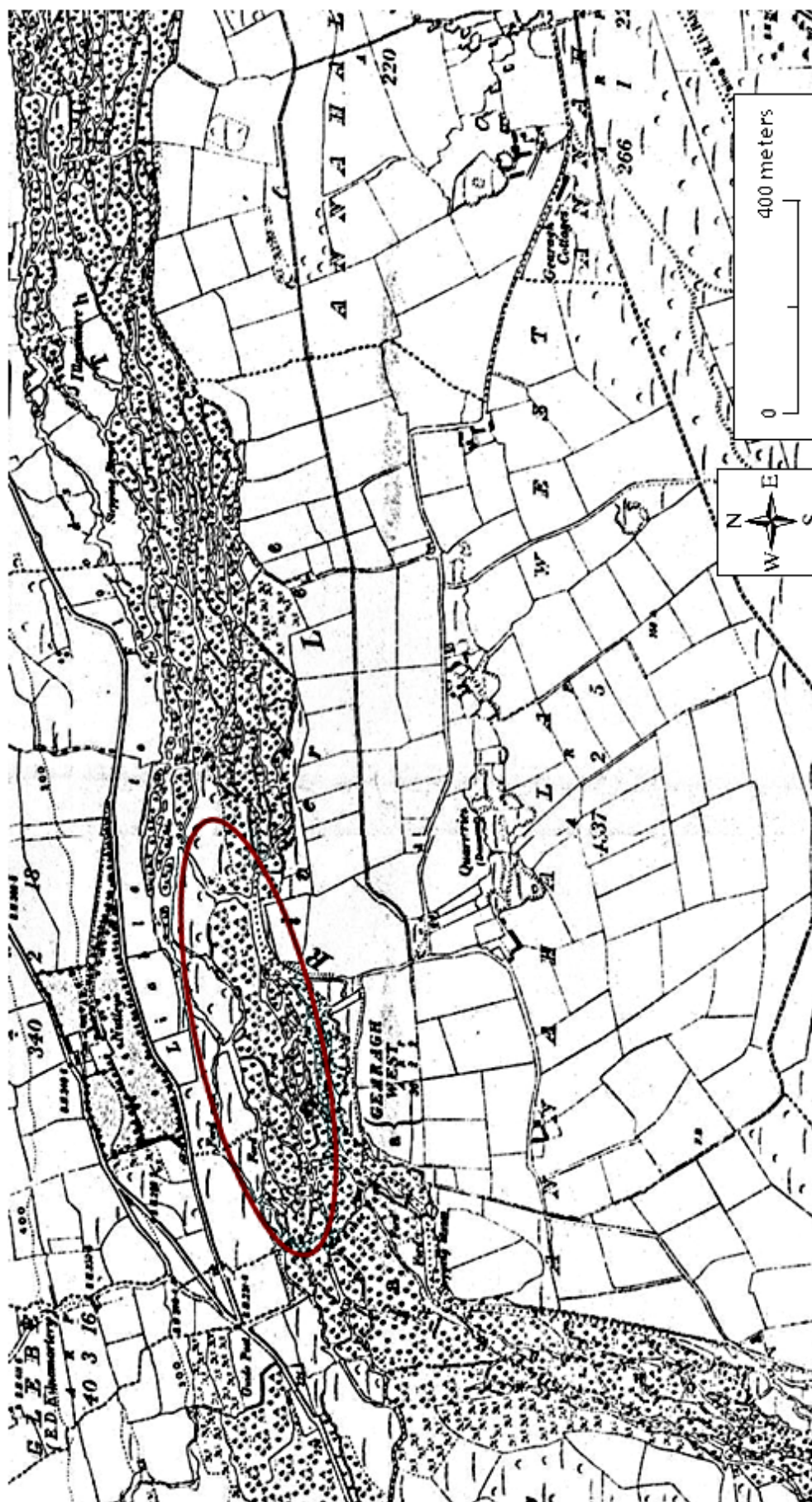


Fig. 2.9 Extract of the second Ordnance Survey map from 1904 showing a section of the Gearagh, Co. Cork. Islands in the northern section of the Gearagh that had previously been clear of woodland (Figs. 2.7 and 2.8) are now shown to have tree or scrub symbols (circled in red).

had been erected along the southern side of the Gearagh to reduce flooding in adjacent farmland. Although this embankment was probably quite old, it was only marked for the first time on the second Ordnance Survey map. Embankments such as these were difficult to maintain and eventually deteriorated (O'Donoghue, 1996). Other more successful drainage works were carried out in the interval since 1842. The old river channel in Annahala East had been straightened into a single large drainage channel that ran to the south of the Gearagh. This undoubtedly helped to reduce flooding in the area and opened up the fields adjacent to the river to more intensive agriculture. Dairying was still one of the most important agricultural activities at this time and a new creamery had been established in Teergay just south of the Toon Bridge. It is likely that farmers in the Gearagh would have delivered their milk to this local creamery.

2.6.4 Landscape of the Gearagh AD 1904 - 1938

The third Ordnance Survey map essentially shows the Irish landscape in the aftermath of World War I and the Irish Civil war. However, only minor changes occurred in the Gearagh since the 1904 map (Fig. 2.10). Areas of the woodland, which had been grassland in 1842 and scrub in 1904, are now shown as mature woodland. Indeed, most islands had reverted to woodland or at least to scrub by the time of the 1938 map. The only significant exceptions are parts of the three large islands in the townland of Raleigh South and the island of Illaunmore. Presumably these areas were still being used to graze cattle. Indeed, accounts reveal that local farmers often allowed their cattle to graze in certain wooded areas of the Gearagh (O'Connell, 2008). Other reports emphasise the inaccessibility of the woodland; regular accounts describe how *poitín*, an illicit spirit, was frequently distilled in the Gearagh so as to avoid detection from the local constabulary (O'Donoghue, 1996; O'Connell, 2008). Several renowned botanists have visited the Gearagh since the late 19th century. These were among the first to document the abundant tree and herb flora there. Many, including Praeger (1907), Braun-Blanquet and Tüxen (1952), and O'Reilly (1955), published reports on their visits to the Gearagh. The ground flora was of particular interest, and several plants which were scarce elsewhere in Ireland were identified in the Gearagh. Despite the initial

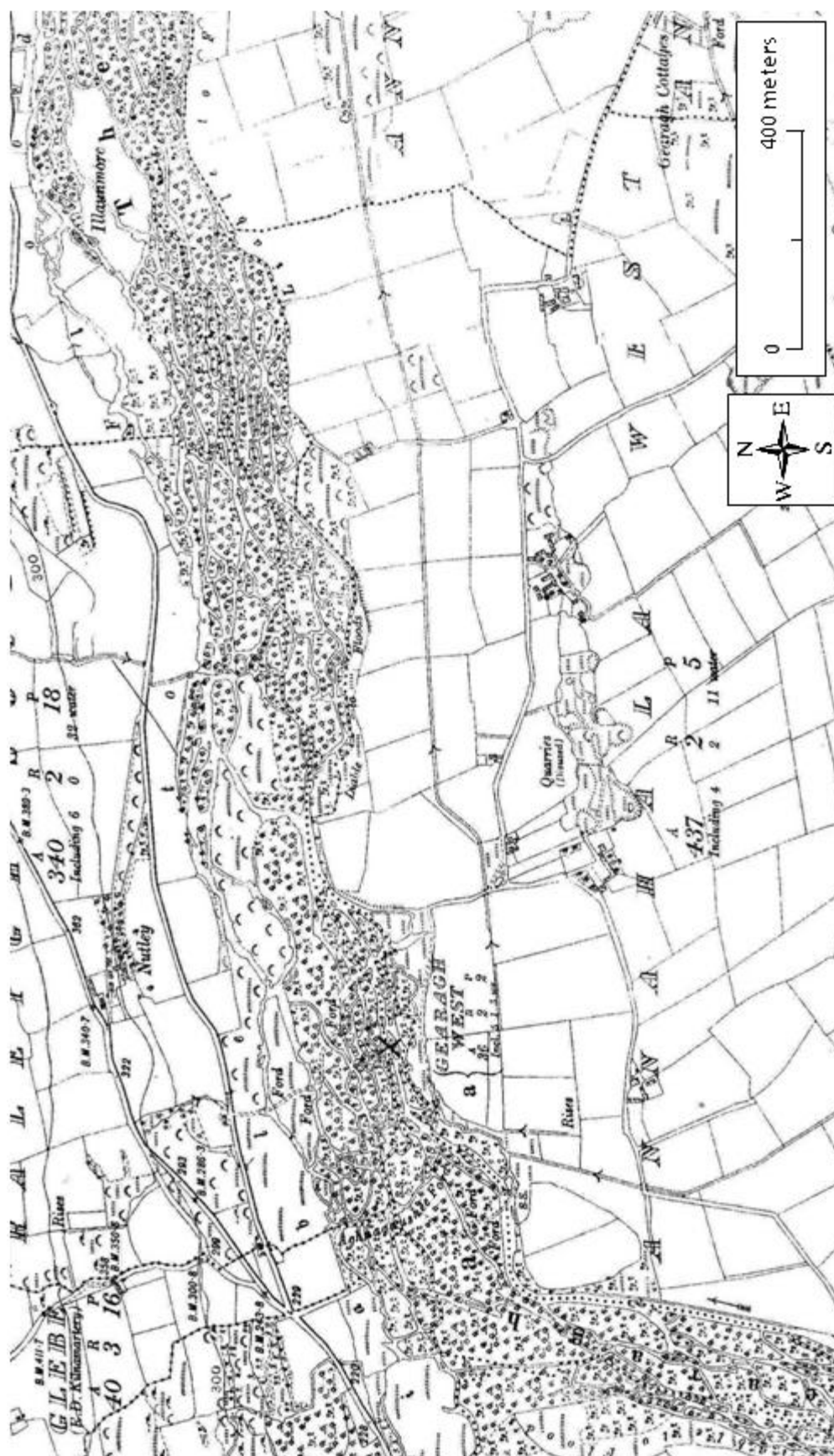


Fig. 2.10. Extract of the third Ordnance Survey map from 1938 showing part of the Gearagh, Co. Cork. Most of the islands are now shown as woodland or scrub.

botanical interest in the woodland, there has been remarkably little ecological work carried out in the Gearagh since these visits.

2.6.5 Landscape of the Gearagh AD 1938 - present

After World War II, the state electricity company, the Electricity Supply Board (ESB), proposed to build a hydro-electric power station on the River Lee as part of a rural electrification scheme. This involved the construction of two dams along the River Lee; one, at Carrigadrohid, created a reservoir that flooded a large section of the Gearagh. Prior to construction, the ESB acquired all of the land that was to be affected by the scheme, including all of the Gearagh woodland. All scrub and trees in the woodland growing below the projected high water level in the Carrigadrohid reservoir were felled (O'Donoghue, 1996). Clearance of the woodland was difficult and took nearly three and a half years to complete (O'Connell, 2008). In the end, approximately 60% of the former woodland was lost (O'Reilly, 1955). On October 1956, the Carrigadrohid reservoir was filled and the felled portion of the woodland was flooded.

For many years, it was generally accepted that Gearagh had been completely destroyed by the creation of the reservoir. It was only after several decades that the importance of the remaining section was highlighted. The Irish Biogeographical Society held a meeting there in 1983 (FitzGerald, 1984), and White (1985) published a paper on it. In 1987, it was declared a statutory nature reserve under the Wildlife Act (1976) with the support of the ESB. Today, the area flooded by the reservoir extends from Lee Bridge to Annahala Bridge and westwards of Illaunmore Island. The reservoir is now home to a diverse range of plants, including rare and naturalised species, and has also become a Wildfowl Sanctuary which supports an extensive bird population.

At present, cattle still graze in parts of the Gearagh woodland during the summer months, but the impacts of this are localised. Little felling has occurred since the early 1950s; in fact, tree regeneration is occurring around the reservoir area. This new woodland community is dominated by *Salix cinerea* spp. *oleifolia*, and has replaced the former *Quercus robur*, *Fraxinus excelsior*, and *Corylus avellana*

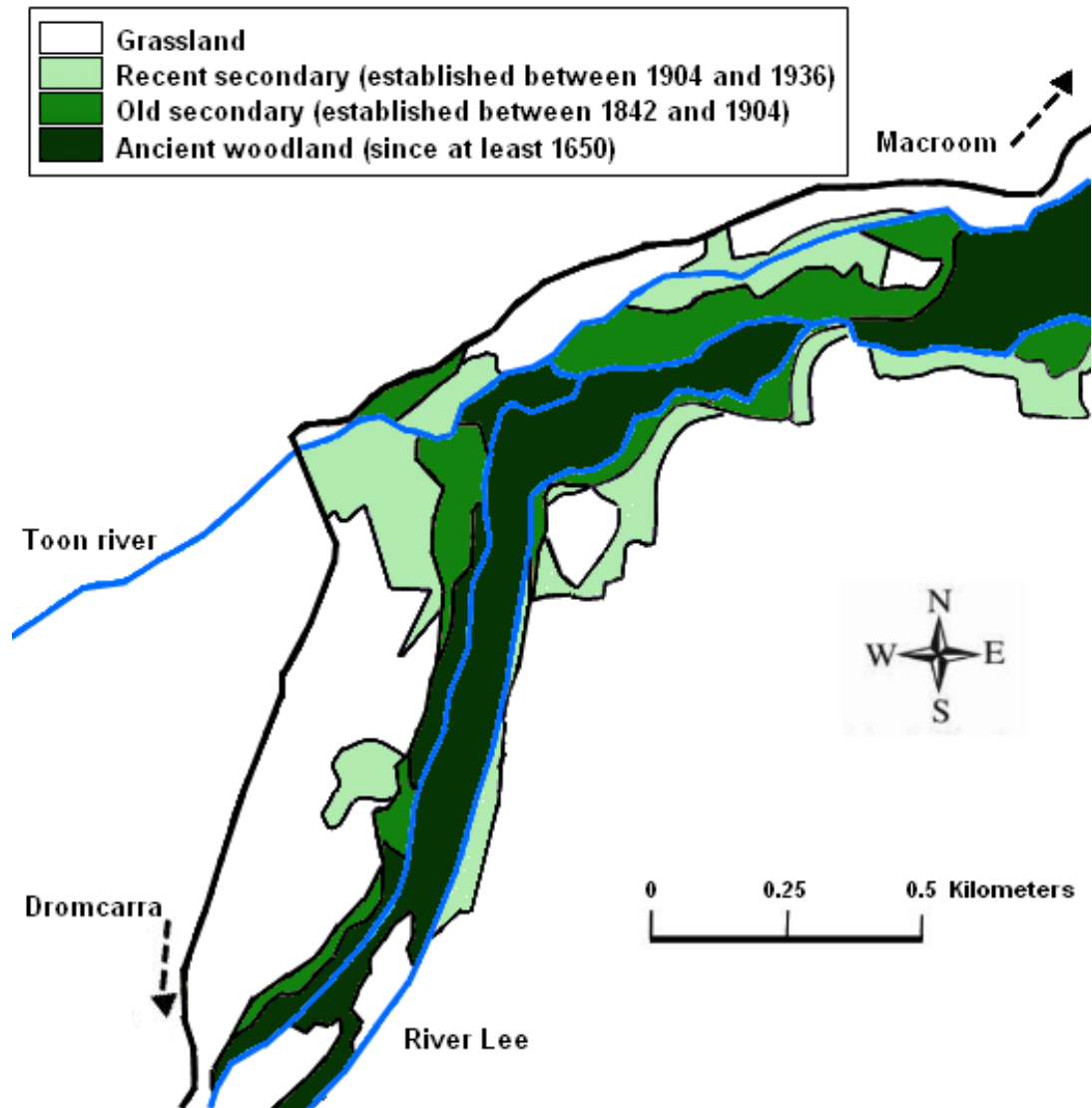


Fig. 2.11 Map showing the boundaries of the different woodland stands and grassland areas in a section of the Gearagh woodland used for this study.

community. Now, the least disturbed part of the woodland occurs in the upper reaches of the Gearagh between Teergay and Toon Bridge, where the core islands are still dominated by *Quercus robur*, *Fraxinus excelsior*, *Corylus avellana*, and *Betula pubescens*. This area forms the central part of the ancient woodland section in the Gearagh (Fig. 2.11). It lies well above the extent of the reservoir and is rarely affected by fluctuations in water level caused by the dam. In wetter depressions and on channel margins, the trees are mainly *Salix* spp. and *Alnus glutinosa*, while

the woodland margins contain *Euonymus europaeus*, *Viburnum opulus*, and *Prunus cerasifera*.

The former Port Road that crossed the Gearagh, linking the Annahala with the main Inchigeelagh road, still survives. It now transects the reservoir as a causeway, and has become a popular recreational site, attracting visitors interested in walking, photography, and bird-watching. It provides an excellent vantage point for people to view the cut stumps of the former woodland as they project out of the water. However, the surviving woodland itself still remains a relatively isolated place and the anastomosing channel pattern continues to protect it from significant human disturbance.

2.7 Conclusions

By combining information from various sources, it has been possible to chart the development of the Gearagh and the surrounding landscape throughout history. Although people have inhabited Ireland since the early Holocene, they have only had an appreciable impact on the landscape since the Bronze Age. While woodlands across Ireland have clearly been affected by human activities throughout prehistoric and early historic times, it remains unclear as to the extent of human impacts on the Gearagh woodland itself. However, it is likely that people have hunted and farmed the land surrounding the woodland since at least the Bronze Age.

Over the last 200 years, human activity around the Gearagh has intensified considerably. While the natural vegetation in the woodland is similar to what it has been for many thousands of years, the overall appearance and structure of the woodland has undergone many changes. Despite the pressures in the surrounding landscape, the Gearagh has survived where many other Irish woodlands have been destroyed. Prior to the construction of the ESB reservoir, most clearances were small and localised. These open areas were only maintained with continuous grazing; when they were abandoned, woodland was able to re-establish. The core of the Gearagh remained relatively intact throughout this period and can now be considered a remnant of ancient woodland.

The Gearagh is unusual as an ancient woodland in that its inaccessibility (and difficulty in exploitation) is not due to steep slopes and remote location, but is instead largely due to the proximity of a large wetland area (Annahalabog) and the anastomosing channel pattern of the River Lee. Although the Gearagh differs from other woodlands in terms of its historical origins and past management, it remains one of the few surviving large stands of native woodland in Ireland; most other native woodlands are either under threat or else are deteriorating. As society becomes increasingly aware of the values associated with such natural woodland, it is likely that greater efforts will be made to conserve and restore this woodland, as well as others throughout the country.

2.8 References

- Aalen, F.H.A. (1978) *Man and the Landscape in Ireland*. Academic Press, London, UK, pp. 342.
- Barnosky, C.W. (1988) A late-glacial and post-glacial pollen record from the Dingle peninsula, County Kerry. *Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science*, **88B**, 23-37.
- Bradshaw, R.H.W. (2004) Past anthropogenic influence on European forests and some possible genetic consequences. *Forest Ecology and Management*, **197**, 203-212.
- Braun-Blanquet, J. & Tüxen, R. (1952) Irische Pflanzengesellschaften. In: *Die Pflanzenwelt Irlands* (ed. W. Ludi), pp. 224-421. Hans Huber, Bern, Switzerland.
- Brinson, M.M. & Verhoeven, J. (1999) Riparian forests. In: *Maintaining Biodiversity in Forest Ecosystems* (ed. M.L. Hunter, Jr), pp. 265-299. Cambridge University Press, Cambridge, UK.
- Brown, A.G. (1999) Biodiversity and pollen analysis: modern pollen studies and the recent history of a floodplain woodland in S. W. Ireland. *Journal of Biogeography*, **26**, 19-32.
- Brown, A.G. (2002) Learning from the past: palaeohydrology and palaeoecology. *Freshwater Biology*, **47**, 817-829.

- Brown, A.G., Stone, P. & Harwood, K. (1995) *The Biogeomorphology of a Wooded Anastomosing River: the Gearagh on the River Lee in County Cork, Ireland*. Occasional Paper 32, Department of Geography, University of Leicester, UK, pp. 76.
- Burt, T.P. (1996) The hydrological role of floodplains within the drainage basin system. In: *Buffer Zones: Their Processes and Potential in Water Protection* (eds N. Haycock, T.P. Burt, K. Goulding & G. Pinay), pp. 21-32. Quest Environmental, Harpenden, UK.
- Caulfield, S. (2005) Forests and people in Ireland's Stone Age. In: *Ireland's Native Woodlands Conference* (eds C. Doyle & D. Little), pp. 48-59. Woodlands of Ireland, Dublin, Ireland.
- Chiverrell, R.C., Innes, J.B., Blackford, J.J., Woodcock, J.J., Davey, P.J., Tomlinson, P.R., Rutherford, M.M. & Thomas, G.S.P. (2004) Palaeoecological and archaeological evidence for Bronze Age human activity on the Isle of Man. *The Holocene*, **14**, 346-360.
- Chiverrell, R.C. & Thomas, G.S.P. (2010) Extent and timing of the Last Glacial Maximum (LGM) in Britain and Ireland: a review. *Journal of Quaternary Science*, **25**, 535-549.
- Cole, E.E. & Mitchell, F.J.G. (2003) Human impact on the Irish landscape during the late Holocene inferred from palynological studies at three peatland sites. *The Holocene*, **13**, 507-515.
- Conry, M.J. & Ryan, P. (1965) Some observations on manganese in west Cork soils. *Irish Journal of Agricultural Research*, **4**, 61-66.
- Coxon, P. (1986) A radiocarbon dated early post glacial pollen diagram from a pingo remnant near Millstreet, County Cork. *Irish Journal of Earth Sciences*, **8**, 9-20.
- Cross, J.R. (2006) The potential natural vegetation of Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy*, **106B**, 65-116.
- Cross, J.R. & Kelly, D.L. (2003) Wetland woods. In: *Wetlands of Ireland: Distribution, Ecology, Uses and Economic Value* (ed. M.L. Otte), pp. 160-173. University College Dublin Press, Dublin, Ireland.

- Dickson, D. (2005) *Old World Colony: Cork and South Munster 1630-1830*. Cork University Press, Cork, Ireland, pp. 726.
- Dupouey, J.L., Dambrine, E., Laffite, J.D. & Moares, C. (2002) Irreversible impact of past land use on forest soils and biodiversity. *Ecology*, **83**, 2978-2984.
- FAO (2011) *State of the World's Forests 2011*. Food and Agriculture Organization of the United Nations, Rome, Italy, pp. 179.
- Farrington, A. (1959) The Lee basin. Part one: glaciation. *Proceedings of the Royal Irish Academy B*, **60**, 135-166.
- Feehan, J. (2005) The woodland vegetation of Ireland, past, present and future. *Irish Forestry*, **62**, 73-87.
- FitzGerald, R. (1984) The Gearagh - a rare habitat in Co. Cork. *BSBI News*, **36**, 8-9.
- Fitzpatrick, H.M. (1966) *The Forests of Ireland: An Account of the Forests of Ireland from Early Times Until the Present Day*. The Society of Irish Foresters, Bray, Ireland, pp. 153.
- Forest Service (2008) *Irish Forests: A Brief History*. Forest Service, Department of Agriculture, Fisheries and Food, Government of Ireland, Dublin, Ireland, pp. 8.
- Fuller, B.S.D. (1990) *Ancient Woodland in Central Ireland: Does it Exist?* M.Sc. thesis, Trinity College Dublin, Dublin, Ireland.
- General Valuation and Boundary Survey Ireland (1852) *General Valuation of Rateable Property in Ireland: County of Cork, Barony of West Muskerry*. H.M. Stationery Office, Dublin, Ireland, pp. 179.
- Hall, V.A. (1995) Woodland depletion in Ireland over the last millennium. In: *Wood, Trees and Forests in Ireland* (eds J.R. Pilcher & S. Mac an tSaoir), pp. 23-33. Royal Irish Academy, Dublin, Ireland.
- Hall, V.A. (1997) The development of the landscape of Ireland over the last two thousand years; fresh evidence from historical and pollen analytical studies. *Chronion*, **1**, 1-22.
- Hall, V.A. (2000) The documentary and pollen analytical records of the vegetational history of the Irish landscape AD 200-1650. *Peritia*, **14**, 342-371.

- Hall, V.A. (2003) Vegetation history of mid- to western Ireland in the 2nd millennium a.d.; fresh evidence from tephra-dated palynological investigations. *Vegetation History and Archaeobotany*, **12**, 7-17.
- Harwood, K. & Brown, A.G. (1993) Fluvial processes in a forested anastomosing river: flood partitioning and changing flow patterns. *Earth Surface Processes and Landforms*, **18**, 741-748.
- Hermý, M. & Verheyen, K. (2007) Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. *Ecological Research*, **22**, 361-371.
- Joyce, P.W. (1887) *The Origin and History of Irish Names of Places*. M.H. Gill, Dublin, Ireland, pp. 573.
- Kelly, D.L. (2005a) Woodland on the western fringe: Irish oakwood diversity and the challenges of conservation. *Botanical Journal of Scotland*, **57**, 21-40.
- Kelly, F. (1997) *Early Irish Farming: A Study Based Mainly on the Law-Texts of the 7th and 8th Centuries AD*. School of Celtic Studies, Dublin Institute for Advanced Studies, Dublin, Ireland, pp. 751.
- Kelly, F. (1999) Trees in early Ireland. *Irish Forestry*, **56**, 58-62.
- Kelly, F. (2005b) The use of Ireland's woodland in medieval times. In: *Ireland's Native Woodlands Conference* (eds C. Doyle & D. Little), pp. 54-59. Woodlands of Ireland, Dublin, Ireland.
- Killen, J. (1997) Components of the Irish landscape: communications. In: *Atlas of the Irish rural landscape* (eds F.H.A. Aalen, K. Whelan & M. Stout), pp. 206-219. Cork University Press, Cork, Ireland.
- Kirby, K.J. & Watkins, C. (1998) *The Ecological History of European Forests*. CAB International, Wallingford, UK, pp. 384.
- Little, D.J., Mitchell, F.J.G., von Engelbrechten, S. & Farrell, E.P. (1996) Assessment of the impact of past disturbance and prehistoric *Pinus sylvestris* on vegetation dynamics and soil development in Uragh Wood, SW Ireland. *Holocene*, **6**, 90-99.
- Lynch, A. (1981) *Man and Environment in South-West Ireland, 4000 B.C. - A.D. 800: A Study of Man's Impact on the Development of Soil and Vegetation*. BAR, Oxford, UK, pp. 175.

- Mac Nally, R., Molyneux, G., Thomson, J.R., Lake, P. & Read, J. (2008) Variation in widths of riparian-zone vegetation of higher-elevation streams and implications for conservation management. *Plant Ecology*, **198**, 89-100.
- Mac Suibhne, M. (1997) *Famine in Muskerry: An Outline of Conditions in the Sixteen Parishes of Macroom Poor Law Union During the Great Famine, 1845-'51*. Litho Press, Middleton, Ireland, pp. 160.
- Makaske, B. (2001) Anastomosing rivers: a review of their classification, origin and sedimentary products. *Earth Science Reviews*, **53**, 149-196.
- McCracken, E. (1959) The woodlands of Ireland circa 1600. *Irish Historical Studies*, **11**, 271-296.
- McCracken, E. (1971) *The Irish Woods since Tudor Times: Distribution and Exploitation*. David and Charles, Plymouth, UK, pp. 184.
- Mighall, T., Timpany, S., Blackford, J., Innes, J., O'Brien, C., O'Brien, W. & Harrison, S. (2008) Vegetation change during the Mesolithic and Neolithic on the Mizen Peninsula, Co. Cork, south-west Ireland. *Vegetation History and Archaeobotany*, **17**, 617-628.
- Mitchell, F. & Ryan, M. (2007) *Reading the Irish Landscape*, 4th edn. TownHouse, Dublin, Ireland, pp. 392.
- Mitchell, F.J.G. (1995) The dynamics of Irish post-glacial forests. In: *Wood, Trees and Forests in Ireland* (eds J.R. Pilcher & S. Mac an tSaoir), pp. 13-22. Royal Irish Academy, Dublin, Ireland.
- Mitchell, F.J.G. (2006) Where did Ireland's trees come from? *Biology and Environment: Proceedings of the Royal Irish Academy*, **106B**, 251-259.
- Naiman, R.J. & Decamps, H. (1997) The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics*, **28**, 621-658.
- Neeson, E. (1991) *A History of Irish Forestry*. Lilliput Press, Dublin, Ireland, pp. 388.
- Neeson, E. (1997) Woodland in history and culture. In: *Nature In Ireland: A Scientific And Cultural History* (ed. J.W. Foster), pp. 133-156. The Lilliput Press, Dublin, Ireland.
- O'Brien, A.F. (1993) Politics, economy and society: the development of Cork and the Irish south-coast region c. 1170 to c. 1583. In: *Cork: History & Society*:

- Interdisciplinary Essays on the History of an Irish County* (eds P. O'Flanagan & C.G. Buttimer), pp. 83-156. Geography Publications, Dublin, Ireland.
- O'Brien, W. (2009) Space and place: the creation of a 'local world'. In: *Local Worlds: Early Settlement Landscapes and Upland Farming in South-West Ireland* (ed. W. O'Brien), pp. 384-432. Collins Press, Cork, Ireland.
- O'Carroll, N. (2004) *Forestry in Ireland: A Concise History* COFORD, Dublin, Ireland, pp. 96.
- O'Connell, J. (2008) *The Gearagh: A Community & Oak Forest Lost Forever; Scéal Beag, Trua Mór*. Googie-Woggie Publishing, Cork, Ireland, pp. 40.
- O'Connell, M. & Molloy, K. (2001) Farming and woodland dynamics in Ireland during the Neolithic. *Biology and Environment: Proceedings of the Royal Irish Academy*, **101B**, 99-128.
- O'Donoghue, S. (1996) *The Flooding of the Lee Valley*. Tower Books, Ballincollig, Ireland, pp. 189.
- O'Flanagan, P. (1993) Three hundred years of urban life: villages and towns in county Cork c. 1600 to 1901. In: *Cork: History & Society: Interdisciplinary Essays on the History of an Irish County* (eds P. O'Flanagan & C.G. Buttimer), pp. 391-469. Geography Publications, Dublin, Ireland.
- O'Reilly, H. (1955) Survey of the Gearagh, an area of wet woodland on the River Lee, near Macroom, Co. Cork. *The Irish Naturalists' Journal*, **11**, 279-286.
- O'Sullivan, A. (1994) The use of trees and woodland in early medieval Ireland. *Irish Forestry*, **51**, 80-94.
- Ó Murchadha, D. (1993) Gaelic land tenure in county Cork: Uíbh Laoghaire in the seventeenth century. In: *Cork: History & Society: Interdisciplinary Essays on the History of an Irish County* (eds P. O'Flanagan & C.G. Buttimer), pp. 213-248. Geography Publications, Dublin, Ireland.
- Overland, A. & O'Connell, M. (2009) Palaeoecological investigations in the Barrees valley. In: *Local World: Early Settlement Landscapes and Upland Farming in South-West Ireland* (ed. W. O'Brien), pp. 285-322. Collins Press, Cork, Ireland.
- Perrin, P., Martin, M., Barron, S., O'Neill, F., McNutt, K. & Delaney, A. (2008) *National Survey of Native Woodlands 2003-2008: Volume I: Main Report*.

- Unpublished report to the National Parks & Wildlife Service, Dublin, Ireland, pp. 187.
- Perrin, P.M. & Daly, O.H. (2010) *A Provisional Inventory of Ancient and Long-Established Woodland in Ireland*, Irish Wildlife Manuals, No. 46. National Parks and Wildlife Service, Department of the Environment, Heritage and Local Government, Dublin, Ireland, pp. 71.
- Peterken, G.F. (1993) *Woodland Conservation and Management*. Chapman & Hall, London, UK, pp. 374.
- Plunkett, G. (2009) Land-use patterns and cultural change in the Middle to Late Bronze Age in Ireland: inferences from pollen records. *Vegetation History and Archaeobotany*, **18**, 273-295.
- Praeger, R. (1907) Irish Field Club Union. Report of the Fifth Triennial Conference and Excursion, Held at Cork, July 11th to 16th, 1907. I. General Account. *The Irish Naturalist*, 253-262.
- PRONI (2007) *Villiers-Stuart Papers: 1215-1945*. Public Record Office of Northern Ireland, Belfast, UK, pp. 61.
- Rackham, O. (1980) *Ancient Woodland: Its History, Vegetation and Uses in England*. Edward Arnold, London, UK, pp. 624.
- Rackham, O. (1995) Looking for ancient woodland in Ireland. In: *Wood, Trees and Forests in Ireland* (eds J.R. Pilcher & S. Mac an tSaoir), pp. 1-12. Royal Irish Academy, Dublin, Ireland.
- Rackham, O. (2000) *The History of the Countryside: The Classic History of Britain's Landscape, Flora and Fauna*. Phoenix Giant, London, UK, pp. 445.
- Rackham, O. (2005) Questions to ask of Irish native woodland. In: *Ireland's Native Woodlands* (eds C. Doyle & D. Little), pp. 11-18. Woodlands of Ireland, Galway, Ireland.
- Ring, D.P. (1991) *The Historical Geography of Macroom: c.1600-1990*. M.A. thesis, National University of Ireland, Cork, Ireland.
- Smith, C. (1774) *The Ancient and Present State of the County and City of Cork: Containing a Natural, Civil, Ecclesiastical, Historical, and Topographical Description Thereof*. W. Wilson, Dublin, Ireland, pp. 443.

- Smyth, W.J. (1993) Social, economic and landscape transformations in county Cork from the mid-eighteenth to the mid-nineteenth century. In: *Cork: History & Society: Interdisciplinary Essays on the History of an Irish County* (eds P. O'Flanagan & C.G. Buttimer), pp. 655-698. Geography Publications, Dublin, Ireland.
- Smyth, W.J. (2006) *Map-Making, Landscapes and Memory: A Geography of Colonial and Early Modern Ireland: c.1530-1750*. Cork University Press, Cork, Ireland, pp. 584.
- Stout, G. & Stout, M. (1997) Early landscapes: from prehistory to plantation. In: *Atlas of the Irish Rural Landscape* (eds F.H.A. Aalen, K. Whelan & M. Stout), pp. 31-63. Cork University Press, Cork, Ireland.
- Taylor, G. (1778) *Taylor and Skinner's Maps of the Roads of Ireland, Surveyed 1777 (George Taylor and Andrew Skinner)*. G. Taylor and A. Skinner, London, UK, pp. 289.
- Tierney, J. (1998) Wood and woodlands in Early Medieval Munster. In: *Early Medieval Munster: Archaeology, History and Society* (eds M.A. Monk & J. Sheehan), pp. 53-58. Cork University Press, Cork, Ireland.
- Toner, M. & Keddy, P. (1997) River hydrology and riparian wetlands: a predictive model for ecological assembly. *Ecological Applications*, **7**, 236-246.
- Vidon, P.G.F. & Hill, A.R. (2004) Landscape controls on the hydrology of stream riparian zones. *Journal of Hydrology*, **292**, 210-228.
- Walsh, T., Ryan, P. & Kilroy, J. (1957) A half century of fertiliser and lime use in Ireland. *Journal of The Statistical and Social Inquiry Society of Ireland*, **XVIX**, 104-136.
- Whelan, K. (1997) The modern landscape: from plantation to present. In: *Atlas of the Irish Rural Landscape* (eds F.H.A. Aalen, K. Whelan & M. Stout), pp. 67-103. Cork University Press, Cork, Ireland.
- White, J. (1985) The Gearagh Woodland, Co. Cork. *The Irish Naturalists' Journal*, **21**, 391-396.
- Yeloff, D. & Van Geel, B. (2007) Abandonment of farmland and vegetation succession following the Eurasian plague pandemic of AD 1347–52. *Journal of Biogeography*, **34**, 575-582.

CHAPTER 3

THE IMPACTS OF LAND-USE HISTORY ON THE SOIL PROPERTIES IN THE GEARAGH

3.1 Abstract

This study sought to compare the soil structure and composition of a stand of ancient woodland with adjacent stands of old secondary woodland (established between 1842 and 1904), recent secondary woodland (established between 1904 and 1936) and grassland to determine if past land-use has had any enduring effect on soil properties. The ancient woodland had a typical brown earth soil and a profile that showed little signs of disturbance, indicating that the canopy of this woodland has never been fully removed. The two stands of secondary woodland and the grassland site were brown podzolic soils, suggesting a trend towards podzolisation. Differences in several soil properties, including pH and calcium content, reflected the former agricultural history of the secondary woodlands. Canopy removal by tree felling also altered the hydrological balance of the soil due to the high precipitation levels in the region. The results of this study indicate that the soils of woodlands with different land-use histories can differ considerably, even on a local scale. The undisturbed soils of the ancient woodland are extremely rare in Ireland and retain features that have developed in the absence of significant human activity. The diagnostic value of soil characteristics as an indicator of ancient woodland is discussed.

3.2 Introduction

During the 18th and 19th centuries, rapid population growth in Europe led to an increase in demand for food. As a result, more land was taken into agriculture, most often in areas that had been previously occupied by woodland (Bellemare *et al.*, 2002). Surviving woodland was generally only found in remote districts that were unsuitable for agriculture or else on private estates. With the development of more intensive forms of agriculture during the late 19th and 20th centuries, much of the farmland that had been established on marginal land was abandoned, and allowed to revert to woodland (Mather *et al.*, 1999). Consequently, present-day natural deciduous woodland can be characterised as either ancient woodland, corresponding to land that has been continuously wooded since at least the Middle Ages (Rackham, 2000), or secondary woodland, which refers to woodland established on former agricultural land. Although many ancient woods today are

small and fragmented, they often retain important features in their soils, plant and animal communities that developed in the absence of human disturbance. They therefore can provide valuable reference points against which to measure the effect of man on woodland ecology.

Soils play a crucial role in woodland structure and functioning, and can affect the abundance and diversity of plant and animal communities within a woodland (Giller, 1996; Hermy and Verheyen, 2007). Ancient woodland soils are regarded as being particularly stable, with most disturbances occurring only as a result of tree fall or burrowing animals (Rackham, 1980). The continuous cover of trees also protects these soils from erosion and ensures that nutrients are efficiently recycled within the system. However, it is well documented that clearance and agriculture can have a significant effect on the properties of these soils. Removal of trees causes an immediate loss of nutrients, and the litter and humus layers are quickly destroyed by cultivation. Continuous crop removal and increased leaching can lead to a further loss of soil fertility. Generally, agricultural activity has been found to result in changes in pH, soil organic matter content, and phosphate content (Koerner *et al.*, 1997; Wilson *et al.*, 1997; Mueller and Koegel-Knabner, 2009).

However, since the 19th century, fertiliser and lime have frequently been applied to agricultural land. This can lead to higher concentrations of nitrogen, phosphorus, potassium, calcium, and magnesium, and to higher pH in the soil (Honnay *et al.*, 1999; Verheyen *et al.*, 1999; Compton and Boone, 2000). Consequently, the altered soil conditions created by agriculture can pose difficulties for subsequent woodland herb establishment, in particular by stimulating the growth of fast-growing competitive species (Hermy and Verheyen, 2007). It is therefore essential to understand any changes in soil properties that may persist even when woodland has re-established.

Although the soils of secondary woodland almost certainly differ from those which formerly occupied the site before the original woodland was cleared, the extent of these changes and their persistence appears to be highly variable. Many studies have shown that agricultural legacies clearly persist for at least a century and that

secondary woodland soils can remain distinct from ancient woodland soils throughout this period (Koerner *et al.*, 1997; Wilson *et al.*, 1997; Verheyen *et al.*, 1999; Compton and Boone, 2000; Flinn and Marks, 2007). Other studies indicate that past human disturbance can lead to elevated soil pH and phosphorus levels that are still apparent even thousands of years after abandonment (Dupouey *et al.*, 2002; Dambrine *et al.*, 2007; Plue *et al.*, 2008). In contrast, some secondary woodlands recover the soil characteristics of nearby ancient woodlands in less than 100 years; they exhibit little difference in soil properties following agriculture (Compton *et al.*, 1998; Dzwonko, 2001; Graae *et al.*, 2003; Matlack, 2009; Sciama *et al.*, 2009). This variation in response is largely due to differences in initial site conditions (Compton and Boone, 2000; Ritter *et al.*, 2003), as well as the nature, duration and intensity of agricultural use (Koerner *et al.*, 1997; Verheyen *et al.*, 1999; Kopecký and Vojta, 2009). On certain soil types, the loss of nutrients due to hay cropping and pasturage is either insignificant or is improved by fertilisation or other natural processes. For instance, naturally highly fertile and non-acidic soils can often obscure the effects of changes in land-use (Sciama *et al.*, 2009). Therefore, the changes in soil properties that occur depend largely on the region concerned.

The effect of land-use legacies on soil development in Ireland has received relatively little attention (Cunningham *et al.*, 1999), despite the acknowledged importance of these effects internationally. Like much of northern Europe, most of the soils in Ireland are relatively young, and only began to form about 10,000 years ago under a cover of deciduous woodland (Culleton and Gardiner, 1985). Nonetheless, a great variability exists in Irish soils, mostly as a result of changing agricultural practices throughout history. The least disturbed soils are therefore only to be found under remnants of ancient woodland. However, very few stands of ancient woodland still remain (Perrin and Daly, 2010). As part of an effort to expand Ireland's native woodlands, the Native Woodlands Scheme was launched in 2001. This involves the creation of new woodlands throughout the country, mostly on former agricultural land. While many of these woods give the appearance of functional woodland communities, it remains unclear whether secondary

woodlands in Ireland have the biological diversity or ecosystem functionality of ancient woodlands. Since most Irish native woodlands will now consist of secondary woodlands, the suitability of soils will be a critical issue in the management of these woodlands.

Even without human disturbance, the humid climate of north-west Europe means that soil development in this region is mainly driven by leaching (the movement of materials down through the soil profile by water). The well developed tree canopy of mature woodland both reduces rainfall reaching the soil surface via canopy interception and enhances the drying of soil through increased evapotranspiration. The removal of woodland cover increases the water percolating through the soil, leading to increased leaching, acidification and, particularly in coarse-textured soils, to eventual podzolisation whereby iron and aluminium oxides are deposited with organic matter at lower depths in the profile (Lynch, 1981). However, the presence of a continuous canopy cover of broadleaved species can retard this podzolisation process so that soil profiles remain relatively undisturbed. Broadleaved woodland can even help to improve soils of former acidic heath by gradually raising the pH (Nielsen *et al.*, 1987). Nonetheless, the effects of acidification and the development of podzols as a result of episodes of deforestation for agriculture can persist for a long time even once woodland has re-established (Froment and Tanghe, 1967; Goovaerts *et al.*, 1990; Koerner *et al.*, 1997). While it is known that woodland clearance in the past 200 years on acidic, upland soils in Ireland resulted in increased leaching and accelerated acidification (Little *et al.*, 1990; Cunningham *et al.*, 1999), few studies have examined the impacts on lowland soils.

This study aims to characterise the properties of an ancient woodland soil and to investigate the changes that have occurred in these soils after the removal of canopy cover for agriculture. The persistence of these changes in the soil properties of secondary woodland will then be quantified. Although most semi-natural woodlands in Ireland are located on infertile, acid soils in remote upland areas (Little *et al.*, 1990), there are a number that survive on more fertile soils. The Gearagh woodland in County Cork is one such woodland, which is also known to contain a remnant of ancient woodland (Perrin and Daly, 2010). The Gearagh

therefore offers an unusual opportunity to compare ancient woodland soils with those of adjacent stands of secondary woodland. In most of the rest of Ireland, and indeed Europe, it is difficult to assess the effects of former land use, since little old-growth woodland remains, and the observed effects are often obscured by the effects of even earlier land-use and soil disturbance (Verheyen *et al.*, 1999). All of the soils in the Gearagh have developed from the same parent material and under the same climatic conditions, so any major differences between them are likely to be due to past land-use legacies. While the data reported are specific to the Gearagh and the soils it contains, it is believed that they reveal many important features associated with the soils of many other woodlands in humid temperate regions of Europe.

3.3 Materials and Methods

3.3.1 Study area and history

Ireland is one of the least wooded countries in Europe, with just 10 % of the land covered by forest (Forest Service, 2008). Most of this is comprised of commercial conifer plantations; only about 2 % is made up of semi-natural woodland (Perrin *et al.*, 2008). The majority of Ireland's native woodlands were cleared between the 17th and 19th centuries in order to create new agricultural land for the rapidly expanding population. Those woodlands that survived this period of clearance occurred mostly on infertile, acid soils that were unsuitable for agriculture, or were otherwise inaccessible. Ireland's population subsequently declined in the late 19th century due to famine and emigration, leading to the abandonment of many marginal agricultural lands, some of which returned to natural woodland.

The Gearagh woodland in County Cork (N 51°52'09", W 9°01'00") extends for about 7 km along the River Lee, and is regarded as one of the few remaining large remnants of native woodland in Ireland (Perrin *et al.*, 2008). The area is characterised by an extreme oceanic climate. It typically has mild winters and cool summers; the monthly mean temperature for January and July being 6°C and 16°C, respectively. Mean annual precipitation is 1200-1400 mm, with a mean annual potential evapotranspiration of 400 mm, giving a maximum moisture surplus of

1000 mm per annum. The average number of rain-days is high, approximately 221 per annum, and rainfall tends to be evenly distributed throughout the year. Although generally classified as alluvial woodland, much of the site is dominated by oak (*Quercus robur*), ash (*Fraxinus excelsior*), and birch (*Betula pubescens*), with an understorey of hazel (*Corylus avellana*), holly (*Ilex aquifolium*) and hawthorn (*Crataegus monogyna*). Alder (*Alnus glutinosa*) and willows (*Salix* spp.) are confined to the wetter depressions and channel margins. The ground flora is diverse, and is dominated by wild garlic (*Allium ursinum*), wood anemone (*Anemone nemorosa*) and lesser celandine (*Ranunculus ficaria*) in the spring. Bryophytes and epiphytes are abundant on tree trunks and on the forest floor. The woodland is located in an area dominated by brown podzolics, with some acid brown earths and gleys, while upland areas are mainly composed of peaty podzols, lithosols, and blanket peats. The soils of the Gearagh are mostly loams or silt loams. The main pedogenic processes along the Lee valley are dominated by acidification and podzolisation (Culleton and Gardiner, 1985).

The existence of the Gearagh in the Civil Survey maps of 1641 confirms that it is an ancient woodland (Chapter 2). However, the Ordnance Survey maps of 1842 show that large parts of the northern section of the woodland had been cleared to create additional pasture land. These marginal fields were subsequently abandoned as the population declined in the late 19th and early 20th century. The land was gradually recolonised by woodland, so that the Gearagh today consists of a mosaic of stands of different age and land-use history. Since abandonment, many of these sites have continued to be used for rough grazing, and marginal grasslands are situated along the edges of the woodland. The wider surrounding landscape is dominated by areas of mixed farming, consisting mostly of pasture and meadow, but also some arable land. Today, the upper reaches of the Gearagh remain largely undisturbed due to the inaccessible nature of the terrain. Although coppicing was a feature of woodland management in the past, little felling has been carried out since the 1950s.

3.3.2 Site selection and sampling

Information on land-use history for the Gearagh was researched using a combination of historical maps, documented accounts, aerial photographs, and fieldwork (see Chapter 2 for more information). Historical Ordnance Survey maps were assembled, dating from 1842, 1904, and 1936. Four habitat types were determined based on this information: (i) ancient woodland, which has been continuously wooded since at least the 1650s, (ii) old secondary woodland, arising in the period 1842-1904 (iii) recent secondary woodland, arising in the period 1904-1936, and (iv) grassland, which remained clear of woodland and continues to be grazed by cattle (Fig. 3.1). The latter was selected so as to aid in interpretation of soil development trends. Many of the woodland boundaries coincided with property lines, suggesting that ownership patterns rather than environmental conditions determined differences in land-use history within the Gearagh. The secondary woodland sites were all abandoned before the widespread use of

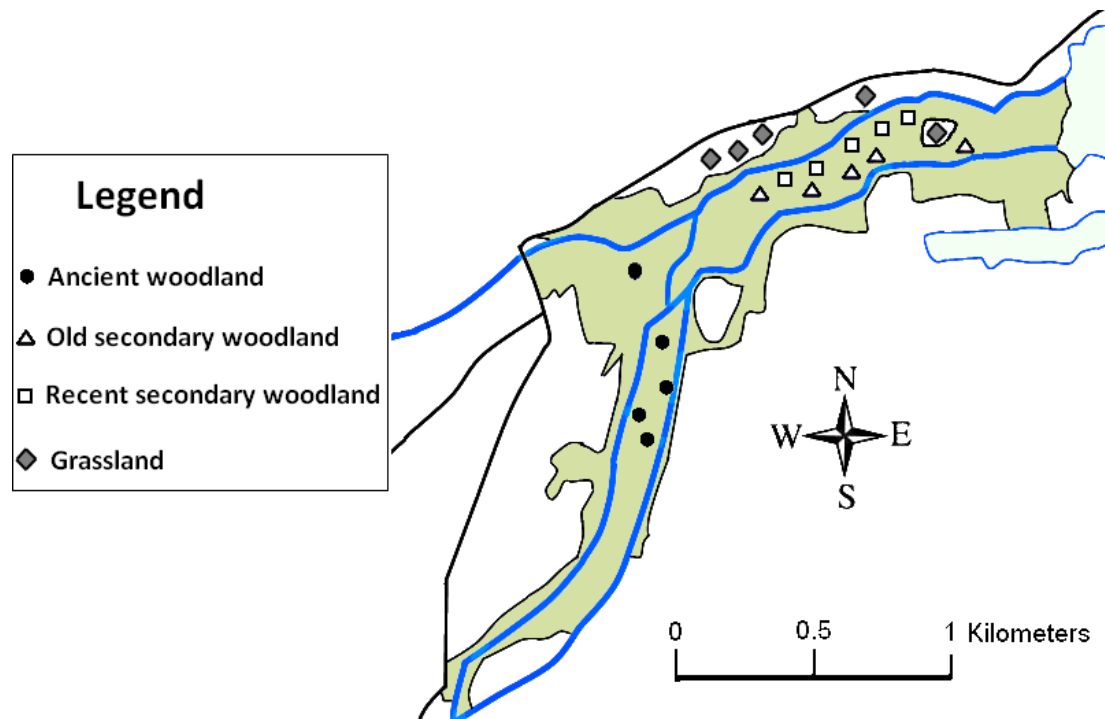


Fig. 3.1 Locations of the habitat types within the Gearagh woodland that were used for investigation, including soil sampling.

inorganic fertilisers, but they most likely received additions of manure and lime, which were common applications in this region in the 19th century. Once the stands of different age had been identified, five replicate sites were located in each of the four habitat types, giving a total of 20 sites in the Gearagh. All of these sites were located within 1 km of each other and so share common characteristics with respect to climate, parent material, slope, altitude, and frequency of flooding from the river, thereby eliminating these as confounding factors in the study (Fig. 3.1). All of these sites are situated beyond the area that is affected by changes in the water levels of the adjacent reservoir (Akumu, 2006).

Sampling took place in 2009 during the winter, a period of low biological activity, in order to reduce temporal variation between sampling times. At each of the replicate study sites, a grid sampling design was established on a 20 × 20 metre area in a homogenous part of the stand. Within this grid, four 1 m² sample points were located randomly (Fig. 3.2). Six subsamples were collected at each sample point using a metallic auger (8 cm diameter) and pooled together to form a composite sample of at least 500 g weight of fresh soil. Samples were taken from four different depths: 0-10 cm, 10-20 cm, 20-40 cm, and 40-80 cm. The depths of the organic (humic) layer and loose litter were measured and then removed at each point prior to the mineral soil sampling. To quantify the amount of leaf litter, all the litter within a 0.25 × 0.25 m frame was collected, oven-dried at 40 °C for 24 hours, and weighed.

Four soil profiles were also studied, one from each of the identified habitat-types of the Gearagh. Soil pits were located in homogenous areas so as to represent, as far as possible, the typical soil profile of each of these habitat-types. Profiles were described using the classification system devised for the Soil Survey of England and Wales (Avery, 1980). Horizons of all profiles were measured and carefully sampled for laboratory analysis. Soil samples from each horizon were collected in metal tubes to determine bulk density.

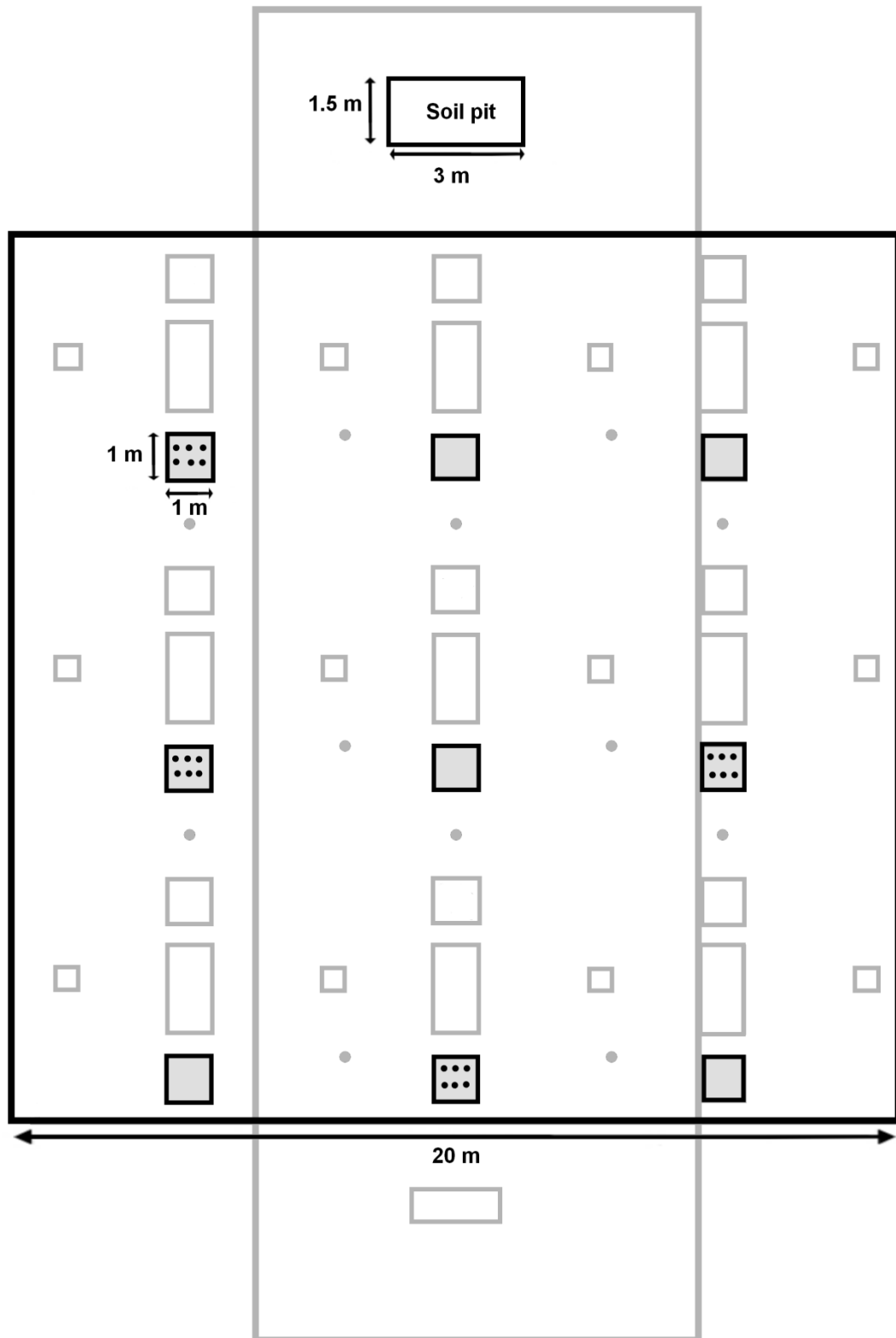


Fig. 3.2 Design of one sampling site, i.e. one of the replicate study sites, with the location of the soil sampling plots (grey plots) and soil pit outlined in black. The sampling designs used in other sections of the thesis are outlined in grey; see Figs. 4.1, 5.2, and 6.1 for further details. Four of the nine 1 m \times 1 m plots were randomly chosen for soil sampling, from which six subsamples were collected (dotted plots).

3.3.3 Laboratory analyses

Soil samples were air-dried in an oven at 40 °C for 24 hours and sieved through a 2-mm mesh sieve prior to analysis. Gravimetric soil moisture was determined for each sample by drying 10 g air-dry subsamples at 105°C for 24 h. Organic matter content was determined by loss-on-ignition (550 °C for 2 hours) (Ball, 1964). Soil pH was measured using a 1:5 air-dry soil : distilled water suspension, and also in 1:5 air-dry soil : CaCl₂ solution (Cools and De Vos, 2006). Extractable phosphorus was extracted with Morgan's solution and measured colorimetrically by the ascorbic acid-molybdenum blue method at 660 nm (Gavlak *et al.*, 1997). Both extractable calcium and magnesium were determined by atomic absorption spectrophotometry after extraction with Morgan's solution (Byrne, 1979). Exchangeable manganese was extracted using a calcium nitrate solution and measured using atomic absorption spectrophotometry (Byrne, 1979). Extractable iron species was determined by the ammonium oxalate method (McKeague and Day, 1966). Ammonium oxalate extracts humic iron complexes (organically bound iron) and also partially extracts poorly crystalline iron oxides, which accounts for most of the iron involved in podzolisation (Farmer *et al.*, 1983). Soil nutrient concentrations were measured on the basis of mass (mg/kg). However, nutrient concentrations per volume may have more biological significance, so nutrient concentrations were converted to a mass per unit area (kg/ha) basis using bulk density values.

Samples representative of the soil horizons from each of the profile were also removed for analysis. The samples were air-dried and all analyses were performed on the fraction passing through a 2 mm mesh. Particle size distribution was determined by sieving techniques (>2 mm fraction) and laser diffraction techniques (<2 mm fraction) after peroxide pre-treatment using a Coulter Malvern Mastersizer 2000. Bulk density was determined by the soil core method (Cools and De Vos, 2006). Samples were dried at 105°C and bulk density calculated on the basis of <2 mm soil. The moist soil colour was recorded using the Munsell colour chart.

3.3.4 Data analyses

Mean values were calculated for each of the soil physical and chemical properties determined at each site. Data were checked for normality and homogeneity and log

transformed where appropriate. Significance of the differences observed between the habitats was assessed using a two-way analysis of variance (ANOVA) with habitat (ancient, old secondary, recent secondary, or grassland) and depth (0-10 cm, 10-20 cm, 20-40 cm, or 40-80 cm) as factors. Pairwise differences among habitat types were evaluated with Tukey's honestly significant difference procedure. PASW Statistics 17 was used for all statistical analyses.

Principal components analyses (PCA) with a correlation matrix were used to summarise variation in the many interrelated soil properties that were measured, using PC-ORD (McCune and Mefford, 2006). Data transformations (log transformation) were applied where appropriate to reduce the effects of outliers and approximate to normality. The axes were interpreted by calculating Pearson coefficients with the original variables to determine their individual degree of influence. The effect of land-use history was tested on site scores for each of the first three principal-component axes with analysis of variance (ANOVA).

3.4 Results

3.4.1 Soil morphological characteristics

The soil profile of the ancient woodland had properties typical of an acid brown earth under deciduous woodland, while the secondary woodland sites as well as the grassland were predominantly brown podzolic soils (Fig. 3.3 and Table 3.1). Brown podzolic soils form under the podzolisation process; however, these soils tend to be less developed and less depleted of materials than typical podzols are. The brown earth of the ancient woodland was a well-drained soil with a rather uniform profile. These soils had not been too extensively leached or degraded; any leaching that had occurred was counteracted by a high degree of biological mixing. Profile depth and thickness of corresponding horizons were variable in each case. The depth to the C horizon was over 70 cm in the ancient and old secondary soil profiles, and only 50 cm in the recent secondary and grassland profiles. All of the soils were predominantly silt-loams and were finely textured. This was reflected in the low bulk density of the soils, particularly for the ancient woodland (Table 3.3).

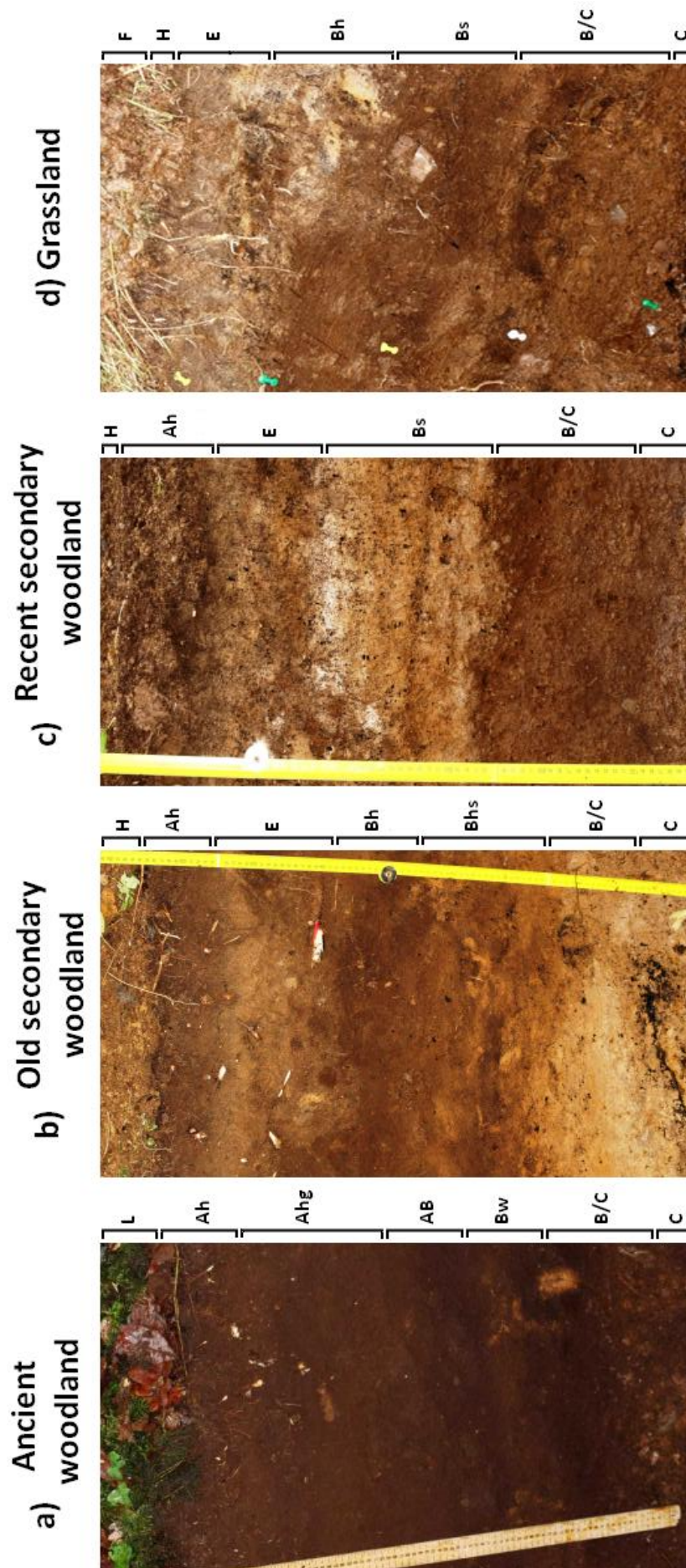


Fig. 3.3 Soil profiles of the a) ancient woodland, b) old secondary woodland, c) recent secondary woodland, and d) grassland habitats in the Gearagh. Horizon notations for each of the profiles are also given. See Table 3.2 for description of soil horizon notation.

Table 3.1 (a) Soil profile description of the ancient woodland. See Table 3.2 for description of soil horizon notation.

Ancient woodland		
Soil type: Acid brown earth		
<hr/>		
Horizons		
5-0 cm	L	Oak, hazel and ash litter. Abrupt, smooth boundary to:
0-7 cm	Ah	Very dark brown (10 YR 2/2) dry, loose silt loam with granular structure. Highly porous. Very few fine but many medium roots; few earthworms observed while digging the profile. Abrupt smooth boundary to:
7-33 cm	Ahg	Black (10 YR 2/1) dry silt loam with granular structure. Very few, fine, faint, sharp mottles. Highly porous. Few fine roots but many medium roots. Few patchy burrows. Clear wavy boundary to:
33-47 cm	AB	Dark brown (7.5 YR 3/2) dry silt loam. Very few, very fine, faint, sharp mottles. Weak, fine subangular blocky structure. Very few, faint clay cutans. Medium porosity. Few fine and few medium roots. Few patchy burrows. Very abrupt wavy boundary to:
47-54 cm	Bw	Very dark brown (10 YR 2/2) dry silt loam. Common coarse, diffuse, prominent mottles. Moderate, fine subangular blocky structure. Common faint clay and iron oxide cutans. Low porosity. Very few fine and very few medium roots. Abrupt smooth boundary to:
54-68 cm	B/C	Black (10 YR 2/1) silt loam. Common, very coarse, prominent, diffuse mottles. Few sub-rounded stones. Moderate, fine subangular blocky structure. Common faint clay, iron and manganese oxide cutans. Low porosity. Very few fine roots only. Very abrupt smooth boundary to:
68 cm +	C	Very dark brown (10 YR 2/2) moist silt loam. Abundant sub-rounded stones. Apedal massive structure. Many distinct iron and manganese oxides with coarse fragments. Very low porosity.

Table 3.1 (b) Soil profile description of the old secondary woodland. See Table 3.2 for description of soil horizon notation.

Old secondary woodland		
Soil type: Brown podzolic soil		
<hr/>		
Horizons		
5–0 cm	H	Decomposing organic material. Many roots. Few patchy burrows. Very abrupt smooth boundary to:
0–7 cm	Ah	Dark brown (10 YR 3/3) silt loam. Common fine, faint, clear mottles. Moderate, fine granular structure. Medium porosity. Very few fine roots and few medium to coarse roots. Few patchy burrows. Clear wavy boundary to:
7–30 cm	E	Dark yellowish brown (10 YR 4/4) silt loam. Common fine to coarse, distinct, clear mottles. Moderate, medium subangular blocky structure. Low porosity. Very few fine to medium roots and few coarse roots. Few patchy burrows. Gradual irregular boundary to:
30–49 cm	Bh	Dark brown (10 YR 3/3) silt loam. Common, fine, prominent, clear mottles. Moderate, medium subangular blocky structure. Low porosity. Very few fine to coarse roots. Few patchy burrows. Clear wavy boundary to:
49–63 cm	Bhs	Brown (10 YR 4/3) silt loam. Common medium, prominent, clear mottles. Moderate, medium subangular blocky structure. Low porosity. Very few fine roots. Few patchy open large burrows. Clear wavy boundary to:
63–77 cm	B/C	Light yellowish brown (10 YR 6/4) silt loam. Common medium, distinct, clear mottles. Common coarse, rounded gravel. Moderate, fine subangular blocky structure. Low porosity. Very few fine roots. Clear broken boundary to:
77 cm +	C	Yellowish brown (10 YR 5/4) silt loam. Common medium, prominent, clear mottles. Common rounded, coarse gravel. Apedal massive structure. Low porosity. Continuous, platy, weakly cemented iron-manganese oxide pan. Very few fibrous roots.

Table 3.1 (c) Soil profile description of the recent secondary woodland. See Table 3.2 for description of soil horizon notation.

Recent secondary woodland		
Soil type: Brown podzolic soil		
<hr/>		
Horizons		
3–0 cm	H	Decomposing organic material. Fibrous with many fine roots. Few patchy burrows. Very abrupt smooth boundary to:
0–10 cm	Ah	Dark brown (10 YR 3/3) silt loam. Few fine, prominent, clear mottles. Very few fine, rounded, weathered gravel. Moderate, very fine subangular blocky structure. Very few prominent manganese oxide cutans. Low porosity. Very few fine and few medium to coarse roots. Few patchy burrows. Abrupt smooth boundary to:
10–19 cm	E	Brown (10 YR 4/3) silt loam. Many medium, prominent, clear mottles. Very few fine, rounded gravel. Moderate, very fine subangular blocky structure. Common manganese oxide cutans. Low porosity. Broken nodular, moderately cemented iron-manganese oxide pan. Very few fine to coarse roots. Few patchy burrows. Clear wavy boundary to:
19–36 cm	Bs	Dark yellowish brown (10 YR 3/6) loam. Many medium, prominent, clear mottles. Few fine, rounded, weathered gravel. Moderate, very fine subangular blocky structure. Common prominent manganese oxide cutans. Low porosity. Very few fine to coarse roots. Few patchy burrows. Clear irregular boundary to:
36–49 cm	B/C	Dark yellowish brown (10 YR 3/4) loam. Common fine, prominent, clear mottles. Few medium, rounded, weathered gravel. Moderate, fine subangular blocky structure. Few distinct manganese oxide cutans. Low porosity. Very few fine to coarse roots. Few patchy burrows. Abrupt wavy boundary to:
49 cm +	C	Dark yellowish brown (10 YR 3/4) sandy loam. Few fine, prominent, clear mottles. Many coarse, rounded, weathered gravel. Apedal massive structure. Common distinct manganese oxide cutans. Very few fine to medium roots.

Table 3.1 (d) Soil profile description of the grassland. See Table 3.2 for description of soil horizon notation.

Grassland		
Soil type: Brown podzolic soil		
Horizons		
6-2 cm	F	Grass and rush litter. High porosity. Extremely abrupt smooth boundary to:
2-0 cm	H	Dark brown (10 YR 3/3) silt loam. Fibrous material with many fine roots. Few fine, rounded weathered gravel. Moderate, medium subangular blocky structure. Slightly plastic texture. Medium porosity. Extremely abrupt smooth boundary to:
0-8 cm	E	Dark greyish brown (10 YR 4/2) silt loam. Many medium, prominent, clear mottles. Few coarse, rounded, weathered gravel. Moderate, fine subangular blocky structure. Low porosity. Few fine and very few medium to coarse roots. Very abrupt wavy boundary to:
8-21 cm	Bh	Brown (10 YR 4/3) silt loam. Common, medium, prominent, very diffuse mottles. Common coarse, rounded, weathered gravel. Moderate, fine subangular blocky structure. Few prominent manganese oxide cutans. Medium porosity. Very few fine to medium roots. Clear irregular boundary to:
21-34 cm	Bs	Dark brown (10 YR 3/3) silt loam. Common fine, distinct, diffuse mottles. Many coarse, rounded, weathered gravel. Moderate, medium subangular blocky structure. Very few prominent manganese oxide cutans. Medium porosity. Very few fine roots. Gradual irregular boundary to:
34-51 cm	B/C	Dark brown (10 YR 3/3) loam. Many coarse, prominent, very diffuse mottles. Many coarse, rounded gravel. Moderate, fine subangular blocky structure. Few prominent manganese oxide cutans. Medium porosity. Very few fine roots. Gradual broken boundary to:
51 cm +	C	Dark yellowish brown (10 YR 3/4) sandy clay loam. Common, coarse prominent very diffuse mottles. Many coarse, rounded, weathered gravel. Apedal massive structure. Many prominent manganese oxide cutans. Medium porosity. Very few fine roots.

Table 3.2 Description of selected soil horizon notation (adapted from Avery, 1980)

Notation	Description
L	Fresh leaf litter
F	Partly decomposed litter
H	Well decomposed litter, often mixed with mineral matter
Ah	Uncultivated A horizon (mineral horizon near the surface)
Ahg	A horizon with evidence of mottling
AB	Transitional subsurface horizon between A and B
E	Subsurface mineral horizon with less organic matter, iron or clay than the immediately underlying horizon
Bw	B horizon (mineral subsurface horizon without rock structure) that shows evidence of alteration under well-aerated conditions
Bh	B horizon containing translocated organic matter, associated with aluminum or iron, in coats on particles and aggregates
Bs	B horizon enriched in aluminum and iron complexed with organic matter
Bhs	B horizon with properties of Bh and Bs
B/C	Horizon in which areas with characteristics of B horizons mix with C horizon material
C	Unconsolidated or weakly consolidated mineral horizon that retains rock structure

However, the bulk density of the grassland soil was appreciably higher than for the other soils. The bulk density was lowest in the surface horizon of all soils and generally increased with depth.

The surface humic layer (H in the soil profile descriptions) of both secondary woodlands and grassland profiles consisted mostly of well decomposed organic matter, but was not significantly developed. This layer was a similar depth in all of the soils studied and was generally quite thin, ranging on average from 1 to 2 cm. Much of the humified organic matter was intimately mixed with the mineral matter of the surface horizon. In contrast, there was a significant difference in the litter layer between sites; the ancient and old secondary both had a greater depth ($F = 5.423$; $d.f. = 3,16$; $P < 0.01$) and density ($F = 27.956$; $d.f. = 3,16$; $P < 0.001$) of litter than the recent secondary and grassland sites.

Table 3.3 Physical properties of the mineral soil profiles from the four habitat types of the Gearagh. The bulk density and coarse fragment contents from the C horizon in the ancient woodland and old secondary woodland could not be measured due to inadequate samples.

Horizon	Particle size distribution			Organic matter (%)	Bulk density (g/cm)	Coarse fragments ⁽ⁱ⁾ (%)
	Clay (%)	Silt (%)	Sand (%)			
Ancient woodland						
Ah	11.8	72.5	15.6	23.7	0.47	0.0
Ahg	18.5	77.3	4.2	12.6	0.68	0.0
AB	22.1	72.2	5.7	10.5	0.57	0.0
Bw	22.9	72.6	4.4	13.3	0.48	0.0
B/C	19.8	69.5	10.7	20.1	0.50	0.0
C	17.4	70.1	12.5	16.2	-	-
Old secondary woodland						
Ah	16.6	74.5	8.9	17.3	0.51	0.0
E	21.4	74.4	4.1	12.2	0.54	0.0
Bh	21.8	64.2	14.0	13.5	0.55	0.7
Bhs	21.0	67.1	11.9	14.7	0.52	0.8
B/C	16.1	53.5	30.4	9.7	0.58	2.8
C	20.5	56.1	23.4	7.8	-	-
Recent secondary woodland						
Ah	12.0	77.4	10.6	21.5	0.57	0.0
E	16.3	68.2	15.5	12.8	0.70	0.0
Bs	16.5	48.9	34.6	9.7	0.72	0.5
B/C	14.4	45.6	40.0	8.6	0.72	0.2
C	8.4	24.2	67.4	2.2	0.78	1.8
Grassland						
E	14.3	74.5	11.1	22.2	0.85	0.4
Bh	17.6	69.3	13.1	13.9	0.76	0.1
Bs	21.1	57.2	21.6	9.3	0.85	2.5
B/C	22.9	67.9	9.3	11.0	0.73	3.0
C	25.7	49.4	25.0	10.7	0.82	2.3

⁽ⁱ⁾ Greater than 2 mm

In the brown podzolic soils, the horizons immediately below the surface mineral horizon were the eluvial E horizons (Fig. 3.3 and Table 3.1). They were a lighter colour than the horizons immediately above and below, and sometimes had a bleached and mottled appearance characteristic of more poorly-drained soils. These were the horizons that had undergone the greatest degree of leaching; the

lighter colour reflected the partial removal of iron and manganese. They ranged in thickness from 8-23 cm, but were weakly expressed in comparison with horizons typical of fully developed podzols. The most distinct E horizon occurred in the recent secondary woodland. The E horizons rested on B horizons in which some of the leached material had accumulated. Stronger colours were apparent in the B horizons, mostly due to the accumulation of iron oxides and organic matter. In contrast, the higher concentration and more uniform distribution of free iron oxides throughout the soil profile of the ancient woodland gave the brown earth its characteristic brown colour throughout the profile. Iron and/or manganese pans had not formed under the ancient woodland canopy, but were often observed on or within the subsurface horizons of both the secondary and grassland soils. These varied in thickness, but most were around 1 cm thick, and had a black lustrous metallic surface. These pans represented the maximum degree of iron and/or manganese accumulation in the profile. The only difference among C horizons was in their stone content with the grassland having a slightly greater quantity of coarse fragments than the recent secondary.

Particle size analyses were similar for all soils with respect to the content of sand, silt, and clay (Table 3.3). Clay content generally increased with depth, although this was most pronounced in the grassland soil, which reached a maximum clay content of over 25 % in the deepest horizon. The recent secondary soil had the lowest clay content in all but the surface horizon. All of the soils had a high silt content (mostly over 40 %), but ancient woodland had a particularly high silt content throughout the soil profile (approximately 70 %). Stone content was greatest in the grassland soil, whereas no stones were found in the upper surfaces of the ancient soil. The C horizons all contained gravels and larger stones.

3.4.2 Soil chemical properties

The principal component analyses of the soil properties clearly separated out the four habitat types (Fig. 3.4). The first principal component axis, which explained 28 % of the variation, correlated strongly with litter quantity and depth, as well as soil moisture content at all four depths (Table 3.4). Many other soil properties aligned

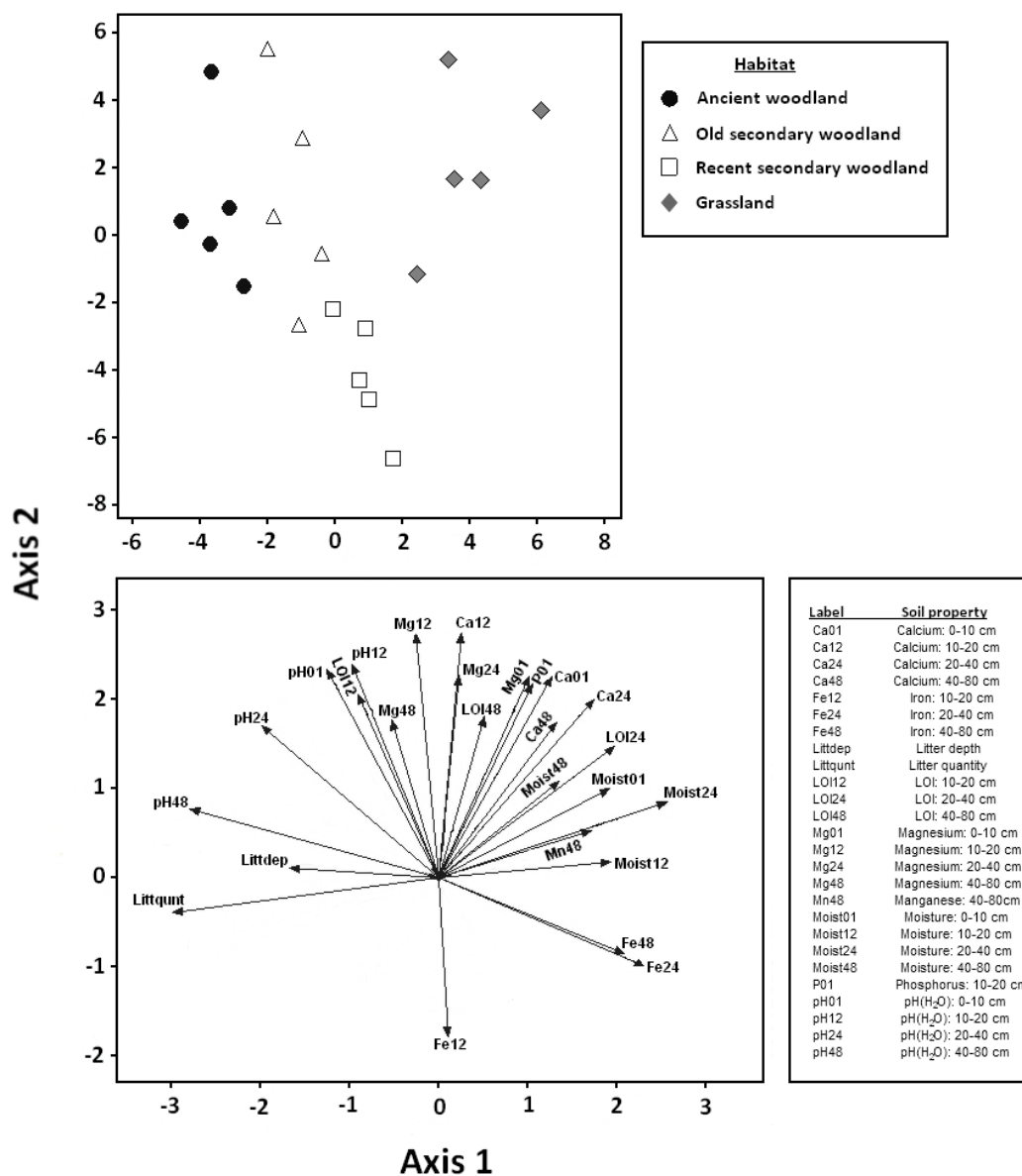


Fig. 3.4 Principal components analysis of soil properties. The upper panel shows axis 1 and axis 2 plots for the soil property data collected from the four habitat types of the Gearagh. The lower panel is a joint plot showing the Pearson correlations between axes 1 and 2 and the most influential soil properties. Axis 1 = 28%, Axis 2 = 22 %, cumulative = 50 %.

Table 3.4 Pearson's Product Moment correlation coefficient matrix of PCA axis 1, 2 and 3 scores of soil properties in the Gearagh. Significance levels of Pearson's Product Moment correlation coefficient shown where applicable: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Soil property	Axis 1	Axis 2	Axis 3
Humus layer depth	0.001	0.159	0.159
Litter quantity	-0.887 ***	-0.161	-0.161
Litter depth	-0.541 *	0.020	0.020
pH(H ₂ O) at 0-10 cm	-0.383	0.791 ***	0.791
pH(H ₂ O) at 10-20 cm	-0.307	0.809 ***	0.809
pH(H ₂ O) at 20-40 cm	-0.614 **	0.566 **	0.566
pH(H ₂ O) at 40-80 cm	-0.840 ***	0.239	0.239
pH(CaCl ₂) at 0-10 cm	-0.535 *	0.722 ***	0.722
pH(CaCl ₂) at 10-20 cm	-0.403	0.678 ***	0.678
pH(CaCl ₂) at 20-40 cm	-0.761 ***	0.082	0.082
pH(CaCl ₂) at 40-80 cm	-0.646 **	-0.254	-0.254
LOI at 0-10 cm	-0.436	0.265	0.265 ***
LOI at 10-20 cm	-0.238	0.698 ***	0.698 *
LOI at 20-40 cm	0.569 **	0.520 *	0.520
LOI at 40-80 cm	0.114	0.622 **	0.622
Moisture at 0-10 cm	0.629 **	0.365	0.365 **
Moisture at 10-20 cm	0.652 **	0.086	0.086 ***
Moisture at 20-40 cm	0.803 ***	0.317	0.317 *
Moisture at 40-80 cm	0.458 *	0.388	0.388 **
Phosphorus at 0-10 cm	0.332	0.759 ***	0.759
Phosphorus at 10-20 cm	0.165	0.163	0.163
Phosphorus at 20-40 cm	0.253	-0.431	-0.431
Phosphorus at 40-80 cm	0.171	-0.332	-0.332
Calcium at 0-10 cm	0.321	0.778 ***	0.778
Calcium at 10-20 cm	0.049	0.941 ***	0.941
Calcium at 20-40 cm	0.450 *	0.694 ***	0.694
Calcium at 40-80 cm	0.314	0.605 **	0.605
Magnesium at 0-10 cm	0.255	0.781 ***	0.781
Magnesium at 10-20 cm	-0.102	0.938 ***	0.938
Magnesium at 20-40 cm	-0.006	0.776 ***	0.776
Magnesium at 40-80 cm	-0.230	0.598 **	0.598 *
Manganese at 0-10 cm	0.165	0.367	0.367 *
Manganese at 10-20 cm	-0.370	0.186	0.186
Manganese at 20-40 cm	0.303	0.070	0.070
Manganese at 40-80 cm	0.464 *	0.191	0.191
Iron at 0-10 cm	-0.146	-0.411	-0.411 **
Iron at 10-20 cm	0.107	-0.604 **	-0.604 *
Iron at 20-40 cm	0.752 ***	-0.313	-0.313 **
Iron at 40-80 cm	0.676 ***	-0.267	-0.267

with this axis as well, particularly in the subsoil. These included pH at 20-40 cm and, 40-80 cm depth, calcium at 20-40 cm, manganese at 40-80 cm, and iron at 20-40 cm and 40-80 cm. This axis separated the grassland soils from the three woodland soils ($F = 61.246$; $d.f. = 3,16$; $P < 0.001$). The second axis, which explained another 22 % of the variation, correlated most strongly with calcium and magnesium at all depths surface pH, subsoil organic matter content (LOI), and iron at 10-20 cm (Table 3.4). This second axis distinguished the woodland soils from each other, particularly the recent secondary soils from the old secondary and ancient woodland soils ($F = 6.537$; $d.f. = 3,16$; $P < 0.01$). Axis three corresponded to variation in surface organic matter content, moisture at all depths, iron to 40 cm depth, surface manganese, and magnesium at 40-80 cm depth (Table 3.4). This represented 14 % of the variation, and further separated out the ancient woodland from the old secondary woodland soils ($F = 4.116$; $d.f. = 3,16$; $P > 0.05$).

Table 3.5 shows the results for the two-way ANOVA on the soil properties for the Gearagh. Organic matter content differed significantly between the four habitats. The greatest content by far occurred in the surface layer of the ancient woodland (Fig. 3.5); the old secondary, recent secondary, and grassland soils had on average 24 %, 25 %, and 24 % organic matter content at 0-10 cm, respectively, whereas the ancient woodland contained 28 % in the top 10 cm of soil. However, in the 20-40 cm layer, the ancient woodland had the lowest LOI value of all four habitats. Yet all four habitats showed the same trend of decreasing organic matter content with depth. Generally, organic matter decreased by 51- 59 % from the surface layers to 40-80 cm depth. Measurements of the OL horizon revealed that the ancient and old secondary woodlands had built up a deeper litter layer ($F = 5.423$; $d.f. = 3,16$; $P < 0.001$) and a greater quantity of litter ($F = 27.956$; $d.f. = 3,16$; $P < 0.001$) than the other study sites. Soil moisture content showed no significant variation with depth, but there was a difference between the habitats (Table 3.4). The ancient woodland and old secondary had the lowest soil moisture contents (Fig. 3.5). Moisture was higher in the recent secondary soils, and even more so in the grassland sites.

Table 3.5 Results from two-way ANOVA on (a) pH(H₂O), (b) pH(CaCl₂), (c) loss-on-ignition, (d) moisture, (e) phosphorus, (f) calcium, (g) magnesium, (h) manganese, and (i) iron with Habitat (Ancient, Old secondary, Recent secondary, or Grassland) and Depth (0-10 cm, 10-20 cm, 20-40 cm, or 40-80 cm) as treatments. Data that were ln-transformed prior to analysis are indicated with *.

	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
(a) pH(H ₂ O)				
Corrected model	15	0.23	12.42	< 0.001
Habitat	3	0.25	13.33	< 0.001
Depth	3	0.78	41.59	< 0.001
Habitat × Depth	9	0.05	2.39	< 0.05
Error	64	0.02		
(b) pH(CaCl ₂)				
Corrected model	15	0.13	9.70	< 0.001
Habitat	3	0.18	13.94	< 0.001
Depth	3	0.30	22.96	< 0.001
Habitat × Depth	9	0.05	3.86	< 0.001
Error	64	0.01		
(c) Loss-on-ignition *				
Corrected model	15	0.56	50.06	< 0.001
Habitat	3	0.04	3.48	< 0.05
Depth	3	2.70	241.71	< 0.001
Habitat × Depth	9	0.02	1.70	0.106
Error	64	0.01		
(d) Moisture *				
Corrected model	15	0.20	7.56	< 0.001
Habitat	3	0.86	32.37	< 0.001
Depth	3	0.06	2.26	0.090
Habitat × Depth	9	0.03	1.06	> 0.05
Error	64	0.03		
(e) Phosphorus *				
Corrected model	15	1.02	61.57	< 0.001
Habitat	3	0.04	2.62	0.058
Depth	3	4.89	293.97	< 0.001
Habitat × Depth	9	0.06	3.75	< 0.001
Error	64	0.02		
(f) Calcium *				
Corrected model	15	1.84	11.30	< 0.001
Habitat	3	4.67	28.70	< 0.001
Depth	3	2.56	15.73	< 0.001
Habitat × Depth	9	0.65	4.02	< 0.001
Error	64	0.16		
(g) Magnesium *				
Corrected model	15	1.14	8.37	< 0.001
Habitat	3	2.18	16.02	< 0.001
Depth	3	2.77	20.37	< 0.001
Habitat × Depth	9	0.25	1.82	0.082
Error	64	0.14		
(h) Manganese *				
Corrected model	15	0.10	1.50	> 0.05
Habitat	3	0.11	1.68	> 0.05
Depth	3	0.16	2.43	0.073
Habitat × Depth	9	0.07	1.14	> 0.05
Error	64	0.07		
(i) Iron *				
Corrected model	15	2.25	69.30	< 0.001
Habitat	3	0.77	23.73	< 0.001
Depth	3	10.04	309.48	< 0.001
Habitat × Depth	9	0.14	4.43	< 0.001
Error	64	0.03		

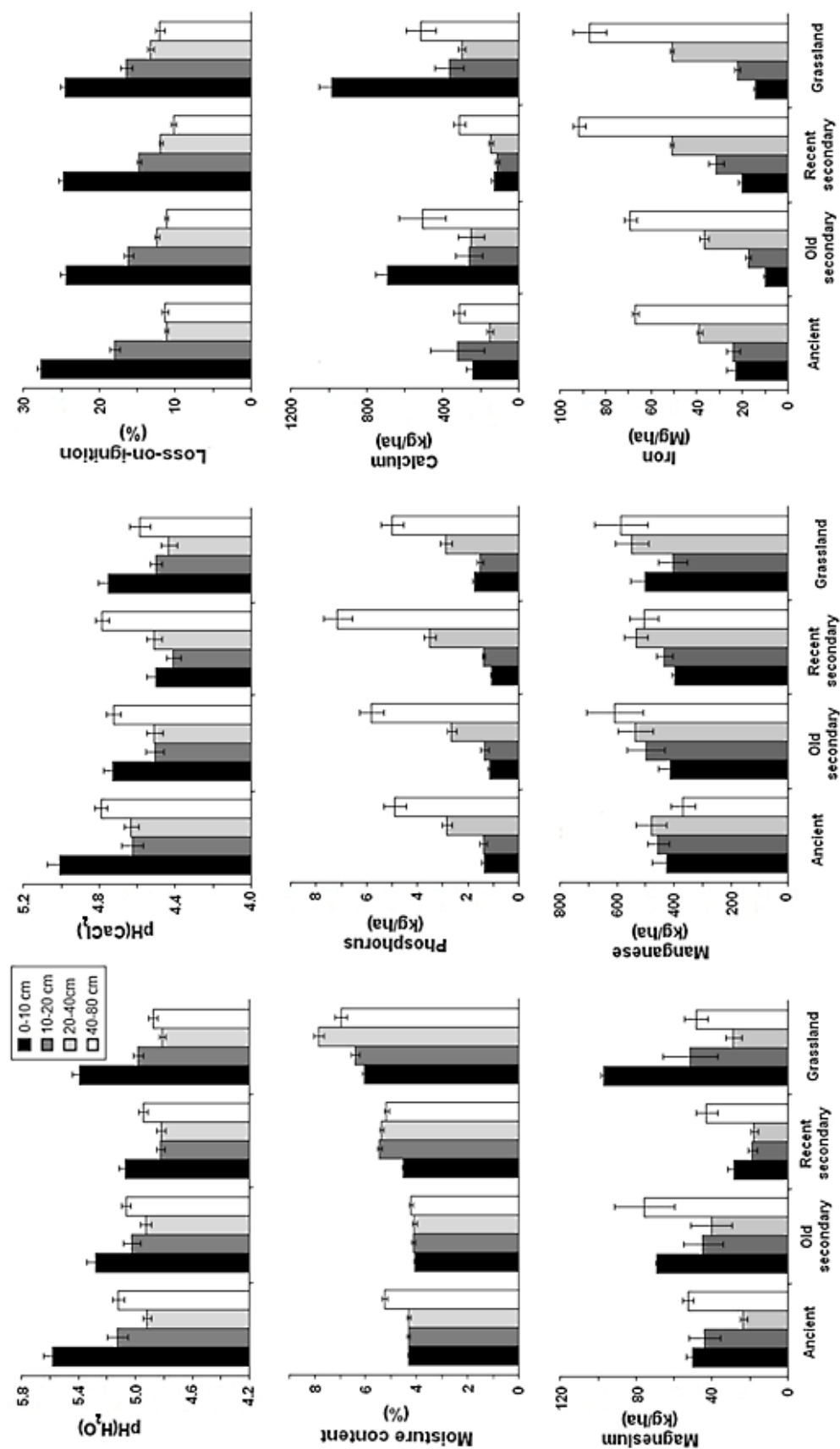


Fig 3.5 Variation in soil properties at different depths (0-10 cm, 10-20 cm, 20-40 cm and 40-80 cm below the soil surface) for the four different habitat-types of the Gearagh: Ancient woodland; Old secondary woodland; Recent secondary woodland; and Grassland. Mean values with standard error are shown

All soils in the Gearagh can be classified as acidic. However, the ancient woodland contained the least acidic soil (Table 3.5 and Fig. 3.5), most noticeably at the surface layer (0-10 cm) for both pH(H₂O) ($F = 8.008$; $d.f. = 3,16$; $P < 0.01$) and pH(CaCl₂) ($F = 9.938$; $d.f. = 3,16$; $P < 0.001$). Values of pH were similar for all soils at 10-20 cm depth, but differed again below that, with the ancient soil again having a higher pH(H₂O) than sites under secondary woodland and grassland ($F = 12.556$; $d.f. = 3,16$; $P < 0.001$). Soil pH showed a similar pattern through the soil profile at all habitat types; pH was greatest at the surface and decreased with depth, before showing a slight increase again at the deepest layer (40-80 cm). All soils fell below pH(H₂O) 5.6, which is the level at which manganese becomes available to plants, and all but the surface levels of the ancient, old secondary, and grassland soils were at pH levels (soil pH 5.2) where aluminium begins to become solubilised and available to plants.

All woodland soils were somewhat similar in available phosphorus content, although there was a significant interaction between habitat and depth (Table 3.5). Available phosphorus content remained at similar concentrations at all depths in the ancient woodland soils (1.2-1.4 kg/ha at 0- 10 cm of soil), increased with depth in both the secondary woodlands (33-42 %), but decreased from the surface to 40-80 cm depth in the grassland soils by 25 %. Surface calcium and magnesium content was greater in the old secondary and grassland soils than in the ancient and recent secondary soils (Table 3.5 and Fig. 3.5). However, there was little difference in subsoil magnesium contents between the habitat types ($F = 2.616$; $d.f. = 3,16$; $P > 0.05$). No mineral horizon had a Ca:Mg ratio less than 4; the 0-10 cm layer in the recent secondary soil had the lowest Ca:Mg ratio, while the old secondary and grassland had high Ca:Mg ratios. Calcium, magnesium, and manganese were all greatest in concentration at the soil surface across all sites, particularly in the old secondary and grassland sites. However, manganese contents were similarly high between all habitat-types at each depth ($F = 2.267$; $d.f. = 3,16$; $P > 0.05$).

Ammonium oxalate is considered to extract both organic Fe and poorly crystalline Fe and thus most of the iron involved in podzolisation. Distribution patterns for extractable iron show that maximum values occurred in the subsoil horizons for the

old secondary, recent secondary, and grassland sites (Fig. 3.5). This corresponds to the darker colour recorded for the B horizons in the soil profiles, in comparison with the lighter coloured E horizons. The maximum iron value in the ancient woodland, however, occurred in the uppermost horizons and decreased with depth. Ammonium oxalate also extracts humic-iron complexes; the high values recorded in subsoil layers of the secondary and grassland soils indicate that humic-iron complexes have moved down the profile.

3.5 Discussion

This study has shown that soil properties clearly differed between the grassland, ancient woodland and secondary woodlands. Many of these changes in soil characteristics can be related to land-use history, in particular, the removal of woodland cover for the creation of agricultural land. The acid brown earths of the ancient woodland had a remarkably undisturbed profile, indicating that this part of the woodland has been subject to minimal human interference. However, past and present clearance of woodland cover in other parts of the Gearagh has caused the original acid brown earths to develop features of brown podzolic soils. The high precipitation levels of this part of Europe mean that the hydrological balance of the system was significantly altered once the canopy cover was removed. This caused a reduction in both the transpiration demand of the vegetation and in the interception rates, the latter accounting for as much as 15 % of total precipitation in Irish oak woods (Little, 2004). This led to an increase in soil water content, leaching rates, and the gradual loss of nutrients in the open grasslands. This development of brown podzolics in the Gearagh is consistent with the trend towards podzolisation after woodland clearance for agriculture in Ireland (Lynch, 1981; Little *et al.*, 1990) and England (Dimbleby and Gill, 1955). Despite subsequent reforestation, the soils of the secondary woodland sites have not regained all of the characteristics of the soils in the ancient woodland. Nonetheless, the old secondary soils are the most similar to the ancient woodland, probably a result of a combination of a shorter duration of agricultural use and a longer period under secondary woodland (Matlack, 2009).

The relatively uniform distribution of iron throughout the ancient woodland profile indicates that this soil was not greatly influenced by the podzolisation process. Any leaching that did occur was probably effectively counterbalanced by biological mixing. Yet, the natural acidic nature of the soil meant that when significant leaching did occur, such as after clear-felling of trees, then the soil began to podzolize relatively easily (Cunningham *et al.*, 1999). This led to increased surface acidity, as recorded in the present-day soils at the secondary woodland and grassland sites. Moreover, the high amounts of extractable iron content in these soils confirmed that they were in the early stages of the podzolisation process; humic iron complexes had moved down the profile and redeposited in the lower horizons. The clear visual difference between the profile horizons further indicated that intensive leaching had occurred in these sites (Little *et al.*, 1997). The podzolisation process also resulted in the formation of iron and manganese pans in parts of the secondary woodland and grassland sites. Such iron pans are generally only found in woodlands that are known to have been cleared in the past (Cruickshank and Cruickshank, 1981; Little *et al.*, 1997). Indeed, the formation of iron pans can even be triggered by cattle grazing on pasture land without the application of amendments (Cunningham *et al.*, 2001), as occurs in the present-day grassland sites. Under present climatic conditions, it is likely that podzolisation will continue to be the dominant soil process in this region. However, the presence of a broadleaved woodland canopy can delay the podzolisation process in comparison with a non-wooded site (Little *et al.*, 1997). Podzols can even potentially return to a brown earth soil under a continuous cover of deciduous vegetation, but this process may take up to 1,000 years to complete (Willis *et al.*, 1997).

In this study, past woodland clearance is associated with an overall decrease of surface pH. These results contrast with other studies which have found woodlands to become more acidic with age (Verheyen *et al.*, 1999; Matlack, 2009) or else to show little difference in acidity (Dzwonko, 2001; Flinn and Marks, 2007; Sciamia *et al.*, 2009). Generally, in drier parts of Europe and North America, which are less prone to leaching, long-term use of agriculture raises pH independent of soil type, resulting in less acidic soils in recent woodlands than in old-growth woodlands. For

instance, Wilson (1997) found that the pH of recent woodland soil on previously cultivated land was significantly higher than that of an adjacent ancient woodland. However, in the Gearagh, although the ancient woodland soil can still be classified as acidic, woodland clearance for agriculture led to further degradation and acidification of the soil. The subsequent growth of woodland on such acidic soils probably improved acidity to some extent (Nielsen *et al.*, 1987); previous research has shown that the colonisation of highly acidic heaths by broadleaved species such as *Betula* can retard podzolisation and reduce overall soil acidity (Miles, 1981). Nonetheless, in this study, 70-150 years of woodland cover have been insufficient to allow the development of the lower acidity of the undisturbed, ancient woodland soil. The lower pH in the secondary and grassland sites is particularly problematic as manganese is more likely to occur in amounts that are toxic to plants. The natural levels of manganese are quite high in this area (Conry and Ryan, 1965) and the toxicity can be further increased by waterlogged conditions and high organic matter contents. However, in the well-drained soils of the ancient woodland, oxidised conditions generally prevail, and manganese is more likely to occur in amounts that are less toxic to plants.

The high calcium values at the surface of the old secondary and the grassland soils presumably result from previous management of the land. Lime was frequently applied to agricultural land during the 19th century (Walsh *et al.*, 1957); indeed, a number of lime kilns were in use in Anahala just to the south of the Gearagh at that time. Lime was applied in order to raise availability of macronutrients. It also would have helped to reduce the availability of most micronutrients in the soil. Without such amendments, continuous grazing of pasture would eventually lead to a reduction in pH and nutrients due to the export of plant material (Verheyen *et al.*, 1999). The high calcium concentration in the grassland sites are probably as a result of heavier application of lime late in the abandonment period. Indeed, elevated levels of basic cations have been observed as long as 75-200 years after abandonment (Wilson *et al.*, 1997). However, the calcium content of the grassland soils is much less than that of pastures which continue to be limed today (Little and Bolger, 1995); it is unlikely that lime is still applied here. Despite these past

applications of lime, the secondary woodland and grassland sites still display podzolic characteristics. This confirms other studies which found evidence of podzolisation within 50-150 years after agricultural abandonment (Little and Collins, 1995). The comparatively low concentrations of calcium and magnesium in the recent secondary soils can be attributed to a combination of leaching and the sequestration of nutrients in woody biomass (Bellemare *et al.*, 2002). Both calcium and magnesium are stored in the woody tissue of broadleaf trees. Therefore, the large standing biomass, particularly in the ancient woodland, may act to withdraw these nutrients from the decomposition system.

Phosphorus additions from manuring are known to persist for hundreds (Koerner *et al.*, 1997; Compton and Boone, 2000; Dupouey *et al.*, 2002) or even thousands (Dupouey *et al.*, 2002; Dambrine *et al.*, 2007) of years in the soil. Consequently, woodland soils on former arable land or pasture often contain significantly more phosphorus than those of old-growth woodlands. However, secondary woodland soils in this study were not greatly enriched with phosphorus in comparison with the ancient woodland soil, as reported by other authors (Sciama *et al.*, 2009). This suggests that any manure additions in the past must have been quite small (Flinn and Marks, 2007), or at least enough to compensate for the net export of phosphorus by grazing cattle. Other studies have reported higher phosphorus contents under woodland (Wilson *et al.*, 1997). Under these conditions, phosphorus is usually tightly conserved within the vegetation-litter-soil cycle and little is lost from the system. Although not significant, the ancient woodland here did have the greatest phosphorus content of all of the woodland soils. However, the greatest amount of available phosphorus at the surface occurred in grassland sites. Phosphorus can be remarkably immobile in soil and so these high quantities may be a legacy of past nutrient amendments.

Past land-use also appears to have affected the organic matter content of the soils, which was greatest in the ancient woodland sites, particularly in the surface layers. This is indicative of the large quantities of organic matter that are cycled through the ancient woodland system and are returned to the soil mostly as leaf litter. The removal of trees and other vegetation in the past would have disrupted this close-

cycling system, leading to a decrease in soil organic matter that is still detectable in the secondary woodlands today. Nonetheless, the organic matter content in the old secondary and recent secondary soils was still quite high; this is consistent with other studies which have found organic matter to be high in woodlands that were preceded by pastures (Koerner *et al.*, 1997; Verheyen *et al.*, 1999; Compton and Boone, 2000) as opposed to tillage (Wilson *et al.*, 1997; Flinn and Marks, 2007). In Ireland, grassland soils have a much higher organic matter content than do tillage soils (Collins *et al.*, 2004). The dense root system of the grasses is an important contributor of organic matter to the subsoil as they decompose. These high concentrations were still detected in the secondary woodlands up to 80 years after abandonment. Finally, the organic matter content in the subsoil gives further indication of leaching. The slightly greater content in the 20-40 cm layer of the secondary and grassland soils in comparison with the ancient woodland suggests that there is a greater downward movement of water in these soils. Over time, this action would carry and deposit particles of organic matter at greater depths in the soil.

The continuous presence of woodland cover, with active biological and nutrient cycling, has preserved the acid brown earths in the ancient woodland and counterbalanced the natural tendency towards leaching (Collins *et al.*, 2004). Indeed, the fertility of the ancient woodland does not appear to be unusually low. This indicates that coppicing and removal of underwood has never been carried out extensively in the woodland (Rackham, 1980; Peterken, 1993). Although relatively undisturbed, it should be remembered that this woodland is not the equivalent of primary forest. Even the most remote woodlands in Europe have been subject to some form of anthropogenic disturbance during their history (Peterken, 1996). Nonetheless, it appears that woodland clearance for agriculture can alter soil properties to the extent that these changes still persist in stands of secondary woodland over 150 years after abandonment.

3.6 Conclusions

The soil characteristics of the ancient woodland indicate that it is unlikely that this stand has ever been permanently cleared. The lack of disturbance is reflected in the soil profile; this proved to be a useful method to elucidate soil development and consequently past land-use history of the woodland. The secondary woodland stands still reflect former agricultural history in their soil properties. It appears that soil alteration was facilitated by canopy removal as well as subsequent agricultural development. The effects of canopy removal on acid soil properties in high rainfall areas (700-3000 mm per annum) and the persistence of these differences, even a century later, should be taken into account in woodland management.

3.7 References

- Akumu, C.E. (2006) *Conservation Assessment of Plant Communities in a Flooded Riverine Forest, the Gearagh*. M.Sc. thesis, University College Cork, Ireland.
- Avery, B.W. (1980) *Soil classification for England and Wales (higher categories)*. Soil Survey Technical Monograph No. 14, Harpenden, UK, pp. 67.
- Ball, D.F. (1964) Loss-on-ignition as an estimate of organic matter and organic carbon in non-calcareous soils. *Journal of Soil Science*, **15**, 84-92.
- Bellemare, J., Motzkin, G. & Foster, D. (2002) Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. *Journal of Biogeography*, **29**, 1401-1420.
- Byrne, E. (1979) *Chemical Analysis of Agricultural Materials*. An Foras Taluntais, Johnstown Castle Research Centre, Wexford, Ireland, pp. 194.
- Collins, J.F., Larney, F.J. & Morgan, M.A. (2004) Climate and soil management. *Climate, Weather and Irish Agriculture* (eds T. Keane & J.F. Collins), pp. 119-160. AGMET, Dublin, Ireland.
- Compton, J.E. & Boone, R.D. (2000) Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. *Ecology*, **81**, 2314-2330.
- Compton, J.E., Boone, R.D., Motzkin, G. & Foster, D.R. (1998) Soil carbon and nitrogen in a pine-oak sand plain in central Massachusetts: Role of vegetation and land-use history. *Oecologia*, **116**, 536-542.

- Conry, M.J. & Ryan, P. (1965) Some observations on manganese in west Cork soils. *Irish Journal of Agricultural Research*, **4**, 61-66.
- Cools, N. & De Vos, B. (2006) Sampling and analysis of soil. Manual IIIa. In: *Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests* (eds R. Fischer & M. Lorenz), pp. 89-115. ICP Forests, UNECE, Hamburg, Germany.
- Cruickshank, J.G. & Cruickshank, M.M. (1981) The development of humus-iron podsol profiles, linked by radiocarbon dating and pollen analysis to vegetation history. *Oikos*, **36**, 238-253.
- Culleton, E.B. & Gardiner, M.J. (1985) Soil formation. *The Quaternary History of Ireland* (eds K.J. Edwards & W.P. Warren), pp. 141-182. Academic Press, London, UK.
- Cunningham, D.A., Collins, J.F. & Cummins, T. (2001) Anthropogenically-triggered iron pan formation in some Irish soils over various time spans. *Catena*, **43**, 167-176.
- Cunningham, D.A., Farrell, E.P. & Collins, J.F. (1999) Soil responses to land-use change - a study in south-west Ireland. *Forest Ecology and Management*, **119**, 63-76.
- Dambrine, E., Dupouey, J.L., Laut, L., Humbert, L., Thinon, M., Beaufils, T. & Richard, H. (2007) Present forest biodiversity patterns in France related to former Roman agriculture. *Ecology*, **88**, 1430-1439.
- Dimbleby, G.W. & Gill, J.M. (1955) The occurrence of podzols under deciduous woodland in the New Forest. *Forestry*, **28**, 95-106.
- Dupouey, J.L., Dambrine, E., Laffite, J.D. & Moares, C. (2002) Irreversible impact of past land use on forest soils and biodiversity. *Ecology*, **83**, 2978-2984.
- Dzwonko, Z. (2001) Assessment of light and soil conditions in ancient and recent woodlands by Ellenberg indicator values. *Journal of Applied Ecology*, **38**, 942-951.
- Farmer, V.C., Russell, J.D. & Smith, B.F.L. (1983) Extraction of inorganic forms of translocated Al, Fe and Si from a podzol Bs horizon. *Journal of Soil Science*, **34**, 571-576.

- Flinn, K.M. & Marks, P.L. (2007) Agricultural legacies in forest environments: tree communities, soil properties, and light availability. *Ecological Applications*, **17**, 452-463.
- Forest Service (2008) *Irish Forests: A Brief History*. Forest Service, Department of Agriculture, Fisheries and Food, Government of Ireland, Dublin, Ireland, pp. 8.
- Froment, A. & Tanghe, M. (1967) Répercussion des formes anciennes d'agriculture sur les sols et la composition floristique. *Bulletin de la Société Royale Botanique de Belgique*, **100**, 335-351.
- Gavlak, R.G., Horneck, D.A. & Miller, R.O. (1997) *Western States Laboratory Proficiency Testing Program: Soil and Plant Analytical Methods, Version 3.00*. Western Regional Extension Publication, Utah, USA, pp. 93.
- Giller, P.S. (1996) The diversity of soil communities, the 'poor man's tropical rainforest'. *Biodiversity and Conservation*, **5**, 135-168.
- Goovaerts, P., Frankart, R. & Gérard, G. (1990) Effet de la succession de différentes affectations sur les propriétés chimiques de pedons en Fagne de Chimay (Belgique). *Pédologie*, **40**, 179-194.
- Graae, B.J., Sunde, P.B. & Fritzboøger, B. (2003) Vegetation and soil differences in ancient opposed to new forests. *Forest Ecology and Management*, **177**, 179-190.
- Hermý, M. & Verheyen, K. (2007) Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. *Ecological Research*, **22**, 361-371.
- Honnay, O., Hermý, M. & Coppin, P. (1999) Impact of habitat quality on forest plant species colonization. *Forest Ecology and Management*, **115**, 157-170.
- Koerner, W., Dupouey, J.L., Dambrine, E. & Benoit, M. (1997) Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. *Journal of Ecology*, **85**, 351-358.
- Kopecký, M. & Vojta, J. (2009) Land use legacies in post-agricultural forests in the Doupovské Mountains, Czech Republic. *Applied Vegetation Science*, **12**, 251-260.

- Little, D. (2004) A new dawn for native woodlands: Brackloon wood, Co. Mayo - pilot site for the native woodland scheme. In: *Ireland's Native Woodlands* (eds C. Doyle & D. Little), pp. 176-183. Woodlands of Ireland, Galway, Ireland.
- Little, D. & Bolger, T. (1995) The effects of contrasting land uses on soil properties and animal communities in brown earth soils. *Biology & Environment: Proceedings of the Royal Irish Academy*, 183–193.
- Little, D., Farrell, E. & Collins, J. (1997) Land-use legacies and soil development in semi-natural ecosystems in the marginal uplands of Ireland. *Catena*, **30**, 83-98.
- Little, D.J. & Collins, J.F. (1995) Anthropogenic influences on soil development at a site near Pontoon, Co. Mayo. *Irish Journal of Agricultural and Food Research*, **34**, 151-163.
- Little, D.J., Farrell, E.P., Collins, J.F., Kreutzer, K. & Schierl, R. (1990) Podzols and associated soils in semi-natural oak woodlands: a preliminary report. *Irish Forestry*, **47**, 79-89.
- Lynch, A. (1981) *Man and Environment in South-West Ireland, 4000 B.C. - A.D. 800: A Study of Man's Impact on the Development of Soil and Vegetation*. BAR, Oxford, UK, pp. 175.
- Mather, A.S., Fairbairn, J. & Needle, C.L. (1999) The course and drivers of the forest transition: the case of France. *Journal of Rural Studies*, **15**, 65-90.
- Matlack, G.R. (2009) Long-term changes in soils of second-growth forest following abandonment from agriculture. *Journal of Biogeography*, **36**, 2066-2075.
- McCune, B. & Mefford, M.J. (2006) *PC-ORD: Multivariate Analysis of Ecological Data, Version 5*. MjM Software Design, Gleneden Beach, USA.
- McKeague, J. & Day, J. (1966) Dithionite-and oxalate-extractable Fe and Al as aids in differentiating different classes of soil. *Canadian Journal of Soil Science*, **46**, 13-22.
- Miles, J. (1981) *The Effect of Birch on Moorlands*. Institute of Terrestrial Ecology, Cambridge, UK, pp. 18.

- Mueller, C. & Koegel-Knabner, I. (2009) Soil organic carbon stocks, distribution, and composition affected by historic land use changes on adjacent sites. *Biology and Fertility of Soils*, **45**, 347-359.
- Nielsen, K.E., Dalsgaard, K. & Nørnberg, P. (1987) Effects on soils of an oak invasion of a *Calluna* heath, Denmark, I: morphology and chemistry. *Geoderma*, **41**, 79-95.
- Perrin, P., Martin, M., Barron, S., O'Neill, F., McNutt, K. & Delaney, A. (2008) *National survey of native woodlands 2003-2008*. Unpublished report to the National Parks & Wildlife Service, Dublin, Ireland, pp. 187.
- Perrin, P.M. & Daly, O.H. (2010) *A Provisional Inventory of Ancient and Long-Established Woodland in Ireland*. Irish Wildlife Manuals, No. 46. National Parks and Wildlife Service, Department of the Environment, Heritage and Local Government, Dublin, Ireland, pp. 71.
- Peterken, G.F. (1993) *Woodland Conservation and Management*. Chapman & Hall, London, UK, pp. 374.
- Peterken, G.F. (1996) *Natural Woodland: Ecology and Conservation in Northern Temperate Regions*. Cambridge University Press, Cambridge, UK, pp. 522.
- Plue, J., Hermy, M., Verheyen, K., Thuillier, P., Saguez, R. & Decocq, G. (2008) Persistent changes in forest vegetation and seed bank 1,600 years after human occupation. *Landscape Ecology*, **23**, 673-688.
- Rackham, O. (1980) *Ancient Woodland: Its History, Vegetation and Uses in England*. Edward Arnold, London, UK, pp. 624.
- Rackham, O. (2000) *The History of the Countryside: The Classic History of Britain's Landscape, Flora and Fauna*. Phoenix Giant, London, UK, pp. 445.
- Ritter, E., Vesterdal, L. & Gundersen, P. (2003) Changes in soil properties after afforestation of former intensively managed soils with oak and Norway spruce. *Plant and Soil*, **249**, 319-330.
- Sciama, D., Augusto, L., Dupouey, J.-L., Gonzalez, M. & Moares Domínguez, C. (2009) Floristic and ecological differences between recent and ancient forests growing on non-acidic soils. *Forest Ecology and Management*, **258**, 600-608.

- Verheyen, K., Bossuyt, B., Hermy, M. & Tack, G. (1999) The land use history (1278-1990) of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. *Journal of Biogeography*, **26**, 1115-1128.
- Walsh, T., Ryan, P. & Kilroy, J. (1957) A half century of fertiliser and lime use in Ireland. *Journal of The Statistical and Social Inquiry Society of Ireland*, **XVIX**, 104-136.
- Willis, K.J., Braun, M., Sümegi, P. & Tóth, A. (1997) Does soil change cause vegetation change or vice versa? A temporal perspective from Hungary. *Ecology*, **78**, 740-750.
- Wilson, B.R., Moffat, A.J. & Nortcliff, S. (1997) The nature of three ancient woodland soils in southern England. *Journal of Biogeography*, **24**, 633-646.

CHAPTER 4

THE IMPACTS OF LAND-USE HISTORY ON VEGETATION COMPOSITION IN THE GEARAGH

4.1 Abstract

Secondary woodlands often differ considerably from ancient woodlands in terms of their ground flora community. Several plant species which are closely associated with ancient woodlands are often thought to be absent from secondary woodlands either because of dispersal limitation or because historical disturbances have created unsuitable habitat conditions for recruitment in these sites. This study compares the canopy and ground flora composition of a stand of ancient woodland with adjacent stands of secondary woodland and grassland of a similar local ecology. While the species richness of the ground flora vegetation was similar across all sites, ordination analysis revealed that each of the study sites represented distinct vegetation communities. Most of the species that were found in the ancient woodland were also found in the secondary woodland stands, indicating that dispersal ability was not a limiting factor in the colonisation of new woodland. However, the differences in community composition between the sites were likely due to altered environmental conditions. Many species that were only found in the secondary woodlands are associated with wetter conditions. It is suggested that past woodland clearance and conversion to agriculture had altered edaphic conditions, leading to variations in plant community composition. While secondary woodlands have the potential to recover much of the vegetation characteristics of ancient woodlands, changes in site conditions as a result of past land-use can have a considerable effect on the extent of this recovery.

4.2 Introduction

Ancient woodlands have become increasingly rare habitats in the European landscape (Rackham, 1980). Many typical woodland plant species, such as *Mercurialis perennis*, *Hyacinthoides non-scripta* and *Sanicula europaea* (in Europe) and *Prenanthes altissima*, *Cardamine diphylla* and *Cimicifuga racemosa* (in North America), are restricted to these isolated woodlands (Wulf, 1997; Hermy *et al.*, 1999; Dyer, 2010), and in recent years there has been a greater interest in the ecology of these plants. For instance, it is acknowledged that ancient woodland species are generally adapted for growth in stable woodland ecosystems that are characterised by local, small-scale disturbances. They tend to have limited seed

production and dispersal ability, and many species can live for over 60 years (Hermý *et al.*, 1999; Hermý and Verheyen, 2007). Many are dispersed by ants (myrmecochory), or have no morphological adaptations for dispersal (barochores). Some also have specific germination requirements or exhibit mainly clonal growth, and often have no persistent seed banks (Sciama *et al.*, 2009). These characteristics make them sensitive to habitat loss; consequently they are poorly adapted for rapid population recovery and recolonisation following severe disturbances, such as clearance for agricultural land-use (Flinn and Vellend, 2005). Therefore, ancient woodlands are regarded as highly important habitats for the preservation of these rare species.

In addition to the ground flora community, the tree structure and composition of naturally regenerating woodlands may also differ considerably from those that were never cleared. Several studies in eastern North America have found that the tree communities of continuously wooded areas remain distinct in terms of their species composition and canopy structure from those that were established more than a century ago on agricultural land (Bellemare *et al.*, 2002; Flinn and Marks, 2007; Dyer, 2010). Differences in canopy structure and composition may also affect the ground flora community composition through changes in light availability and the quantity and quality of litter (Verheyen and Hermý, 2001; Van Oijen *et al.*, 2005). However, in much of western Europe the structure of ancient woodlands has often been carefully managed (e.g. through selective felling, coppicing, pollarding) so that there is little difference in the canopy layer of stands with diverse land-use histories. Most studies investigating the vegetation composition of secondary and ancient stands have therefore focused on woodlands where the shrub and tree layer developed as a result of active tree planting and intensive woodland management (Verheyen *et al.*, 2003; Wulf, 2004). However, woodlands where the shrub and tree layer was allowed to develop spontaneously offer a greater opportunity to investigate the direct effect of past land-use on current community composition without the additional effect of a particular management regime.

Woodland plant species may also occur in grasslands adjacent to woodlands, particularly in the presence of individual trees or on grasslands that were formerly

wooded (Peterken and Game, 1984; Inghe and Tamm, 1985). Grasslands have a very low intensity of disturbance in comparison with arable fields. This may enable some woodland species to survive as very small populations in pastures and meadows (e.g. *Anemone nemorosa*, *Geum urbanum*, *Carex remota*), allowing them to recolonise new woodland more efficiently on these sites (Wulf, 2004). Species richness in woodlands can also be higher when networks of hedgerows are present in the surrounding landscape (Petit *et al.*, 2004). Even woodland species with limited seed dispersal may form remnant populations, which could expand should habitat conditions improve (Honnay *et al.*, 1999).

The variability observed among previous studies in terms of the distribution of plants in secondary woodlands highlights the importance of regional variation in environmental conditions and woodland history (Verheyen *et al.*, 2006). However, few studies have examined this topic outside of central Europe or eastern North America. In Ireland, an assessment of ancient woodlands was only recently completed (Perrin and Daly, 2010), and plants associated with these woodlands remain poorly studied. In addition, much of what is known about ancient woodland flora may not be applicable to Ireland due to the impoverished nature of the Irish flora. Indeed, many specialist plant species do not occur in Ireland (e.g. *Actaea spicata*, *Helleborus viridis*, *Paris quadrifolia*), while other species occupy a broader niche than they do elsewhere (Kelly, 2004). Therefore, the differences between ancient and secondary woodland may be less distinct than in other regions. Nonetheless, the scarcity of ancient woodlands makes them a conservation priority throughout Ireland. A better understanding of the floristic difference between ancient woodland and adjoining stands of more recent origin will therefore help to improve schemes aimed at restoring Irish native woodlands (Kelly, 2005).

This study assessed the impact of historical land-use on the current vegetation composition of the Gearagh woodland with adjoining secondary stands. By focusing on a single area, the impact of broad ecological influences (climate, altitude) is reduced and the more immediate determinants of species composition can be ascertained. In this study, the secondary woodland stands established naturally rather than being planted. The objectives of this research study were: (i) to assess

the effects of past land-use on the canopy and ground flora composition of the Gearagh and the distribution and abundance of individual taxa in adjacent stands; (ii) to determine if adjacent grasslands act as refugia for woodland species; and (iii) to examine the life-history, dispersal and ecological characteristics of plant species associated with each habitat in the study.

4.3 Materials and methods

4.3.1 Vegetation sampling

Details about the site history and sampling methods can be found in the previous chapter (Sections 3.3.1 and 3.3.2). Five replicate sites were located in each of the four habitat-types, giving a total of 20 sites in the Gearagh, all of which were located beyond the area that is affected by changes in the water level of the adjacent reservoir (Akumu, 2006). Nine 1 × 2 m plots were placed within each of these sites in a grid design (Fig. 4.1). This was chosen as the minimal area to capture ground flora diversity after examining the species-area relationship from preliminary samples (see Appendix A). In each of these plots, floristic data was recorded using a species percentage cover method on a 1-100 % scale with 1% increments up to 10%, and with 10% increments from there on. Unidentified species were collected and identified in the laboratory. Species nomenclature is after Webb *et al.* (1996). Species were recorded for every plot in both May and July of the same year. The highest number on the two occasions was recorded as the species frequency.

To describe the tree communities and structure, a single 10 × 30 m transect was arranged in the centre of each site (Fig. 4.1). Tree species and diameter at breast height (dbh) were recorded for all the living tree species with a dbh ≥ 5 cm. Tree height was estimated using a clinometer. Three structural classes were identified: shrub (2 – 5 m); lower canopy (5 – 15 m), and upper canopy (15 – 20 m). Percentage cover of vegetation within each structural class was described to the nearest 5 %. Vegetation data were summarised by calculating stem density, basal area, frequency, and height, as well as relative basal area for each species recorded. The occurrence of individual trees with more than one main stem was also noted, as

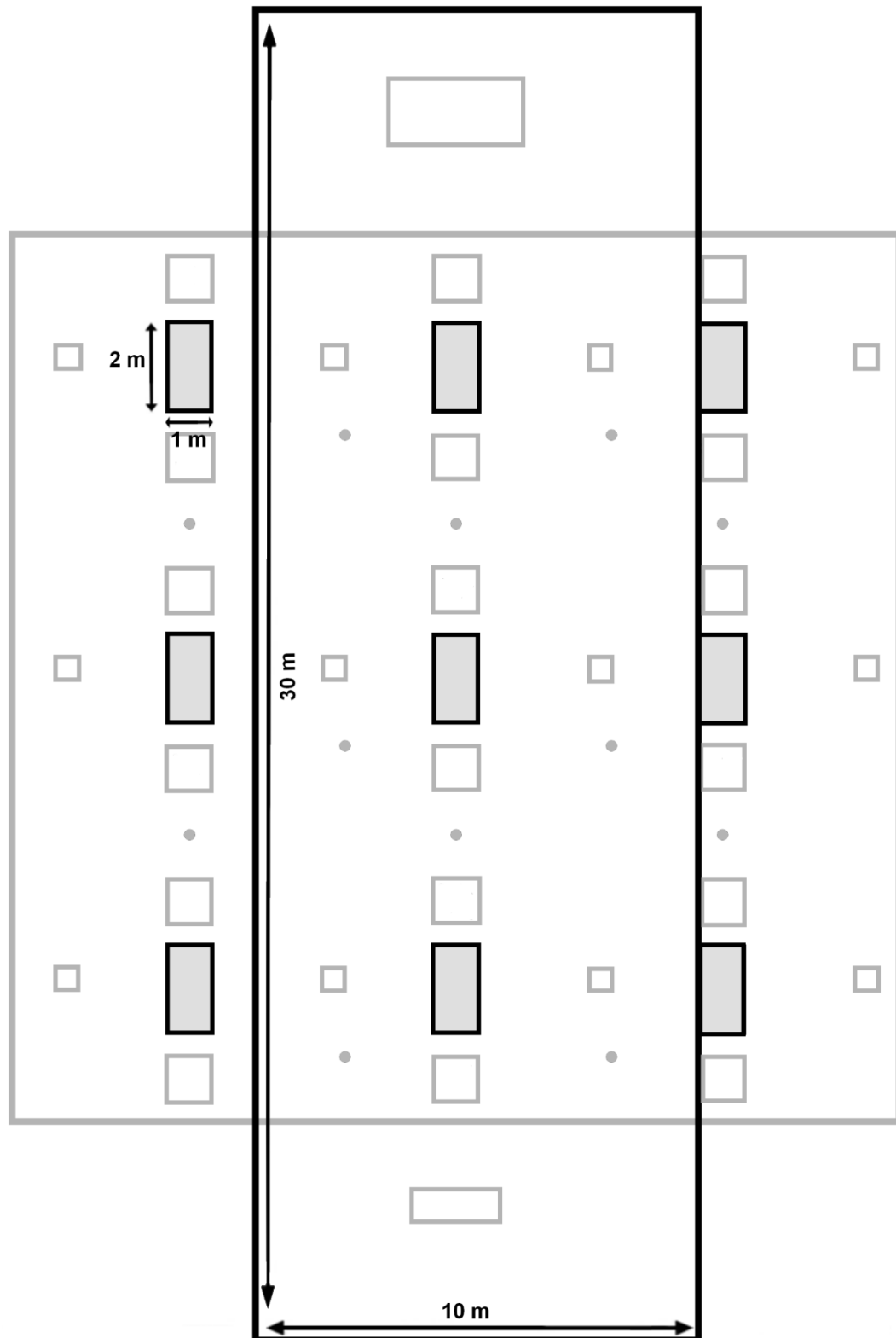


Fig. 4.1 Design of one sampling site, i.e. one of the replicate study sites, with the location of the nine ground flora sampling plots (grey plots) and the transect for sampling tree communities outlined in black. The sampling designs used in other sections of the thesis are outlined in grey; see Figs. 3.2, 5.2, and 6.1 for further details.

this may be indicative of a coppice regime. All dead standing or fallen stems with a dbh ≥ 10 cm were counted. Coarse woody debris was subsequently classified in three categories: (i) intact standing dead trees and broken snags; (ii) logs; and (iii) stumps.

Understorey light availability was quantified using hemispherical photographs of the woodland canopy. Six photographs were taken at each site, spaced evenly throughout the site. Photographs were taken on overcast days to avoid glare from direct sunlight. For each photograph, the camera was aligned north and levelled horizontally. A Nikon Coolpix E5700 digital camera with a Fisheye Converter was used. The digital images were analysed with the Gap Light Analyser programme (Frazer *et al.*, 2000). A single observer analysed all images to minimise error in threshold determination. For each habitat, the mean amount of radiation reaching the understorey ($\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) was calculated.

4.3.2 Data analysis

The nested sampling design provided abundance data from nine 2 m^2 quadrats; this was used to provide robust summary data at the level of each of the replicate sites. The total cover as the sum of the individual species' cover, the number of species, Shannon-Wiener diversity and Pielou's evenness (Magurran, 2004) of each plot were calculated and differences between habitat types were tested with a Kruskal-Wallis test. All recorded species were classified as either woodland species or non-woodland species, based on information from Webb *et al.* (1996). The species richness of woodland and non-woodland species was then calculated and analysed with a Kruskal-Wallis test. Differences in canopy variables were assessed using ANOVA tests after examination for normality and homogeneity of variance. The type of coarse woody debris was expressed as a percentage of total dead stems and tested with a Kruskal-Wallis test.

In order to investigate the modes of species dispersal, all species were divided into six dispersal groups: anemochores (wind-dispersed seed), barochores (species without a specific dispersal agent), endozoochores (fruits consumed and dispersed by vertebrates), epizoochores (dispersed by adhesion to animals), hydrochores

(water-dispersed seed), and myrmecochores (ant-dispersed seed). Species were also classified by life-forms (chamaephyte, geophyte, hemicryptophyte, phanerophyte, therophyte). Information on species traits were taken from the Ecological Flora of the British Isles (Fitter and Peat, 1994). The relative number and abundance of dispersal groups and life-form classes were calculated by summing the number or cover of species of each category and dividing that by the total number of species or cover in each plot. Differences in colonisation ability and life-form types between age classes were tested separately with Kruskal-Wallis tests.

In order to characterise the environmental conditions of the stands, the indicator value of vegetation for soil pH (*R*), nitrogen content (*N*), light (*L*), and moisture (*F*) was assessed using Ellenberg's scoring system, as modified for British and Irish vegetation (Hill *et al.*, 1999). Although not without limitations, indicator values provide a useful means of assessing the values of environmental variables (Diekmann, 2003). For each vegetation plot, a weighted average was calculated for each of these four indicator values, using cover-abundance of each species as the weighting factor. Variations of Ellenberg's indicator values between the different former land-use categories were compared using Kruskal-Wallis tests.

Plant communities were analysed using non-metric multidimensional scaling (NMS) ordination (Kruskal, 1964) using PC-ORD (McCune and Mefford, 2006). Data were first screened by Outlier Analysis using Sørensen (Bray-Curtis) distance measure. None of the plots or species were identified as outliers and all were included in the analysis. Data were then modified to include only those species that occurred in more than two sites so as to reduce noise in the dataset (McCune and Grace, 2002). NMS was run from a starting configuration in 'slow and thorough' autopilot mode, with Sørensen (Bray-Curtis) selected as the distance measure. The stability criterion was set at 0.00001 and the number of iterations to evaluate stability was set at 15. A Monte-Carlo test was carried out with 250 randomised runs.

Habitat sites were compared with non-metric MRPP (Multi-response Permutation Procedures) and Indicator Species Analysis, based on Sørensen (Bray-Curtis) distances. MRPP provides a nonparametric multivariate test of differences between

groups (Mielke and Berry, 2007), while Indicator Species Analysis identifies the species which are most characteristic of each group (Dufrene and Legendre, 1997). Non-metric MRPP is the same as MRPP except that the distance matrix is converted to ranks before calculating the test statistic. Indicator Species Analysis calculates an indicator value (IV) for each species in a group based on their abundance and frequency, ranging from 0 (no indication) to 100 (perfect indication). The highest indicator value (IV_{max}) for a given species across groups is treated as an indicator value of that species. Analysis was conducted using PC-ORD (McCune and Mefford, 2006) and was tested for significance using Monte-Carlo techniques. This was used to draw up a table of species typical of each habitat type.

4.4 Results

4.4.1 Tree stand composition and structure

A total of ten species of woody plants ($\text{dbh} \geq 5 \text{ cm}$) were recorded in the tree stratum, of which *Acer pseudoplatanus* (an alien species), *Prunus spinosa*, and *Viburnum opulus* were infrequent. All the woodland habitats had a similar stem density, about 1050 trees/ha ($F = 0.059$; $d.f. = 2,12$; $P > 0.05$; Table 4.1). Tree size distributions also appeared similar in the three woodland types, although both secondary woodlands had more small trees of 5-10 cm dbh than the ancient woodland (Fig. 4.2). Although not significant, there was a trend of decreasing total basal area with woodland age ($F = 1.760$; $d.f. = 2,12$; $P = 0.214$). Understorey light levels were similar in all woodlands, and the only significant difference in canopy cover occurred in the upper layer, which was greatest in the ancient woodland (Table 4.1). No difference was detected in mean height between stands.

Quercus robur comprised 38 % of the relative basal area in the ancient woodland stands and occurred in all of the woodland habitats, although not in all sites of the recent secondary woodland (Table 4.2). Ancient woodland was also dominated by *Corylus avellana* (28 % of the relative basal area), *Fraxinus excelsior* (13 %), and *Ilex aquifolium* (11 %). The latter occurred in significantly greater densities in the ancient woodland than in either of the two secondary woodland stands. In the old

Table 4.1 Mean values (\pm standard error) of the structural characteristics in the three woodland types in the Gearagh. Results of ANOVA tests are shown.

Site variables	Ancient woodland	Old secondary woodland	Recent secondary woodland	<i>P</i>
Density (stems ha ⁻¹)	1007 \pm 55.3	1087 \pm 148.6	1053 \pm 104.2	> 0.05
Basal area (m ² ha ⁻¹)	67 \pm 8.2	96 \pm 14.8	107 \pm 26.0	> 0.05
Height (m)	9.56 \pm 0.49	9.55 \pm 0.48	8.44 \pm 0.43	> 0.05
Cover of shrub layer (%)	14 \pm 4.8	27 \pm 7.5	8 \pm 3.4	0.095
Cover of lower canopy (%)	75 \pm 8.4	86 \pm 4.0	79 \pm 5.1	> 0.05
Cover of upper canopy (%)	87 \pm 2.5	62 \pm 11.5	40 \pm 14.3	0.007
Radiation (mol m ⁻² d ⁻¹)	4.07 \pm 0.11	4.10 \pm 0.10	4.04 \pm 0.11	> 0.05

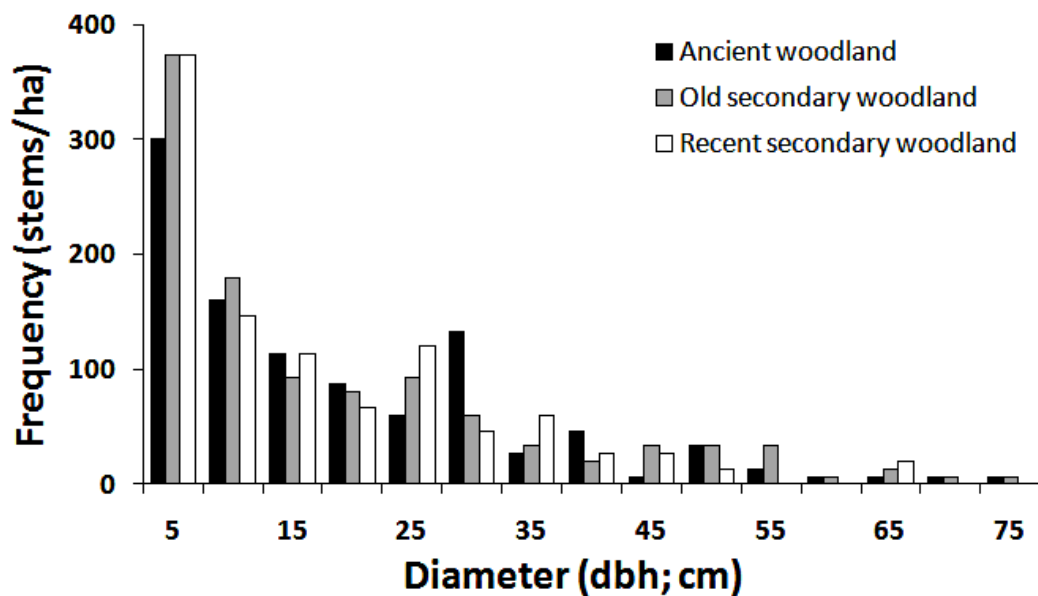


Fig. 4.2 Tree size distributions of the three historical woodland types in the Gearagh (dbh \geq 5 cm; ten trees with dbh > 80 cm are not shown).

Table 4.2 Characteristics of the most frequent tree and shrub species in the three historical woodland types of the Gearagh (stems ≥ 5 cm dbh). Mean values and results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different superscript letters; any two with a common letter within a row are not significantly different ($P \geq 0.05$).

	Ancient woodland	Old secondary woodland	Recent secondary woodland	<i>P</i>
Density (stems ha ⁻¹)				
<i>Betula pubescens</i>	133.20	99.80	126.80	> 0.05
<i>Corylus avellana</i>	420.00	660.00	526.60	> 0.05
<i>Crataegus monogyna</i>	60.00 ^a	60.20 ^a	240.00 ^b	< 0.05
<i>Fraxinus excelsior</i>	53.40	53.40	53.20	> 0.05
<i>Ilex aquifolium</i>	140.00 ^b	40.00 ^a	0.00 ^a	0.005
<i>Quercus robur</i>	200.20	140.00	46.80	0.056
<i>Salix cinerea</i> spp. <i>oleifolia</i>	0.00	33.20	53.20	> 0.05
Relative density (%)				
<i>Betula pubescens</i>	13.24	10.18	12.03	> 0.05
<i>Corylus avellana</i>	41.37	60.24	52.09	> 0.05
<i>Crataegus monogyna</i>	6.18 ^a	6.05 ^a	21.99 ^b	< 0.05
<i>Fraxinus excelsior</i>	5.51	4.53	4.18	> 0.05
<i>Ilex aquifolium</i>	14.02 ^b	3.07 ^a	0.00 ^a	< 0.01
<i>Quercus robur</i>	19.67	11.84	5.00	0.068
<i>Salix cinerea</i> spp. <i>oleifolia</i>	0.00	4.07	4.18	> 0.05
Basal area (m ² ha ⁻¹)				
<i>Betula pubescens</i>	5.80	30.60	13.60	> 0.05
<i>Corylus avellana</i>	17.60 ^a	38.60 ^{ab}	72.60 ^b	< 0.05
<i>Crataegus monogyna</i>	0.93 ^a	0.90 ^a	10.25 ^b	< 0.01
<i>Fraxinus excelsior</i>	7.87	6.88	3.80	> 0.05
<i>Ilex aquifolium</i>	7.23 ^b	1.73 ^{ab}	0.00 ^a	< 0.01
<i>Quercus robur</i>	27.55	11.64	6.05	0.093
<i>Salix cinerea</i> spp. <i>oleifolia</i>	0.00	5.09	1.08	> 0.05
Relative basal area (%)				
<i>Betula pubescens</i>	8.34	27.24	14.05	> 0.05
<i>Corylus avellana</i>	28.00	41.81	64.62	0.085
<i>Crataegus monogyna</i>	1.76 ^a	1.04 ^a	10.99 ^b	< 0.05
<i>Fraxinus excelsior</i>	12.69	8.34	3.62	> 0.05
<i>Ilex aquifolium</i>	11.34 ^b	2.36 ^{ab}	0.00 ^a	< 0.01
<i>Quercus robur</i>	37.87 ^b	12.13 ^{ab}	5.71 ^a	< 0.05
<i>Salix cinerea</i> spp. <i>oleifolia</i>	0.00	7.09	0.99	> 0.05
Height (m)				
<i>Betula pubescens</i>	7.97	15.85	12.30	> 0.05
<i>Corylus avellana</i>	6.09	6.80	7.74	> 0.05
<i>Crataegus monogyna</i>	3.09	4.88	5.92	> 0.05
<i>Fraxinus excelsior</i>	15.16	9.37	6.11	> 0.05
<i>Ilex aquifolium</i>	6.04 ^b	3.65 ^{ab}	0.00 ^a	< 0.05
<i>Quercus robur</i>	13.68	10.94	5.88	> 0.05
<i>Salix cinerea</i> spp. <i>oleifolia</i>	0.00	4.74	2.65	> 0.05

secondary woodland, *C. avellana* comprised 42 % of the relative basal area, followed by *Betula pubescens* (27 %), and *Q. robur* (12 %). The recent secondary woodland was dominated by *C. avellana* (65 % of relative basal area), which occurred in significantly greater amounts there than it did in the ancient woodland. Although not one of the most dominant species in the woodland, *Crataegus monogyna* occurred in significantly greater quantities in the recent secondary woodland than in either the ancient or old secondary woodland stands. *F. excelsior*, *I. aquifolium* and *Q. robur* all increased in density and basal area from the recent secondary to the old secondary and then to the ancient woodland (Table 4.2). *Q. robur*, *F. excelsior* and *B. pubescens* were generally the tallest species in each of the woodlands. The only woodland habitat in which *Prunus spinosa* occurred was the recent secondary, but this was only in very small numbers and most individuals had a dbh of less than 5 cm.

Although there was no overall difference in the total amount of dead stems between the woodland types (Table 4.3), there appeared to be greater production of coarse woody debris in the ancient and old secondary woodland than in the recent secondary woodland. This likely explains the slightly lower density and basal area recorded in the ancient woodland (Table 4.1). The percentage of total dead stems that occurred as stumps was significantly greater in both the ancient and old secondary woodland than in the recent secondary woodland.

Table 4.3 Main types of coarse woody debris as a percentage of total dead stems in each of the three historical woodland types of the Gearagh. Mean values and results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different letters; any two with a common letter within a row are not significantly different ($P \geq 0.05$).

	Ancient woodland	Old secondary woodland	Recent secondary woodland	<i>P</i>
Dead stem density (pieces ha ⁻¹)	440	460	286	> 0.05
Dead stem (% of total stems)	30	24	21	> 0.05
Stumps (% of total dead stems)	12.0 ^b	17.6 ^b	0.0 ^a	< 0.05
Snags (% of total dead stems)	55.3	68.2	79.3	> 0.05
Logs (% of total dead stems)	31.7	14.1	20.7	> 0.05

Stumps: broken or cut stumps of trees; snags: standing dead trees; logs: fallen dead trees.

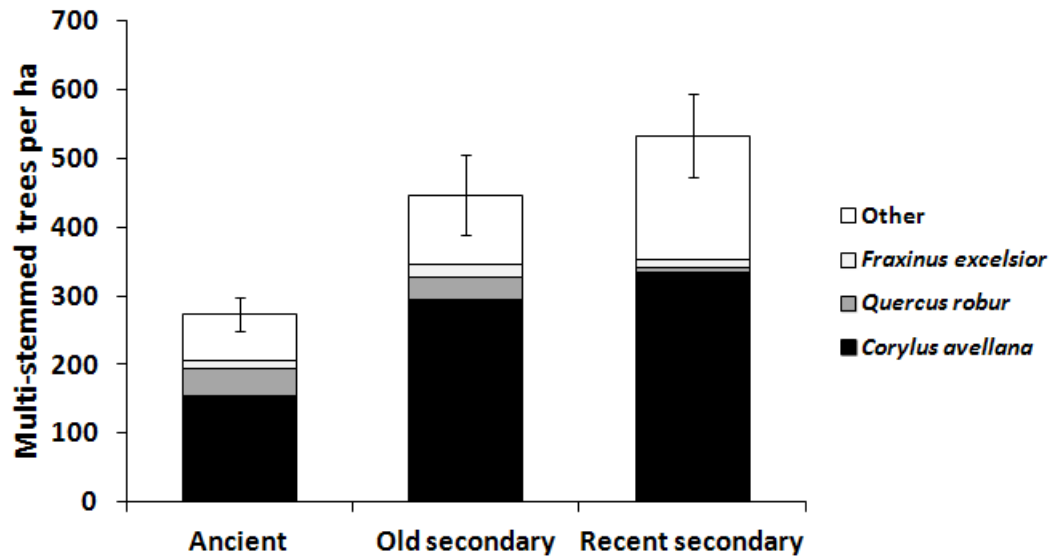


Fig. 4.3 Total number of multi-stemmed trees (possessing more than one primary stem) in the ancient, old secondary, and recent secondary woodland areas of the Gearagh; the main tree species are indicated. *B. pubescens*, *C. monogyna*, *I. aquifolium*, and *S. cinerea* spp. *oleifolia* are combined under Other.

Many of the trees that were recorded possessed more than one main stem (Fig. 4.3). In the ancient woodland 27 % of the trees were noted as being multi-stemmed, while this figure rose to 41 % in the old secondary woodland and 51 % in the recent secondary. In all three woodland areas, *C. avellana* accounted for over half of all multi-stemmed trees recorded. However, multiple stems were also found to occur on *Q. robur* and *F. excelsior* individuals, particularly in the ancient woodland where 20 % of *Q. robur* and 30 % of *F. excelsior* individuals were multi-stemmed.

4.4.2 Ground flora characteristics

Over all habitats, a total of 71 species of ground flora were found. There was little variation in total ground flora species richness between the four habitat types of the Gearagh (Table 4.4). However, the species richness of plants typically associated with woodlands (both generalists and specialists), as defined by Webb *et al.* (1996), was lower in the grassland sites; woodland species richness was similar in the three woodland habitats. Conversely, as expected, the species richness of non-woodland plants was greatest in the grassland, while the recent secondary had the highest non-woodland species richness of the three woodland habitats. The Shannon-

Wiener diversity index and Pielou's evenness showed little difference between the habitats. Total herb cover was also similar in the three woodland habitats, but was significantly greater in the grassland; this value can often be over 100% as it represents the sum of individual species' cover. Yet, of the total number of species recorded in just the three woodland habitats, only 45 % were common to all three stands. These included: *Ajuga reptans*, *Allium ursinum*, *Anemone nemorosa*, *Blechnum spicant*, *Circaea lutetiana*, *Conopodium majus*, *Crataegus monogyna*, *Deschampsia caespitosa*, *Dryopteris filix-mas*, *Euphorbia hyberna*, *Filipendula ulmaria*, *Fraxinus excelsior*, *Geum urbanum*, *Hedera helix*, *Ilex aquifolium*, *Lonicera periclymenium*, *Poa trivialis*, *Primula vulgaris*, *Quercus robur*, *Ranunculus ficaria*, *Rubus fruticosus*, *Sanicula europea*, *Veronica montana*, *Viburnum opulus*, and *Viola riviniana*.

Unsurprisingly, an NMS ordination performed on vegetation data from all habitats clearly distinguished between grassland and woodland (87% of variation explained). To discriminate between woodland types, a second NMS ordination was performed using only plant data from the three woodland types. This NMS ordination yielded a three-dimensional solution with a final stress of 5.8 that explained 92 % of the variation in woodland ground flora composition (Fig. 4.4). The first axis, which

Table 4.4 Differences in average number of ground flora species, total cover, Shannon-Wiener diversity index, and Pielou's evenness between the four habitat types in the Gearagh. Median values and results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different letters; any two with a common letter within a row are not significantly different ($P \geq 0.05$).

	Ancient woodland	Old secondary woodland	Recent secondary woodland	Grassland	<i>P</i>
Total herb species richness	23	23	25	19	> 0.05
Woodland species richness	17 ^b	18 ^b	18 ^b	9 ^a	< 0.05
Non-woodland species richness	4 ^a	6 ^a	7 ^{ab}	10 ^b	< 0.01
Total herb cover (%)	79 ^a	83 ^a	73 ^a	113 ^b	< 0.01
Shannon-Wiener diversity	2.33	2.33	2.27	1.97	> 0.05
Pielou's evenness	0.75	0.75	0.70	0.67	> 0.05

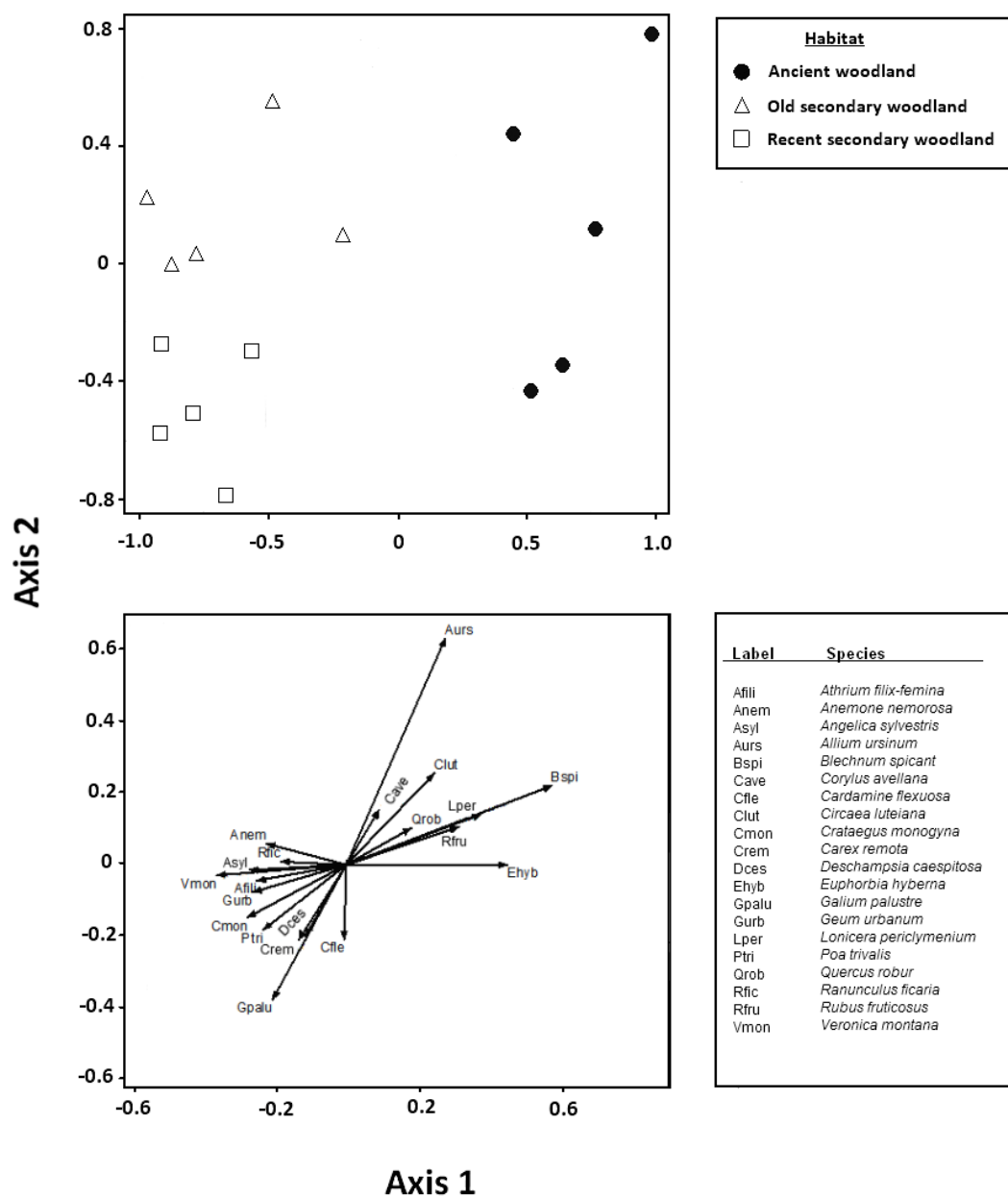


Fig. 4.4 NMS ordination of woodland ground flora vegetation. The upper panel shows axis 1 and 2 plots for the three woodland sites in the Gearagh. The lower panel is a joint plot showing the correlations between the axes and the key species. Cumulative variation in the original dataset explained by the ordination is 47 %: Axis 1 = 39 %, Axis 2 = 8 %, Final Stress = 5.8; Final Instability = 0.00001.

explained 39 % of the variation, described a gradient between key species from *Blechnum spicant* ($r = 0.80$) and *Euphorbia hyberna* ($r = 0.71$) to *Veronica montana* ($r = -0.64$). The second axis indicated dominance by *Allium ursinum* ($r = 0.84$) rather than *Galium palustre* ($r = -0.65$). Axis 3, explaining 45 % of the variation, primarily represented *Hedera helix* ($r = 0.79$) vs. *Ranunculus ficaria* ($r = -0.78$).

The first two ordination axes distinctly separated the three woodland habitats from each other (Fig. 4.4). The ancient woodland was separated from both secondary woodlands along the first axis, while the two secondary woodlands separated along the second. This separation confirmed results from the non-metric MRPP, which showed that the species composition of each habitat type differed markedly overall, although the two secondary woodlands showed the greatest similarity to each other (Table 4.5).

The distinctness of each of the habitat communities resulted from the differential distributions of many individual species. Indicator species analysis distinguished 31 significant species (40 % of all species recorded) associated with each of the habitats in the Gearagh (Table 4.6). The grassland had the greatest number of indicator species (17) out of all the habitats. This reflects the large number of species that are confined to grassland sites. *Juncus effusus* had an indicator value of 100 for the grassland, which suggests that this species is a diagnostic indicator for

Table 4.5 Summary of the multi-response permutation procedures analysis comparing all habitat types of the Gearagh.

Groups compared	<i>P</i>	<i>A</i>
Grassland v Recent secondary	0.002	0.45
Grassland v Old Secondary	0.002	0.45
Grassland v Ancient	0.002	0.45
Ancient v Old Secondary	0.002	0.30
Ancient v Recent Secondary	0.003	0.30
Old Secondary v Recent Secondary	0.021	0.17

The *A* statistic is a descriptor of within-group homogeneity compared with the random expectation. A maximum value of *A* = 1 indicates that all species within the group are identical. In community ecology, values for *A* are commonly below 0.1 and an *A* > 0.3 is regarded as fairly high.

Table 4.6 Indicator species and their indicator values of ground flora vegetation for each of the four habitat types in the Gearagh. Species with a significant indicator value ($P \leq 0.05$) are shown in bold. Significance of 1000 permutations in a Monte-Carlo test: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Indicator species	Indicator Value (%)			
	Ancient woodland	Old secondary woodland	Recent secondary woodland	Grassland
Ancient woodland				
<i>Blechnum spicant</i>	90 **	1	2	0
<i>Lonicera periclymenium</i>	83 **	11	2	0
<i>Euphorbia hyberna</i>	79 **	8	0	0
<i>Rubus fruticosus</i> agg.	68 *	2	9	9
<i>Hyacinthoides non-scripta</i>	60 *	0	0	0
<i>Dryopteris filix-mas</i>	60 *	0	0	0
<i>Quercus robur</i>	52	15	4	0
<i>Allium ursinum</i>	49	38	13	0
<i>Ilex aquifolium</i>	47	11	15	0
<i>Sanicula europea</i>	45	13	13	0
<i>Solidago virgurea</i>	40	0	0	0
<i>Circaea luteiana</i>	37	12	1	0
<i>Corylus avellana</i>	37	3	0	0
<i>Galium odoratum</i>	37	0	0	0
<i>Cardamine pratensis</i>	25	7	0	0
<i>Ajuga reptans</i>	19	17	10	0
Old secondary woodland				
<i>Anemone nemorosa</i>	11	66 ***	23	0
<i>Ranunculus ficaria</i>	10	62 **	18	2
<i>Primula vulgaris</i>	4	62 *	1	0
<i>Dryopteris dilatata</i>	12	38	22	0
<i>Chrysosplenium oppositifolium</i>	0	30	10	0
<i>Equisetum hyemale</i>	0	29	6	0
<i>Betula pubescens</i>	0	20	0	0
<i>Caltha palustris</i>	0	20	0	0
<i>Heracleum sphondylium</i>	0	20	0	0
<i>Lysimachia nemorum</i>	0	20	0	0
<i>Prunella vulgaris</i>	0	20	0	0
<i>Scrophularia nodosa</i>	0	20	0	0
<i>Viola palustris</i>	0	20	0	0
<i>Conopodium majus</i>	10	13	2	0

Table 4.6 continued.

	Indicator Value (%)			
	Ancient woodland	Old secondary woodland	Recent secondary woodland	Grassland
Recent secondary woodland				
<i>Carex remota</i>	0	0	98 ***	0
<i>Athyrium filix-femina</i>	0	30	63 *	0
<i>Crataegus monogyna</i>	3	30	55 *	0
<i>Galium palustre</i>	0	0	65 *	7
<i>Geum urbanum</i>	2	35	52 *	0
<i>Veronica montana</i>	5	44	50	0
<i>Angelica sylvestris</i>	0	32	46	0
<i>Hedera helix</i>	26	32	42	0
<i>Viola riviniana</i>	15	33	41	0
<i>Malus sylvestris</i>	0	0	40	0
<i>Fraxinus excelsior</i>	26	36	38	0
<i>Viburnum opulus</i>	28	16	30	0
<i>Ranunculus auricomus</i>	0	0	20	0
Grassland				
<i>Galium aparine</i>	0	0	3	93 ***
<i>Rumex acetosa</i>	0	0	0	98 ***
<i>Valeriana officinalis</i>	0	0	1	95 ***
<i>Agrostis stolonifera</i>	0	0	1	98 ***
<i>Juncus effusus</i>	0	0	0	100 ***
<i>Prunus spinosa</i>	0	0	0	80 **
<i>Ranunculus acris</i>	0	0	0	80 **
<i>Ranunculus repens</i>	1	0	0	75 **
<i>Rumex conglomerates</i>	0	0	0	80 **
<i>Urtica dioica</i>	0	0	0	80 **
<i>Lycopus europaeus</i>	4	0	0	64 *
<i>Plantago lanceolata</i>	0	0	0	60 *
<i>Myosotis scorpioides</i>	0	0	0	60 *
<i>Ranunculus flammula</i>	0	0	0	60 *
<i>Trifolium dubium</i>	0	0	0	60 *
<i>Brachypodium sylvaticum</i>	0	0	0	60 *
<i>Veronica chamaedrys</i>	0	3	3	56 *
<i>Deschampsia caespitosa</i>	2	5	16	57
<i>Poa trivialis</i>	1	9	23	50
<i>Epilobium montanum</i>	0	0	0	40
<i>Filipendula ulmaria</i>	25	20	25	30
<i>Cardamine flexuosa</i>	4	0	18	20
<i>Ulex europaeus</i>	0	0	0	20
<i>Taraxacum officinale</i>	0	0	0	20
<i>Trifolium repens</i>	0	0	0	20
<i>Verbascum thapsus</i>	0	0	0	20

the habitat. The ancient, old secondary and recent secondary woodland sites each had 6, 3, and 5 indicator species, respectively. Species which were indicators of old secondary woodland also occurred in the ancient and recent secondary woodlands, but had their greatest indicator value in the old secondary. Some of the indicators for the recent secondary were also associated with the old secondary woodland, but few others were also associated with the ancient.

4.4.3 Life-history characteristics

Ellenberg's indicator values were significantly different between the four habitat types for light, moisture, and reaction (pH), but not for nitrogen (Table 4.7). All indicators showed a similar trend of increasing values from ancient woodland to grassland, with the two secondary habitats in intermediate places. Ancient woodland therefore had the lowest indicator values for light, moisture, reaction, and also nitrogen, while grassland had the highest. The Ellenberg indicator values were recalculated based on the indicator species for each habitat. In this way, the common species could be excluded. The indicator values for light, moisture, soil reaction and nitrogen were all significantly higher for the grassland indicators compared to the ancient woodland indicator species (Fig. 4.5). These results showed that species in the ancient woodland were more tolerant of shade, acidity, lower nitrogen contents in the soils and a lower water level. In contrast, the grassland and secondary site indicators seem to be favoured by a higher light

Table 4.7 Differences in Ellenberg indicator values between the four habitat types in the Gearagh. Median values and results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different letters; any two with a common letter within a row are not significantly different ($P \geq 0.05$).

Ellenberg indicator	Ancient woodland	Old secondary woodland	Recent secondary woodland	Grassland	<i>P</i>
Light (<i>L</i>)	4.8 ^a	4.9 ^a	5.1 ^a	6.7 ^b	< 0.05
Moisture (<i>F</i>)	5.8 ^a	5.9 ^{ab}	5.9 ^{ab}	6.3 ^b	< 0.05
pH (<i>R</i>)	5.9 ^a	6.1 ^{ab}	6.3 ^b	6.3 ^b	< 0.05
Nitrogen (<i>N</i>)	5.5	5.5	5.6	5.7	> 0.05

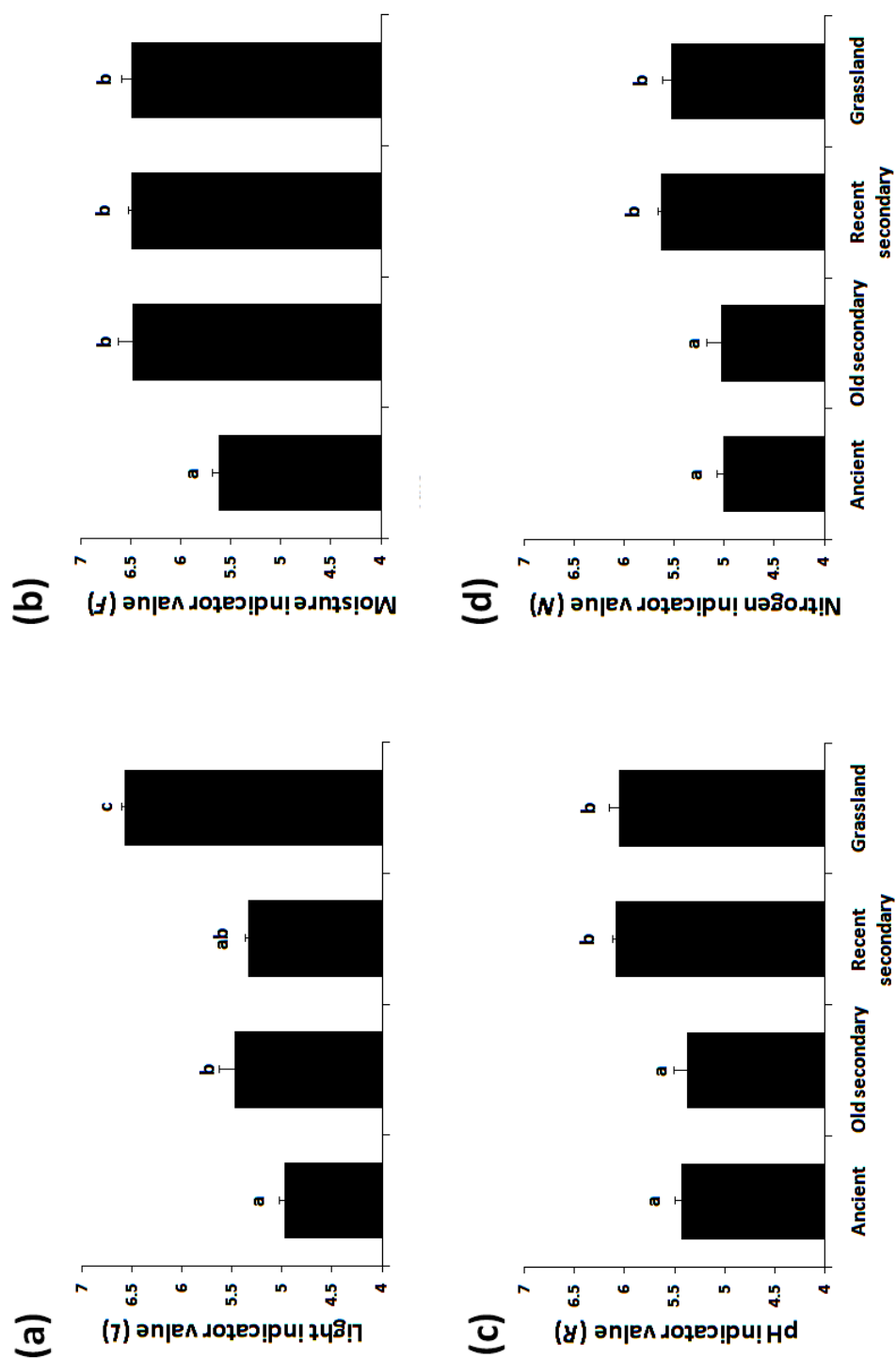


Fig. 4.5 Mean (\pm standard error) Ellenberg indicator values for a) light, b) moisture, c) soil reaction, and d) nitrogen of indicator species for each of the four habitat types of the Gearagh. Any bars with a common letter within a figure are not significantly different using Tukey's honestly significant difference test ($P < 0.05$).

intensity, moist conditions, and a good supply of nitrogen and basic cations. While the old secondary woodland indicators also require more light and water than those associated with the ancient woodland, they are more similar to the ancient woodland indicators in terms of their tolerance of soil acidity and lower nitrogen contents.

Ancient woodland sites contained the greatest number of geophytes, although this was not reflected in percentage cover values; on that basis, the old secondary woodland was instead richest in geophytes (Table 4.8). The number of species of hemicryptophytes, phanerophytes, and therophytes was similar in all woodland sites, but differed in the grassland. The grassland was poor in all but hemicryptophytes, while all three woodlands were only poor in chamaephytes and therophytes.

Table 4.8 Differences in the relative contribution of the life-forms expressed as species and cover values between the habitat types of the Gearagh. Mean values and results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different letters; any two with a common letter within a row are not significantly different ($P \geq 0.05$).

	Ancient woodland	Old Secondary woodland	Recent Secondary woodland	Grassland	<i>P</i>
Number of species (%)					
Chamaephytes	3.5	7.9	6.4	4.1	> 0.05
Geophytes	19.2 ^c	18.6 ^{bc}	13.8 ^b	2.6 ^a	< 0.01
Hemicryptophytes	43.8 ^a	45.2 ^a	50.7 ^a	76.4 ^b	< 0.01
Phanerophytes	33.5 ^b	28.3 ^b	27.6 ^b	8.8 ^a	< 0.05
Therophytes	0.0 ^a	0.0 ^a	1.5 ^a	8.1 ^b	< 0.001
Cover (%)					
Chamaephytes	0.6 ^a	5.1 ^{ab}	5.7 ^b	0.8 ^a	< 0.01
Geophytes	24.5 ^b	42.0 ^c	15.6 ^{ab}	0.3 ^a	< 0.001
Hemicryptophytes	30.5 ^a	20.7 ^a	31.4 ^a	92.1 ^b	< 0.01
Phanerophytes	44.4 ^b	32.2 ^{ab}	46.9 ^b	3.3 ^a	< 0.01
Therophytes	0.0 ^a	0.0 ^a	0.3 ^a	3.5 ^b	< 0.01

Table 4.9 Differences in the dispersal modes expressed as species and cover values between the habitat types of the Gearagh. Mean values and results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different letters; any two with a common letter within a row are not significantly different ($P \geq 0.05$).

	Ancient woodland	Old secondary woodland	Recent secondary woodland	Grassland	<i>P</i>
Number of species (%)					
Anemochores	21.8	22.4	18.8	28.1	> 0.05
Barochores	14.9	15.8	16.8	20.8	> 0.05
Endozoochors	26.1	20.5	21.9	15.5	> 0.05
Epizoochors	12.6 ^a	9.7 ^a	10.4 ^a	17.7 ^b	< 0.05
Hydrochors	0.8 ^a	4.3 ^a	12.1 ^b	15.3 ^b	< 0.001
Myrmecochors	23.8 ^{bc}	27.3 ^c	20.0 ^b	2.6 ^a	< 0.01
Cover (%)					
Anemochores	12.2	9.0	13.6	19.5	> 0.05
Barochores	12.4 ^a	12.3 ^a	19.2 ^a	52.5 ^b	< 0.01
Endozoochors	40.4 ^b	27.3 ^{ab}	40.9 ^b	6.3 ^a	< 0.05
Epizoochors	2.9 ^a	3.4 ^a	3.4 ^a	18.1 ^b	< 0.05
Hydrochors	0.4 ^a	1.3 ^b	4.6 ^b	3.2 ^b	< 0.05
Myrmecochors	31.7 ^b	46.6 ^c	18.2 ^b	0.3 ^a	< 0.001

In the analysis of colonisation ability, significant differences were identified among all of the diaspore dispersal types, other than the anemochores (Table 4.9). Comparison of dispersal types indicated that the ancient woodland had the fewest number of barochores; these accounted for most of the cover in the grassland sites. The number and abundance of hydrochors was greatest in the grassland and recent secondary, but few were found in the old secondary or ancient woodland. The woodland sites were richest in endozoochors and myrmecochors, although there were fewer myrmecochors in the recent secondary woodland.

4.5. Discussion

4.5.1 Tree characteristics

The results of this study indicate that the structure and composition of vegetation in the secondary woodland still differs from that of the ancient woodland, even up to 150 years after agricultural abandonment. This is similar to previous studies

which have shown that past land-use remains an important factor in shaping the structure and function of present-day woodlands in North America (Bellemare *et al.*, 2002; Gerhardt and Foster, 2002; Flinn and Marks, 2007; Dyer, 2010); land-use change is rarely the dominant factor for the overstorey development in European woodlands as most secondary stands are actively planted (Verheyen and Hermy, 2001). Nonetheless, the old secondary woodland in the Gearagh does show a certain degree of recovery and is more similar to ancient woodland than to the recent secondary. While the total density and size distribution of trees in the secondary woodland is comparable to that of the ancient woodland, these secondary woodlands also have a greater total basal area. All three woodlands types have a similar canopy structure, despite a slightly more complex upper canopy in the ancient woodland; ultimately, this has resulted in similar light regimes in all woodland understoreys. Due to the greater amount of dead stems, the mean basal area and density in the ancient woodland is somewhat lower than in the secondary woodlands.

The Gearagh has seemingly been subject to low-intensity management in the past; there seems to be little or no evidence of planting in the woodland. Smith (1774) described a mature woodland containing oak, ash, hazel, and birch, with an abundance of ferns, similar to the surviving remnants of the ancient stands today. The continuation of this low-level woodland maintenance, along with a favourable climate for tree growth, would have enabled the stem density and basal area of the secondary woodlands to increase to the extent that they are now similar to that of the ancient woodland. The rapid recovery of basal area in the secondary woodlands was also likely facilitated by the species composition of the habitats. *B. pubescens*, for instance, shares characteristics of pioneer species that can easily disperse into open areas (Dyer, 2010); it is relatively short-lived, its seedlings are intolerant of shade and it can grow rapidly in open conditions. *C. avellana*, which commonly forms the understorey in the ancient woodland, often grows to greater heights in the recent secondary than in either the old secondary or ancient stands. It has the ability to produce multiple stems, which may account for its large basal area. It

typically reaches 50-70 years of age, so the majority of trees in the recent secondary would currently be at a mature stage.

While the same tree species occurred in all three woodland types, there was a notable difference in the frequencies of these species. As with other studies, much of the variation in vegetation can be explained by the different disturbance histories of the three woodlands (Bellemare *et al.*, 2002; Flinn and Marks, 2007). The prominence of *Corylus avellana* and *Crataegus monogyna* in the recent secondary indicate that it is still developing from a post-agricultural community; *C. monogyna* and *P. spinosa* in particular are common invaders of cleared and disturbed sites in Ireland (Webb *et al.*, 1996). The vegetation in the old secondary reflects its greater maturity than the recent secondary in which the canopy is more strongly dominated by *B. pubescens* and *Q. robur*. In the old secondary, the understorey includes *C. avellana*, *I. aquifolium*, and *C. monogyna*. Species such as *F. excelsior* and *I. aquifolium* are slower to colonise abandoned agricultural land. Their presence in the old secondary woodland indicates that it is gradually becoming more like the ancient woodland in tree structure and composition. However, the abundance of trees in the smaller size classes in the secondary woodlands indicates that considerable regeneration is continuing in these sites. *Alnus glutinosa*, which had previously been used to classify the Gearagh as a wet woodland (Kelly and Iremonger, 1997), was not recorded in any of the sites; this is more likely to be found near the woodland margins, away from the core of the woodland and the study sites.

This study also indicates that a great deal of dead wood is present in the Gearagh, unlike in other woodlands in Ireland (Sweeney *et al.*, 2010) and Britain (Kirby *et al.*, 1998), where many woodlands have been cut at least once in the past hundred years and large timber removed. The large number of snags recorded suggests that trees in all parts of the woodland often die standing, as has previously been reported for Irish woodlands (Iremonger, 1990). Consequently, spaces in the canopy are formed gradually by the dieback of individuals. This allows more slow-growing suppressed species such as *Q. robur* to subsequently develop. However, there do appear to be slightly more fallen dead trees in the ancient woodland than

in the other sites; these are more likely to create sudden large gaps in the canopy. This explains the continued presence of fast-growing pioneer species such as *B. pubescens* in the ancient woodland which may be found following the creation of a large canopy gap.

The frequent occurrence of multi-stemmed trees in the Gearagh, particularly of *Q. robur* and *F. excelsior* in the ancient woodland, is suggestive of coppicing within the site. Indeed, the majority of ancient woodlands in Ireland either contain coppice stools or some other evidence of a past coppicing regime (Perrin & Daly, 2010). It is likely that many of these woods, including the Gearagh, were managed for coppice around the time of the Irish famine in 1845, which was a period of intense human pressure on the land (Rackham, 1995). The multi-stem growth form may be particularly advantageous to understorey trees such as *C. avellana*, which may persist in that growth form for up to 100 years after cessation of coppicing (Tanentzap *et al.*, 2012). The presence of stumps in the ancient and old secondary woodland may also be evidence of past coppicing and timber harvesting. However, it is also possible that the stand structure is the result of a single past felling event rather than a systematic coppice regime, or may even simply be due to the natural growth and development of trees within the site (Perrin & Daly, 2010).

4.5.2 Ground flora characteristics

Previous studies have indicated that significant differences in vegetation communities exist between ancient and secondary woodlands (Hermy *et al.*, 1999; Vellend, 2003; Hermy and Verheyen, 2007), and that these differences may persist for hundreds or even thousands of years after abandonment (Dupouey *et al.*, 2002; Dambrine *et al.*, 2007). Unlike many studies (Matlack, 1994; Sciama *et al.*, 2009), however, there is no evidence that past land-use has altered the species richness of the Gearagh. Nonetheless, the results here suggest that the four habitats in the study can be described as distinct vegetation types, despite the similarities in species richness (Bossuyt *et al.*, 1999). Although increased species richness is often associated with areas that have been disturbed by human activities, this may depend on the type of past activity under investigation (Koerner *et al.*, 1997; Kopecký and Vojta, 2009). The secondary woodlands of the Gearagh were all

formerly used as cattle pastures, which is regarded as being less disruptive than many other agricultural activities (Flinn and Vellend, 2005). Past human activities can therefore lead, under some circumstances but not others, to an increase in species richness.

Woodland clearance and conversion to agriculture in the 19th century resulted in the severe reduction in local populations of woodland plant species. The current composition and structure of the secondary woodland stands indicate that they have still not fully recovered from this past disturbance event. However, part of the difference in secondary plant communities is also probably a consequence of former colonisation of abandoned fields. Some of the plants in these stands may therefore be relics from earlier stages of the succession from old grassland (Verheyen and Hermy, 2001). Indeed, a number of plants that are associated with the grassland sites were also found in the secondary woodland stands (for example, *Filipendula ulmaria*, *Deschampsia caespitosa*, and *Poa trivialis*). Species with strong competitive ability often rapidly establish, and indeed persist, in secondary woodlands at the expense of ancient woodland species (Baeten *et al.*, 2010a).

Many woodland species that are common in Britain and the rest of Europe are absent from Ireland. As a result, many species are able to occupy a broader ecological range here than they do elsewhere. For instance, many of the species that are found in the secondary woodland are also able to grow in woodland edges, clearings, and even on grassland that has not been intensively used. Consequently, many woodland species can be found in non-woodland habitats (Rackham, 1980). It should also be acknowledged that in the 19th century, woodland species had a greater chance of growing on grassland since land use was less intensive compared to nowadays. In some regions of Europe, woodland plants can be found that grow on meadows or pastures which have not been intensively managed by agriculture, particularly in humid climates (Graae, 2000). Woodland species, including those associated with ancient woodlands, generally have a great potential to survive outside closed woodlands, particularly in humid climates where they are less restricted by drying winds.

4.5.3 Life-history traits

Overall, most of the differences in life-form traits occurred between the woodland and grassland habitats. However, differences in the number and abundance of geophytes between ancient and recent secondary woods have been found before (Graae and Sunde, 2000). These plants are typically poorly adapted to disturbances caused by agricultural activity, but can recover with time. Results here confirm previous studies which showed that geophyte numbers in 150-year-old secondary woods resemble those of ancient woodlands (Verheyen *et al.*, 2003). However, the relative cover values of geophytes in the old secondary have overtaken those of the ancient woodland. This is due mostly to the abundance of just two species, *Anemone nemorosa* and *Allium ursinum*. The latter is able to rapidly develop dense stands due to its ability to store nutrients in its perennial buds and its high assimilation rate (Grubb and Marks, 1989). Once established, this dense cover combined with shading by tree canopy later in the season can exclude most other herb species (Jandl *et al.*, 1997). It is also likely that the increased availability of suitable colonisation sites in the newly established woodlands helped the spread of these species (Bossuyt *et al.*, 1999).

During the period of agricultural land-use, species typical of ancient woodland can be lost from the soil seed bank in only a few decades. Therefore, the capacity of woodland species to colonise secondary woods is most frequently attributed to differing modes of diaspore dispersal (Dzwonko, 1993; Matlack, 1994; Hermy and Verheyen, 2007). However, this is also dependant on the degree of isolation of the secondary woodland from the source population. Results here are consistent with earlier studies which found that woodland connectivity had positive effects on the degree of recovery in the plant community of secondary woodlands (Brunet and Von Oheimb, 1998; Jacquemyn *et al.*, 2001; Singleton *et al.*, 2001; Verheyen *et al.*, 2006). For instance, while barochores and myrmecochores were common in the ancient woodland, they were also frequent in both secondary woodlands. Generally, the abundance of barochores and myrmecochores is lower in isolated secondary stands as it can be difficult for these species to cross unwooded areas (Dzwonko and Loster, 1992; Bellemare *et al.*, 2002; Wulf, 2003). In the case of the

Gearagh, many species associated with the ancient woodland have been able to recolonise at least parts of the secondary woodland, regardless of seed dispersal mode. The proximity of the ancient woodland (less than 1 km from the secondary sites) has therefore reduced the effect of dispersal limitation in the recovery of plant species richness. Indeed, much of the understorey vegetation can be restored within a period of 100 years or so (Bossuyt and Hermy, 2000; Brunet, 2007). The percentage cover of anemochores and hydrochores, which are generally good colonisers, was greater in the grassland and recent secondary sites, reflecting results from previous studies (Verheyen *et al.*, 2006).

Despite the success of these colonisers, many species are less abundant in the secondary woodlands than they are in the ancient woodland. Over 80 % of ancient woodland indicator species show a decrease in indicator value from ancient via old to recent secondary woodland. This confirms that the establishment of many species in new woodlands can be a very slow process (Bossuyt *et al.*, 1999; Honnay *et al.*, 1999; Graae *et al.*, 2003). Consequently, although the new woodland stands regenerated close to ancient woodland, the effects of former land-use still remain visible in the present vegetation. Nonetheless, given enough time, the recovery of woodland communities may be possible in areas adjacent to ancient woodlands (Dzwonko and Gawroński, 1994; Singleton *et al.*, 2001).

Colonisation dynamics may also be influenced by woodland herbs that have been able to persist in local refugia within the agricultural landscape (Bellemare *et al.*, 2002). These include hedgerows and other places under low levels of management, particularly in marginal agricultural land (Doogue and Kelly, 2006). In this study, the occurrence of a number of woodland herbs in the grassland sites, chiefly woodland generalists such as *Ranunculus ficaria* and *Filipendula ulmaria*, suggests that they are able to survive outside of the woodland environment. The persistence of such species may have greatly increased rates of recolonisation in the secondary woodlands.

4.5.4 Ellenberg indicator values

Despite the consensus of several authors that the association of certain plants with ancient woodland is due to dispersal limitation (Matlack, 1994; Brunet and Von Oheimb, 1998; Ehrlén and Eriksson, 2000), there are several possible alternative explanations. Differences in local environmental conditions and species interactions in secondary woodlands may also be important (Flinn and Vellend, 2005). Lasting soil differences in particular could contribute to reductions in the frequency and performance of some species (Fraterrigo *et al.*, 2009) and favour other competitive open-habitat species (Hermy *et al.*, 1999; Verheyen and Hermy, 2001; De Keersmaecker *et al.*, 2004). Changes in soil properties may even affect the interactions amongst woodland species (Baeten *et al.*, 2010b), thereby modifying the structure of plant communities. In this study, it is unlikely that the sites which were formerly preferred for agricultural land originally had different soils and topography; all the sites are located within 1 km of each other and the original woodland clearance was carried out in accordance with land ownership boundaries rather than preferential site conditions.

Ellenberg indicator values have often been used to draw conclusions as to site conditions due to significant correlations between indicator values and the measured variables (Wulf, 2003). The results from this study show that the ancient woodland contains species that are tolerant of shade and acidity, and which avoid sites with high nitrogen content. This confirms previous accounts of ancient woodland indicator species from several authors (Koerner *et al.*, 1997; Hermy *et al.*, 1999; Wulf, 2003). In this respect, the species associated with the ancient woodland may also be regarded as stress-tolerant plants. Conversely, the higher light, pH and nitrogen indicator values of the secondary woodland indicators suggests that these plants, particularly those of the recent secondary woodland, have more in common with the grassland species, which are typical plants of open habitats rather than woodlands. These differences might have played a role in plant establishment after agricultural abandonment.

The anastomosing channels of the river Lee that flow through the Gearagh means that it can be subject to flooding, particularly during winter. This explains the abundance of species with moisture indicator values of 5, 6 or 7 that are found throughout the woodland. However, it appears that the hydrology of the site is sensitive to past disturbances, which have ultimately resulted in the proliferation of plant species in the secondary woodlands and grasslands that are particularly tolerant of poorly drained soils. A reduction in transpiration demand of the vegetation has led to a further increase in wetness in the grassland sites. However, despite these changes, there were few species in the ancient woodland (for instance, *Galium odoratum* and *Hyacinthoides non-scripta*) that were not recorded in the secondary woodlands (Matlack, 1994; Bossuyt *et al.*, 1999). Nonetheless, ancient woodland species occur less frequently in the secondary sites; this may be because the soils are unsuitable for growth, or because these species are out-competed by other moisture-tolerant plant species. While other studies have focused on changes in soil chemistry (Honnay *et al.*, 1999; Verheyen and Hermy, 2001), in this study it appears the creation of a poorly-draining soil as a result of past land-use can have a lasting effect on the plant community. These conditions are easily created in Ireland, where high rainfall leads to elevated water-tables in the winter and early spring. Many other secondary woodlands in Europe developed on moist or wet grasslands during the 19th century; the species associated with these sites are also often tolerant of high soil moisture levels (Wulf, 2003).

The ancient woodland has a greater abundance of species that are typical of woods on free-draining base-rich soils, although many of these species are tolerant of acidity. Nonetheless, the abundance of moisture-tolerant species in the secondary woodlands means that they form an important component of Ireland's wetland wood diversity, many of which have developed spontaneously within the past 150 years (Kelly and Iremonger, 1997). The slightly wetter conditions of both secondary woodlands are confirmed by the presence of *Salix cinerea* spp. *oleifolia*, which is absent from the ancient woodland sites. Past land-use, by altering sensitive environmental conditions (in this case, the hydrological balance of the soil), can lead to considerable variation in floristic composition, even on a local scale.

4.6. Conclusions

Past agricultural activity strongly modified plant species composition, to the extent that these differences are still significant over 150 years later. While there is little variation in the species richness, life-form spectra, or dispersal modes, the persistent differences in community composition are most likely due to establishment limitations as a result of altered environmental conditions. Even typically poorly dispersed taxa are able to recolonise secondary woodlands given enough time, as long as they are located near a source population of ancient woodland. It may also be possible for woodland flora to persist among refugia such as hedgerows, particularly in low-intensity landscapes. This study shows that the restoration of a reasonable amount of Irish woodland flora is possible in sites close to source populations, although it must be acknowledged that past land-use has likely altered site conditions to some degree.

4.7. References

- Akumu, C.E. (2006) *Conservation Assessment of Plant Communities in a Flooded Riverine Forest, the Gearagh*. M.Sc. thesis, University College Cork.
- Baeten, L., Hermy, M., Van Daele, S. & Verheyen, K. (2010a) Unexpected understorey community development after 30 years in ancient and post-agricultural forests. *Journal of Ecology*, **98**, 1447-1453.
- Baeten, L., Vanhellemont, M., De Frenne, P., De Schrijver, A., Hermy, M. & Verheyen, K. (2010b) Plasticity in response to phosphorus and light availability in four forest herbs. *Oecologia*, **163**, 1021-1032.
- Bellemare, J., Motzkin, G. & Foster, D. (2002) Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. *Journal of Biogeography*, **29**, 1401-1420.
- Bossuyt, B. & Hermy, M. (2000) Restoration of the understorey layer of recent forest bordering ancient forest. *Applied Vegetation Science*, **3**, 43-50.
- Bossuyt, B., Hermy, M. & Deckers, J. (1999) Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. *Journal of Ecology*, **87**, 628-638.

- Brunet, J. (2007) Plant colonization in heterogeneous landscapes: an 80-year perspective on restoration of broadleaved forest vegetation. *Journal of Applied Ecology*, **44**, 563-572.
- Brunet, J. & Von Oheimb, G. (1998) Migration of vascular plants to secondary woodlands in southern Sweden. *Journal of Ecology*, **86**, 429-438.
- Dambrine, E., Dupouey, J.L., Laut, L., Humbert, L., Thinon, M., Beaufils, T. & Richard, H. (2007) Present forest biodiversity patterns in France related to former Roman agriculture. *Ecology*, **88**, 1430-1439.
- De Keersmaeker, L., Martens, L., Verheyen, K., Hermy, M., De Schrijver, A. & Lust, N. (2004) Impact of soil fertility and insolation on diversity of herbaceous woodland species colonizing afforestations in Muizen forest (Belgium). *Forest Ecology and Management*, **188**, 291-304.
- Diekmann, M. (2003) Species indicator values as an important tool in applied plant ecology-a review. *Basic and Applied Ecology*, **4**, 493-506.
- Doogue, D. & Kelly, D.L. (2006) Woody plant assemblages in the hedges of eastern Ireland: products of history or ecology? *Biology and Environment: Proceedings of the Royal Irish Academy*, **106B**, 237-250.
- Dufrene, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345-366.
- Dupouey, J.L., Dambrine, E., Laffite, J.D. & Moares, C. (2002) Irreversible impact of past land use on forest soils and biodiversity. *Ecology*, **83**, 2978-2984.
- Dyer, J.M. (2010) Land-use legacies in a central Appalachian forest: differential response of trees and herbs to historic agricultural practices. *Applied Vegetation Science*, **13**, 195-206.
- Dzwonko, Z. (1993) Relations between the floristic composition of isolated young woods and their proximity to ancient woodland. *Journal of Vegetation Science*, **4**, 693-698.
- Dzwonko, Z. & Gawroński, S. (1994) The role of woodland fragments, soil types, and dominant species in secondary succession on the western Carpathian foothills. *Plant Ecology*, **111**, 149-160.

- Dzwonko, Z. & Loster, S. (1992) Species richness and seed dispersal to secondary woods in southern Poland. *Journal of Biogeography*, **19**, 195-204.
- Ehrlén, J. & Eriksson, O. (2000) Dispersal limitation and patch occupancy in forest herbs. *Ecology*, **81**, 1667-1674.
- Fitter, A. & Peat, H. (1994) The ecological flora database. *Journal of Ecology*, **82**, 415-425.
- Flinn, K.M. & Marks, P.L. (2007) Agricultural legacies in forest environments: tree communities, soil properties, and light availability. *Ecological Applications*, **17**, 452-463.
- Flinn, K.M. & Vellend, M. (2005) Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and the Environment*, **3**, 243-250.
- Fraterrigo, J.M., Pearson, S.M. & Turner, M.G. (2009) The response of understory herbaceous plants to nitrogen fertilization in forests of different land-use history. *Forest Ecology and Management*, **257**, 2182-2188.
- Frazer, G.W., Canham, C.D. & Lertzman, K.P. (2000) Gap light analyzer (GLA), Version 2.0: image processing software to analyze true-color, hemispherical canopy photographs. *Bulletin of the Ecological Society of America*, **81**, 191-197.
- Gerhardt, F. & Foster, D.R. (2002) Physiographical and historical effects on forest vegetation in central New England, USA. *Journal of Biogeography*, **29**, 1421-1437.
- Graae, B.J. (2000) The effect of landscape fragmentation and forest continuity on forest floor species in two regions of Denmark. *Journal of Vegetation Science*, **11**, 881-892.
- Graae, B.J. & Sunde, P.B. (2000) The impact of forest continuity and management on forest floor vegetation evaluated by species traits. *Ecography*, **23**, 720-731.
- Graae, B.J., Sunde, P.B. & Fritzboøger, B. (2003) Vegetation and soil differences in ancient opposed to new forests. *Forest Ecology and Management*, **177**, 179-190.

- Grubb, P.J. & Marks, P.L. (1989) Spring flowers of eastern North American and European deciduous forests. *Plants Today*, **2**, 89-96.
- Hermý, M., Honnay, O., Firbank, L., Grashof-Bokdam, C. & Lawesson, J.E. (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation*, **91**, 9-22.
- Hermý, M. & Verheyen, K. (2007) Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. *Ecological Research*, **22**, 361-371.
- Hill, M.O., Mountford, J.O., Roy, D.B. & Bunce, R.G.H. (1999) *ECOFAC 2a Technical Annex - Ellenberg's Indicator Values for British Plants*. Department of the Environment, Transport and the Regions (DETR), Norwich, UK, pp. 47.
- Honnay, O., Hermý, M. & Coppin, P. (1999) Impact of habitat quality on forest plant species colonization. *Forest Ecology and Management*, **115**, 157-170.
- Inghe, O. & Tamm, C.O. (1985) Survival and flowering of perennial herbs IV: the behaviour of *Hepatica nobilis* and *Sanicula europaea* on permanent plots during 1943-1981. *Oikos*, **45**, 400-420.
- Iremonger, S.F. (1990) A structural analysis of three Irish wooded wetlands. *Journal of Vegetation Science*, **1**, 359-366.
- Jacquemyn, H., Butaye, J. & Hermý, M. (2001) Forest plant species richness in small, fragmented mixed deciduous forest patches: the role of area, time and dispersal limitation. *Journal of Biogeography*, **28**, 801-812.
- Jandl, R., Kopeszki, H. & Glatzel, G. (1997) Effect of a dense *Allium ursinum* (L.) ground cover on nutrient dynamics and mesofauna of a *Fagus sylvatica* (L.) woodland. *Plant and Soil*, **189**, 245-255.
- Kelly, D.L. (2004) Irish native woodland plant communities. In: *Ireland's Native Woodlands* (eds C. Doyle & D. Little), pp. 91-100. Woodlands of Ireland, Galway, Ireland.
- Kelly, D.L. (2005) Woodland on the western fringe: Irish oakwood diversity and the challenges of conservation. *Botanical Journal of Scotland*, **57**, 21-40.

- Kelly, D.L. & Iremonger, S.F. (1997) Irish wetland woods: the plant communities and their ecology. *Biology and Environment: Proceedings of the Royal Irish Academy*, **97B**, 1-32.
- Kirby, K., Reid, C., Thomas, R. & Goldsmith, F. (1998) Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain. *Journal of Applied Ecology*, **35**, 148-155.
- Koerner, W., Dupouey, J.L., Dambrine, E. & Benoit, M. (1997) Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. *Journal of Ecology*, **85**, 351-358.
- Kopecký, M. & Vojta, J. (2009) Land use legacies in post-agricultural forests in the Doupovské Mountains, Czech Republic. *Applied Vegetation Science*, **12**, 251-260.
- Kruskal, J.B. (1964) Nonmetric multidimensional scaling: a numerical method. *Psychometrika*, **29**, 115-129.
- Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell Publishing, Malden, USA, pp. 256.
- Matlack, G.R. (1994) Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology*, **75**, 1491-1502.
- McCune, B. & Grace, J.B. (2002) *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, USA, pp. 300.
- McCune, B. & Mefford, M.J. (2006) *PC-ORD: Multivariate Analysis of Ecological Data, Version 5*. MjM Software Design, Gleneden Beach, USA.
- Mielke, P. & Berry, K. (2007) *Permutation Methods: A Distance Function Approach*, Second edn. Springer Verlag, New York, USA, pp. 439.
- Perrin, P.M. & Daly, O.H. (2010) *A Provisional Inventory of Ancient and Long-Established Woodland in Ireland*. Irish Wildlife Manuals, No. 46. National Parks and Wildlife Service, Department of the Environment, Heritage and Local Government, Dublin, Ireland, pp. 71.
- Peterken, G.F. & Game, M. (1984) Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *The Journal of Ecology*, **72**, 155-182.

- Petit, S., Griffiths, L., Smart, S.S., Smith, G.M., Stuart, R.C. & Wright, S.M. (2004) Effects of area and isolation of woodland patches on herbaceous plant species richness across Great Britain. *Landscape Ecology*, **19**, 463-471.
- Rackham, O. (1980) *Ancient Woodland: Its History, Vegetation and Uses in England*. Edward Arnold, London, UK, pp. 624.
- Rackham, O. (2005) Questions to ask of Irish native woodland. In: *Ireland's Native Woodlands* (eds C. Doyle & D. Little), pp. 11-18. Woodlands of Ireland, Galway, Ireland.
- Sciama, D., Augusto, L., Dupouey, J.-L., Gonzalez, M. & Moares Domínguez, C. (2009) Floristic and ecological differences between recent and ancient forests growing on non-acidic soils. *Forest Ecology and Management*, **258**, 600-608.
- Singleton, R., Gardescu, S., Marks, P.L. & Geber, M.A. (2001) Forest herb colonization of postagricultural forests in central New York State, USA. *Journal of Ecology*, **89**, 325-338.
- Smith, C. (1774) *The Ancient and Present State of the County and City of Cork: Containing a Natural, Civil, Ecclesiastical, Historical, and Topographical Description Thereof*. W. Wilson, Dublin, Ireland, pp. 443.
- Sweeney, O.F.M., Martin, R.D., Irwin, S., Kelly, T.C., O'Halloran, J., Wilson, M.W. & McEvoy, P.M. (2010) A lack of large-diameter logs and snags characterises dead wood patterns in Irish forests. *Forest Ecology and Management*, **259**, 2056-2064.
- Tanentzap, A.J., Mountford, E.P., Cooke, A.S. & Coomes, D.A. (2012) The more stems the merrier: advantages of multi-stemmed architecture for the demography of understorey trees in a temperate broadleaf woodland. *Journal of Ecology*, **100**, 171-183.
- Van Oijen, D., Feijen, M., Hommel, P., den Ouden, J., de Waal, R. & Hermy, M. (2005) Effects of tree species composition on within-forest distribution of understorey species. *Applied Vegetation Science*, **8**, 155-166.
- Vellend, M. (2003) Habitat loss inhibits recovery of plant diversity as forests regrow. *Ecology*, **84**, 1158-1164.

- Verheyen, K., Bossuyt, B., Honnay, O. & Hermy, M. (2003) Herbaceous plant community structure of ancient and recent forests in two contrasting forest types. *Basic and Applied Ecology*, **4**, 537-546.
- Verheyen, K., Fastenaekels, I., Vellend, M., De Keersmaeker, L. & Hermy, M. (2006) Landscape factors and regional differences in recovery rates of herb layer richness in Flanders (Belgium). *Landscape Ecology*, **21**, 1109-1118.
- Verheyen, K. & Hermy, M. (2001) An integrated analysis of the spatio-temporal colonization patterns of forest plant species. *Journal of Vegetation Science*, **12**, 567-578.
- Webb, D.A., Parnell, J. & Doogue, D. (1996) *An Irish Flora*, 7th edn. Dundalgan Press, Dundalk, Ireland, pp. 337.
- Wulf, M. (1997) Plant species as indicators of ancient woodland in northwestern Germany. *Journal of Vegetation Science*, **8**, 635-642.
- Wulf, M. (2003) Preference of plant species for woodlands with differing habitat continuities. *Flora - Morphology, Distribution, Functional Ecology of Plants*, **198**, 444-460.
- Wulf, M. (2004) Plant species richness of afforestations with different former use and habitat continuity. *Forest Ecology and Management*, **195**, 191-204.

CHAPTER 5

THE IMPACTS OF LAND-USE HISTORY ON THE SEED BANK AND GERMINATION POTENTIAL OF WOODLAND PLANTS IN THE GEARAGH

5.1 Abstract

Past land-use has been shown to have enduring effects on the distribution and abundance of woodland plants in the Gearagh. The differences in community composition between the ancient and secondary woodland sites may be due to the fact that most woodland plants are slow to colonise new sites. At the same time, species associated with more open habitats and woodland edges are thought to have greater colonisation capacities; previous results have shown these species to be more common in younger woodlands of the Gearagh. In this study, the limitations on the colonisation capacity of woodland plants as a contributor to differences in vegetation types between ancient and secondary sites was examined by: (i) investigating the soil seed banks of ancient and secondary woodlands; and (ii) comparing the recruitment ability of three woodland plants (*Anemone nemorosa*, *Hyacinthoides non-scripta*, *Primula vulgaris*) during two growing seasons by means of a seed sowing experiment in ancient and secondary woodland. The soil seed bank study confirmed that most woodland plants did not form a persistent seed bank, while many seeds that were associated with previous, non-woodland, land-use still survived in the secondary woodland. In the seed sowing experiment, while all three woodland plant species successfully recruited new individuals from seed, only a small fraction of the introduced seeds actually germinated after two growing seasons in all woodland habitats. However, each species responded differently to the effects of past land-use. While *Hyacinthoides non-scripta* germinated equally well regardless of woodland history, fewer *Primula vulgaris* seedlings emerged in the secondary woodlands. These results confirm the view of woodland plant community assembly as a two-stage process in which limited seed availability followed by low recruitment reduces colonisation for certain species. Overall, the results indicate that the ability of plants to recruit successfully in woodlands is affected by complex interactions between land-use legacies and species-specific traits.

5.2 Introduction

Deforestation and conversion to agricultural land can have a severe negative impact on woodland plant communities. Even if woodland is restored, numerous studies

have shown that secondary woodland plant communities can still differ considerably from those of undisturbed ancient woodlands (Peterken & Game, 1984; Flinn & Vellend, 2005; Hermy & Verheyen, 2007). These differences are most apparent when the secondary woodlands are isolated from source populations in ancient woodlands; consequently, these changes in community composition are thought to be primarily due to the limited colonisation capacity of many woodland plants (Matlack, 1994; Hermy *et al.*, 1999; Hermy & Verheyen, 2007). This ability to colonise a new site is determined largely by the capability of particular species to disperse in space and/or time (Hermy & Verheyen, 2007). Spatial dispersal refers to the transport of seeds to new sites away from the parent plants, while temporal dispersal corresponds to the ability of a species to form seed banks in the soil. However, few studies have examined how both of these aspects might jointly affect the establishment of plant communities in ancient and secondary woodlands.

The seed bank is generally acknowledged to consist of two types of seed: transient seeds, which persist in the soil for less than one year, and persistent seeds, which can remain viable for much longer (Thompson *et al.*, 1998). Previous research has shown seed size to be negatively correlated with seed longevity in the soil (Bekker *et al.*, 1998; Hodkinson *et al.*, 1998). Large seeds tend to form transient seed banks, partly as their large size makes them more vulnerable to predation (Thompson, 1987). In order to avoid being consumed, it is necessary for large seeds to germinate quite rapidly. Their large stores of resources ensures successful recruitment even under unfavourable or stressful environmental conditions (Eriksson, 1995). Persistent seed banks, on the other hand, are generally composed of smaller seeds. Small seeds avoid detection by predators by becoming buried in the soil (Thompson *et al.*, 1993), where they remain until germination conditions improve.

These buried seeds can play an important role in the natural regeneration of certain plant communities after disturbance (Bossuyt & Honnay, 2008). Accordingly, if the seeds of woodland plant species are able to form persistent seed banks, then they might be able to avoid the adverse effects of temporary agricultural use (Hermy & Verheyen, 2007). Therefore, dispersal in time through seed bank formation could

be a useful strategy by which woodland plants could endure disturbances caused by agriculture. However, this depends both on the duration and intensity of the disturbance event, as well as plant-specific traits relating to dormancy and germination responses. In addition, it is generally accepted that previous land-use and woodland management can greatly alter the composition of the soil seed bank through the introduction of seeds of new species (Bossuyt & Hermy, 2001) and the creation of conditions that modify seed persistence and senescence (Schmidt *et al.*, 2009; Plue *et al.*, 2010b). However, uncertainties remain as to for how long these differences persist. Some studies indicate that the seed banks of secondary woodlands resemble those of ancient woodlands after only 50-100 years (Bossuyt *et al.*, 2002), while others have found distinct differences hundreds (Plue *et al.*, 2009) and even thousands (Plue *et al.*, 2008) of years after human occupation.

Plant species are known to employ a variety of different strategies to facilitate the successful recruitment of new individuals into the population (Baskin & Baskin, 2001). These different strategies are often cited as one of the main reasons for the changes in vegetation communities between woodlands with contrasting land-use histories (Eriksson & Ehrlén, 1992; Baeten *et al.*, 2009b). Many woodland species have the ability for vegetative propagation, while several studies have shown that they are only able to disperse their seeds over short distances (Matlack, 1994; Brunet & Von Oheimb, 1998; Hermy *et al.*, 1999). This has led to the conclusion that dispersal limitation largely accounts for the differences in plant communities between ancient and secondary woodlands (Bradshaw, 2004; Flinn & Vellend, 2005; Hermy & Verheyen, 2007). Indeed, numerous studies have shown that species occurrence decreases with increasing distance from the seed source (Peterken & Game, 1984; Matlack, 1994; Brunet & Von Oheimb, 1998; Verheyen & Hermy, 2001).

However, recruitment may also be constrained by numerous factors that affect the survival of individuals through successive life stages (see Fig. 5.1). Historical land use can result in highly persistent changes in abiotic (e.g. phosphorus availability, pH, and soil moisture content) and biotic (e.g. the diversity and abundance of soil

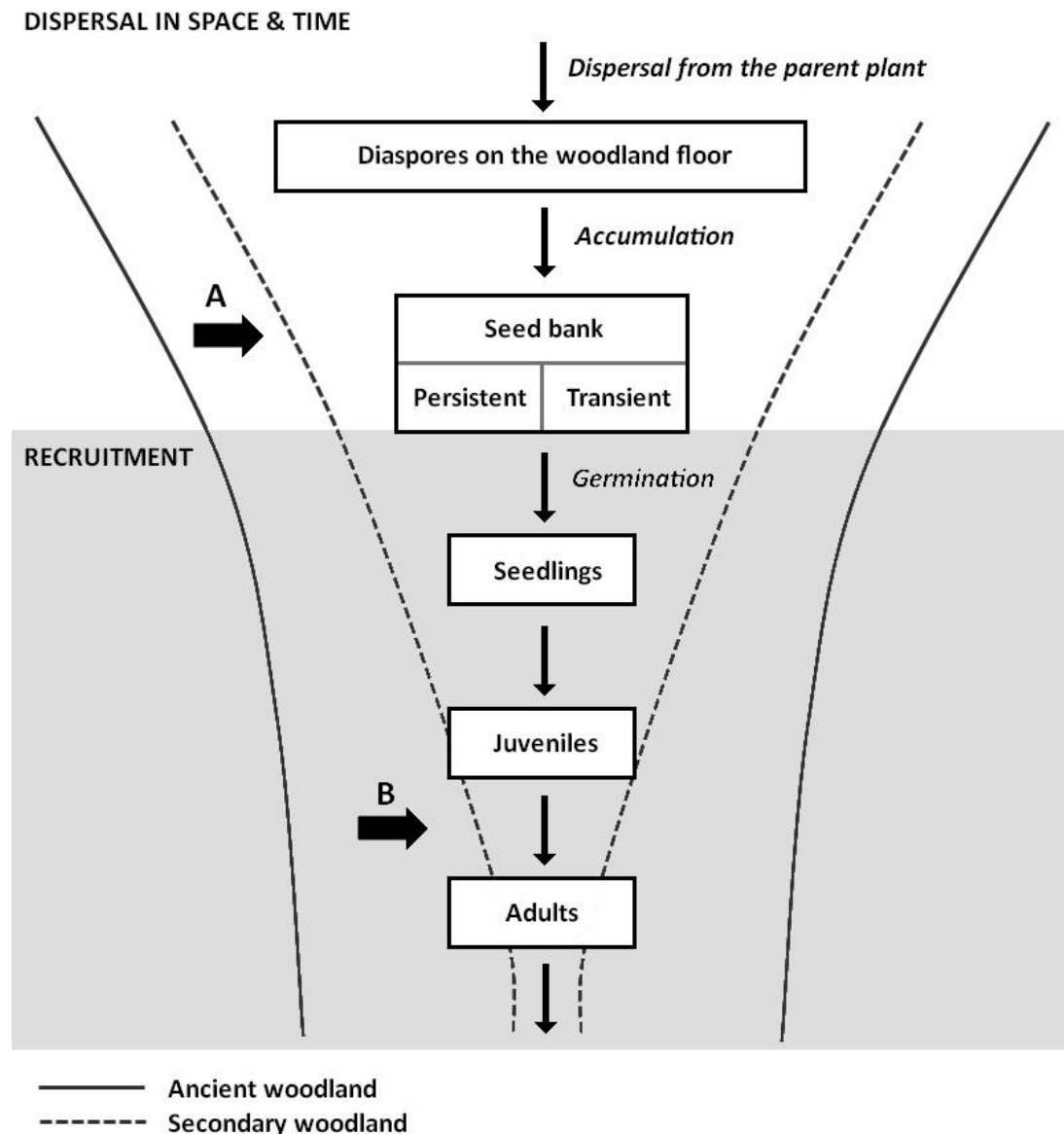


Fig. 5.1 A conceptual diagram showing the bottle-neck model of plant colonisation in ancient and secondary woodland. After dispersal from the parent plant, seeds are incorporated into a seed bank, which may be persistent or transient. From that, seed may germinate and develop into juvenile and then adult plants. The decreasing number of individuals through the various life stages due to mortality and predation is represented by the funnel-shaped lines for both the ancient and secondary woodland. Dispersal limitation (arrow A) causes lower seed availability in the secondary woodland. Establishment limitation, caused by altered environmental conditions, may cause further loss of individuals in the secondary woodland (arrow B). The strength of the environmental effect may vary between species and is highly dependent on the nature of the former land-use (adapted from Hermy & Verheyen, 2007).

seed predators and soil engineers) soil conditions. Such changes in local conditions are likely to further hinder the establishment of woodland species that are adapted to stable environmental conditions (Milcu *et al.*, 2006; Baeten *et al.*, 2010). Furthermore, these changes may actually promote the growth of more disturbance-tolerant species, which may compete with woodland species for new establishment sites (Bossuyt *et al.*, 1999; Endels *et al.*, 2004). Several studies have recorded either an improvement or deterioration in adult plant performance in secondary woodlands (Endels *et al.*, 2004; Vellend, 2005; Flinn, 2007), suggesting that altered environmental conditions can indeed affect the ability of certain plants to recruit successfully (Honnay *et al.*, 1999; Baeten *et al.*, 2009b; Fraterrigo *et al.*, 2009). However, the effects of these land-use legacies can be complex, and depend on a variety of interacting factors, including the traits of the particular species involved as well as the type of environmental changes that have occurred (Baeten *et al.*, 2009a).

In this study, the soil seed banks of the four habitat types in the Gearagh woodland were quantified, by assessing the experimental germination of dormant seeds in a polytunnel, so as to determine the pre-existing seed composition in the study sites (Clark *et al.*, 2007). The *in situ* seed germination potential was assessed by experimentally introducing seeds of three woodland herb species (*Anemone nemorosa*, *Hyacinthoides non-scripta*, and *Primula vulgaris*), none of which tend to form a persistent seed bank (Van der Veken *et al.*, 2007; Jacquemyn *et al.*, 2009; De Frenne *et al.*, 2010). The aims of the study were to determine: (i) the differences in seed bank composition between the ancient, secondary and grassland sites; (ii) the similarity between the seed bank and the existing aboveground vegetation in each site; (iii) the recruitment success of the introduced woodland seeds; (iv) the relative importance of dispersal versus establishment limitation in the ancient and secondary woodland; and (v) potential implications of changes in seed bank composition and seedling recruitment for woodland community development.

5.3 Materials and methods

5.3.1 Study site

The seed bank study and the seed sowing experiment were both carried out in the Gearagh, an area of native deciduous woodland along the River Lee in southwest Ireland. The composition of the seed bank was assessed in a total of 20 sites, five each of ancient woodland, old secondary woodland, recent secondary woodland, and grassland. The seed sowing experiment was only carried out in the woodland sites only. A full description of the study sites can be found in previous chapters (See Sections 3.3.1 and 3.3.2).

5.3.2 Soil seed bank sampling

The composition of the soil seed bank was determined by quantifying seedling emergence from soil samples taken from each habitat type. Sampling for the study was carried out in spring as this is generally regarded as the best sampling period for seed bank analysis (Bossuyt *et al.*, 2002). Three replicate plots of 1 m² were randomly located in each of the 20 study sites (Fig. 5.2). Eight soil cores of 3.5 cm diameter were taken at random from each plot to a depth of 20 cm, after removal of the litter layer. The eight samples were divided into two depths (0-10 cm and 10-20 cm) and the soil from each depth was pooled per plot. This provided a total of 120 soil samples (4 habitats × 5 sites × 3 replicates × 2 depths) and each sample equated to approximately one kilogram fresh weight of soil.

The composition of the soil seed bank was analysed using the concentration method of Ter Heerdt *et al.* (1996). Each soil sample was washed through a coarse (4 mm mesh width) and a fine (0.2 mm mesh width) sieve; this removed all coarse and fine mineral and organic particles, including root and plant material from the samples. The concentrated samples were then mixed with water and spread out into a 2 cm thick layer on trays (38 cm × 24 cm) filled with a 3 cm thick layer of sterilised potting soil (a 50:50 mixture of John Innes No. 1 compost and peat-based compost). A 1 cm layer of vermiculite was placed on the bottom of the tray to improve aeration and reduce waterlogging. The trays were randomly placed in a polytunnel which exposed the seeds to temperature conditions similar to those encountered in the field, with reduced risk of non-target seeds being blown onto

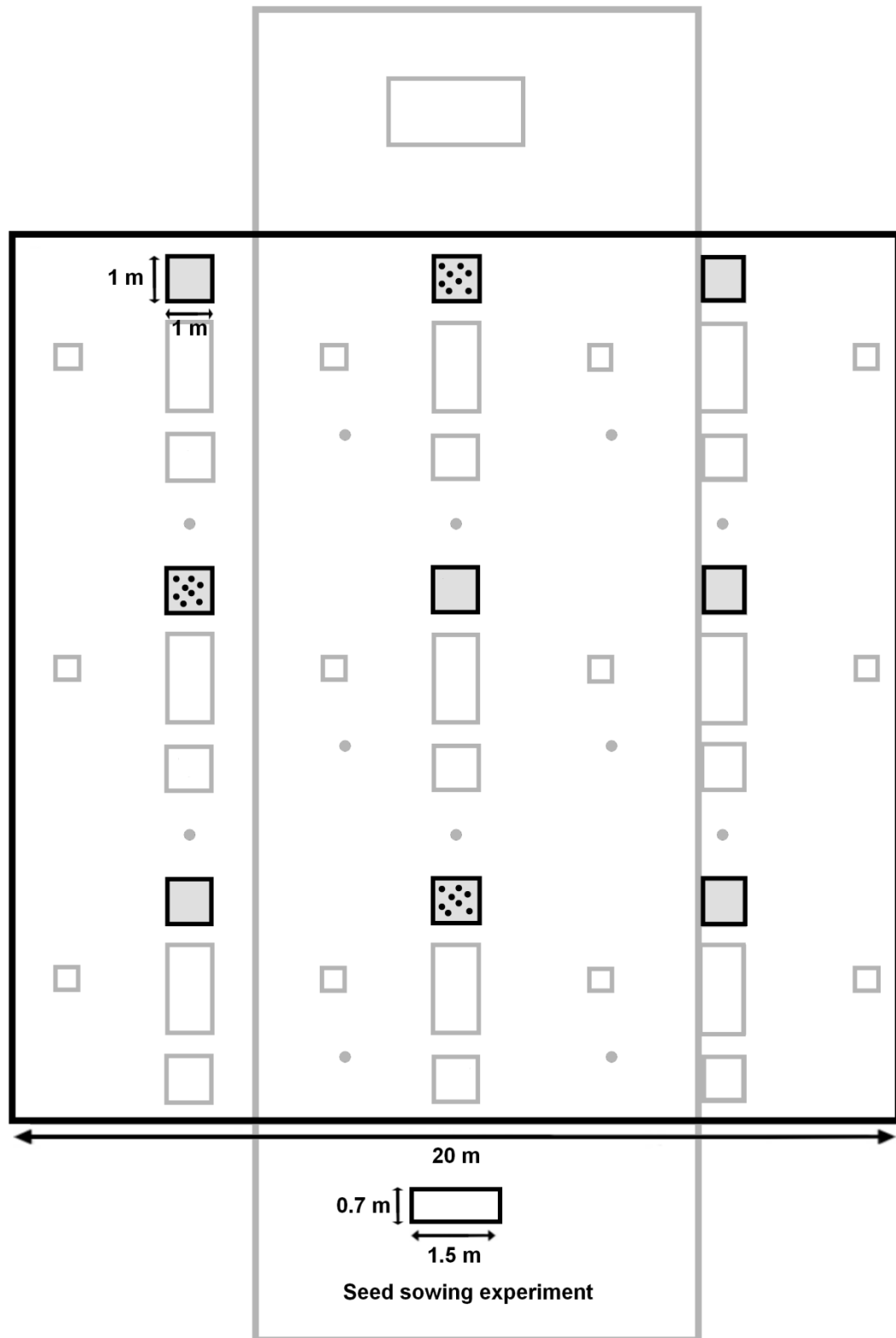


Fig. 5.2 Design of one sampling site, i.e. one of the replicate study sites, with the location of the seed bank sampling plots (grey plots) and the seed sowing experiment outlined in black. The sampling designs used in other sections of the thesis are outlined in grey; see Figs. 3.2, 4.1, and 6.1 for further details. Three of the nine 1 m × 1 m plots were randomly chosen for seed bank sampling, from which eight soil cores were collected (dotted plots).

the trays. Fifteen control trays filled with sterilised potting soil were randomly placed amongst the sample trays; there were used to test for germination of incidental wind-borne seeds. Four taxa were found in the control trays and were excluded from further analyses. All trays were watered regularly.

Seedlings were identified as soon as possible after germination and removed from the trays. Unidentifiable seedlings were removed to a separate pot and allowed to grow until they could be successfully identified. Counts were made on at least a weekly basis over a 10-month period in 2008-2009. If no further seedling emergence was recorded for more than one week, then all the soil samples were allowed to dry out. They were then disturbed and crumbled, before being supplied with more water so as to stimulate germination of the remaining seeds. All seed densities were summed and expressed as seeds per m². Aboveground vegetation was also recorded from the same sites that the soil samples were taken from. Nine 1 × 2 m plots were established within each of the sites and a list of all vascular plant species occurring in each plot was recorded. Further details on the methods used to sample the vegetation are provided in Chapter 4.

5.3.3 Seed germination and survival

Three perennial plants that are common to Irish woodlands were introduced as seeds to the study sites in the autumn of 2008. Details on species traits, including mean seed mass, are given in Table 5.1. Mean seed mass was determined by weighing sets of 100 seeds per species. All three species, particularly *A. nemorosa*

Table 5.1 Woodland plant species included in the study. For each species, the mean seed mass (mg), life-form, seed production, dispersal mode, and leaf phenology are indicated.

Species	Seed mass (mg)	Life-form	Seed production per plant	Dispersal mode	Leaf phenology
<i>Anemone nemorosa</i>	2.10	Geophyte	1-50	Myrmecochory	Vernal
<i>Hyacinthoides non-scripta</i>	8.50	Geophyte	10-100	Barochory	Vernal
<i>Primula vulgaris</i>	0.77	Hemicryptophyte	100-1000	Myrmecochory	Evergreen

and *H. non-scripta*, have proven to be slow-colonising woodland herbs (Verheyen *et al.*, 2003). However, *A. nemorosa* is abundant throughout the Gearagh, while *H. non-scripta* is largely confined to the ancient woodland sites and *P. vulgaris* is an indicator of secondary woodland (Chapter 4). *A. nemorosa* frequently spreads clonally by means of rhizomes (De Frenne *et al.*, 2010), while dispersal by seeds is the main recruitment mechanism of *H. non-scripta* and *P. vulgaris* (Van der Veken *et al.*, 2007; Jacquemyn *et al.*, 2009). Viable seeds of all three species tend to germinate within a year.

Seeds of all three study species were collected from sites within the Gearagh between spring and summer of 2008. Six plots (0.7 m × 0.25 m) were established in each of the woodland study sites, and were permanently marked with wooden stakes. Each of these plots was further divided into three subplots (0.25 m × 0.25 m); see Fig. 5.3. Surface litter was cleared from the experimental sites and seeds of each of the study species were randomly introduced into one such subplot per plot. All species were sown evenly by hand at a density of 400 seeds per m². No seeds were sown into the other subplots, allowing assessment of natural germination of seedlings. The cover of vascular plants, bare ground, bryophytes, and litter were assessed prior to seed sowing (Table 5.2).

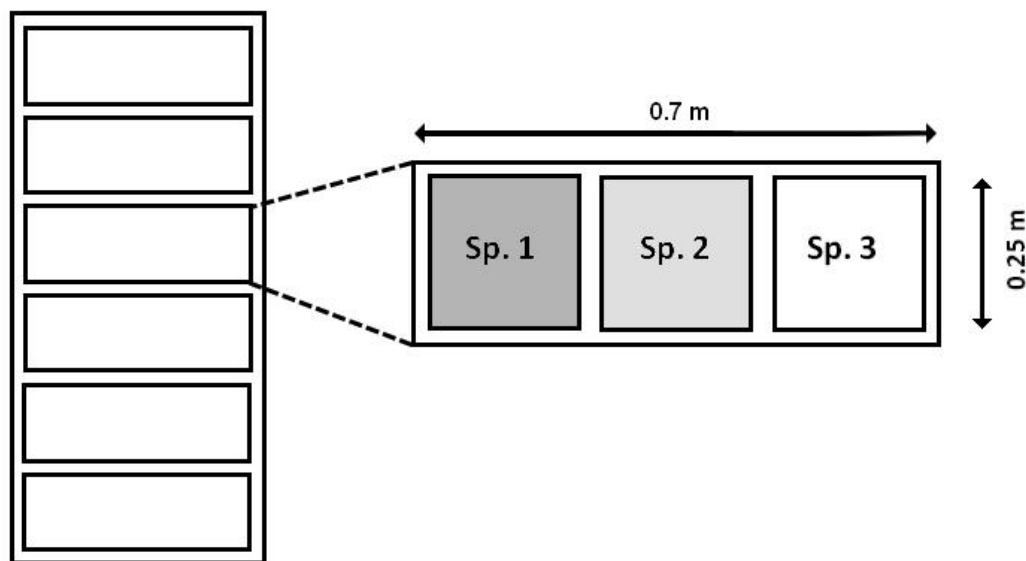


Fig. 5.3 Design of one experimental block, i.e. woodland site. The three species were introduced into the three subplots (Sp. 1-3) as seeds.

Table 5.2 Characterisation of the experimental sites in the ancient, old secondary, and recent secondary woodland stands. Percent cover (mean of 30 subplots \pm standard error) of four ground cover types in the three woodland stands is given. The total ground cover may be over 100 % due to overlap of ground cover types.

Ground cover	Ancient woodland	Old secondary woodland	Recent secondary woodland
Bare ground	1.9 \pm 0.54	7.2 \pm 0.98	6.4 \pm 1.16
Bryophytes	16.6 \pm 1.59	32.8 \pm 4.29	22.5 \pm 3.9
Vascular plants	48.7 \pm 4.24	52.7 \pm 4.83	48.0 \pm 3.41
Litter	55.33 \pm 4.23	36.67 \pm 4.13	45.0 \pm 3.64

To evaluate the germination and survival of the seeds, plots were monitored over a period of two years. This resulted in six census times from both Year 1 and Year 2 which were undertaken from late February to early June in both 2009 and 2010. The numbers of seedlings were counted in each of the three subplots per plot on each sampling date. The emergence of seedlings in the other subplots was also monitored in order to control for the natural dispersion of seedlings into the experimental plots and germination from the seed bank (Reader, 1993; Verheyen & Hermy, 2004). Only for *A. nemorosa* did this correction appear necessary.

5.3.4 Data analysis

Seed bank data were summarised in a number of different ways. Firstly, differences in the total number of species that germinated in each of the four habitat types were tested using a one-way chi-squared test. Next, the species richness, the total seed density, and the density of *Juncus effusus* seeds were calculated. In addition, indicator values for light (*L*), soil moisture (*F*), soil pH (*R*), and soil nitrogen content (*N*) were calculated in order to assess the ecological profile of the seed banks. These were assessed using Ellenberg's scoring system, as modified for British and Irish vegetation (Hill *et al.*, 1999). The mean indicator value of all species present at a site was calculated for each of the four types of indicator. The relative density of large-seeded (> 1 mg) and small-seeded (< 1 mg) species was also calculated. Data on mean seed mass were obtained from the Ecological Flora Database (Fitter & Peat, 1994). *Juncus effusus* was omitted from these calculations, as the data would

otherwise be skewed in favour of small-seeded species. Differences in these variables were tested using a two-way analysis of variance (ANOVA) with habitat (ancient, old secondary, recent secondary or grassland) and depth (0-10 cm or 10-20 cm) as factors. Seed densities for both tests were log transformed prior to analysis to approximate to normality and to achieve homogeneity of variance. Data were analysed using PASW Statistics 17.

The differences in the composition of the soil seed bank were further tested through the use of permutational multivariate analysis of variance (PERMANOVA). This method was used as it can provide an analysis of the effects of multiple factors (in this case, soil depth and habitat) on multi-species data sets (Anderson, 2001) and has proven to be useful for seed bank data (Gioria & Osborne, 2009). Sørensen (Bray-Curtis) was selected as the measure of dissimilarity. The test was done using unrestricted permutations of raw data with 9999 random permutations. Indicator Species Analysis was used to determine species which were affiliated with particular seed bank habitats in the Gearagh (Dufrene & Legendre, 1997). The frequency of each species in the seed bank (number of occurrences over all soil samples of a habitat type) and aboveground vegetation (number of occurrences over all plots of a habitat type) was also calculated. PERMANOVA and Indicator Species Analysis were performed using PC-ORD (McCune & Mefford, 2006).

Sørensen similarity index (SI) was used to analyse the similarity in species composition between the soil seed bank and the corresponding aboveground vegetation for each site: $SI = 2a/(b + c)$, where a refers to the number of species common to both the seed bank and the aboveground vegetation, b represents the number of species in the aboveground vegetation, and c is the number of species in the seed bank. Sørensen's index was chosen because it is simple, effective, and widely used (McCune & Grace, 2002; Magurran, 2004). Differences in Sørensen's index between the four habitat types were analysed with a one-way analysis of variance, after examining data for normality and homogeneity of variance.

The germination and survival of the three study species (*A. nemorosa*, *H. non-scripta*, and *P. vulgaris*) was examined by plotting the mean number of seedlings

that were recorded per habitat on each sampling date over the two-year period. This demonstrated the temporal variation in seedling numbers over time, as well as the differences between each woodland habitat. A two-way ANOVA was used to test the effect of habitat (ancient, old secondary, or recent secondary) and year (year 1 or year 2) on maximum number of seedlings that emerged in each year for each of the three study species. All data were analysed using PASW Statistics 17.

5.4 Results

5.4.1 Seed bank composition

A total of 10,165 seeds (55 species) germinated, of which 1,462 seeds were from the ancient woodland (26 species), 2,484 were from the old secondary woodland (35 species), 2,665 were from the recent secondary woodland (27 species), and 3,554 were from the grassland (38 species). A one-way chi-squared test showed that there was little difference in the total number of species between the habitat types ($\chi^2 = 3.64$, d.f. = 3, $P > 0.05$). 47 seedlings died before they could be identified. *J. effusus* was always the dominant species in the seed bank, and it comprised almost 45% of all seeds that germinated (4,522 seeds). Dominant seed bank species based on the remaining seed numbers were *Carex remota* (18.3%), *Juncus articulatus* (15.1%), *Carex sylvatica* (12.8%), *Hypericum humifusum* (8.5%), and *Poa trivialis* (6.5%). Mean seed density over all plots reached 19,062 seeds m⁻², but was highly variable between samples, ranging from 1,416 to 66,195 seeds m⁻².

Significant differences were found between the seed banks of all four habitats for most variables (Table 5.3 and Fig. 5.4). Seed banks also showed significant differences between the 0-10 cm and 10-20 cm soil layers. Mean species richness increased from the ancient woodland to the secondary sites, with the grassland expressing the largest values for these variables in both the 0-10 cm and 10-20 cm layers. Total seed densities and *J. effusus* seed density were both greater in the 0-10 cm layer than in the 10-20 cm layer. Seed density in particular increased markedly from ancient to secondary and again to grassland for both soil layers (Fig. 5.4). *J. effusus* density was significantly lower in the ancient woodland sites compared with the other habitat types.

Table 5.3 Results from two-way ANOVA on seed data with Habitat (Ancient, Old secondary, Recent secondary, or Grassland) and Depth (0-10 cm or 10-20 cm) as factors. Data that were log transformed prior to analysis are indicated with *.

	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Species richness				
Corrected model	7	79.77	21.78	< 0.001
Habitat	3	82.47	22.52	< 0.001
Depth	1	291.60	79.62	< 0.001
Habitat × Depth	3	6.47	1.77	> 0.05
Error	32	3.66		
Total seed density (seeds m ⁻²) *				
Corrected model	7	4.45	18.70	< 0.001
Habitat	3	8.26	34.72	< 0.001
Depth	1	5.90	24.82	< 0.001
Habitat × Depth	3	0.15	0.64	> 0.05
Error	32	0.24		
<i>Juncus effusus</i> seed density (seeds m ⁻²)*				
Corrected model	7	5.58	14.69	< 0.001
Habitat	3	12.11	31.88	< 0.001
Depth	1	2.13	5.61	< 0.01
Habitat × Depth	3	0.20	0.54	> 0.05
Error	32	0.38		
Ellenberg light value				
Corrected model	7	0.39	5.49	< 0.001
Habitat	3	0.76	10.73	< 0.001
Depth	1	0.01	0.13	> 0.05
Habitat × Depth	3	0.18	2.53	0.075
Error	32	0.07		
Ellenberg moisture value				
Corrected model	7	0.46	3.87	< 0.01
Habitat	3	0.90	7.50	< 0.001
Depth	1	0.12	1.04	> 0.05
Habitat × Depth	3	0.14	1.18	> 0.05
Error	32	0.02		
Ellenberg soil pH value				
Corrected model	7	0.34	4.34	< 0.01
Habitat	3	0.60	7.78	< 0.001
Depth	1	0.14	1.87	> 0.05
Habitat × Depth	3	0.13	1.74	> 0.05
Error	32	0.08		
Ellenberg nitrogen value				
Corrected model	7	0.46	4.82	< 0.001
Habitat	3	0.31	3.24	< 0.05
Depth	1	0.90	9.54	< 0.01
Habitat × Depth	3	0.46	4.82	< 0.01
Error	32	0.09		

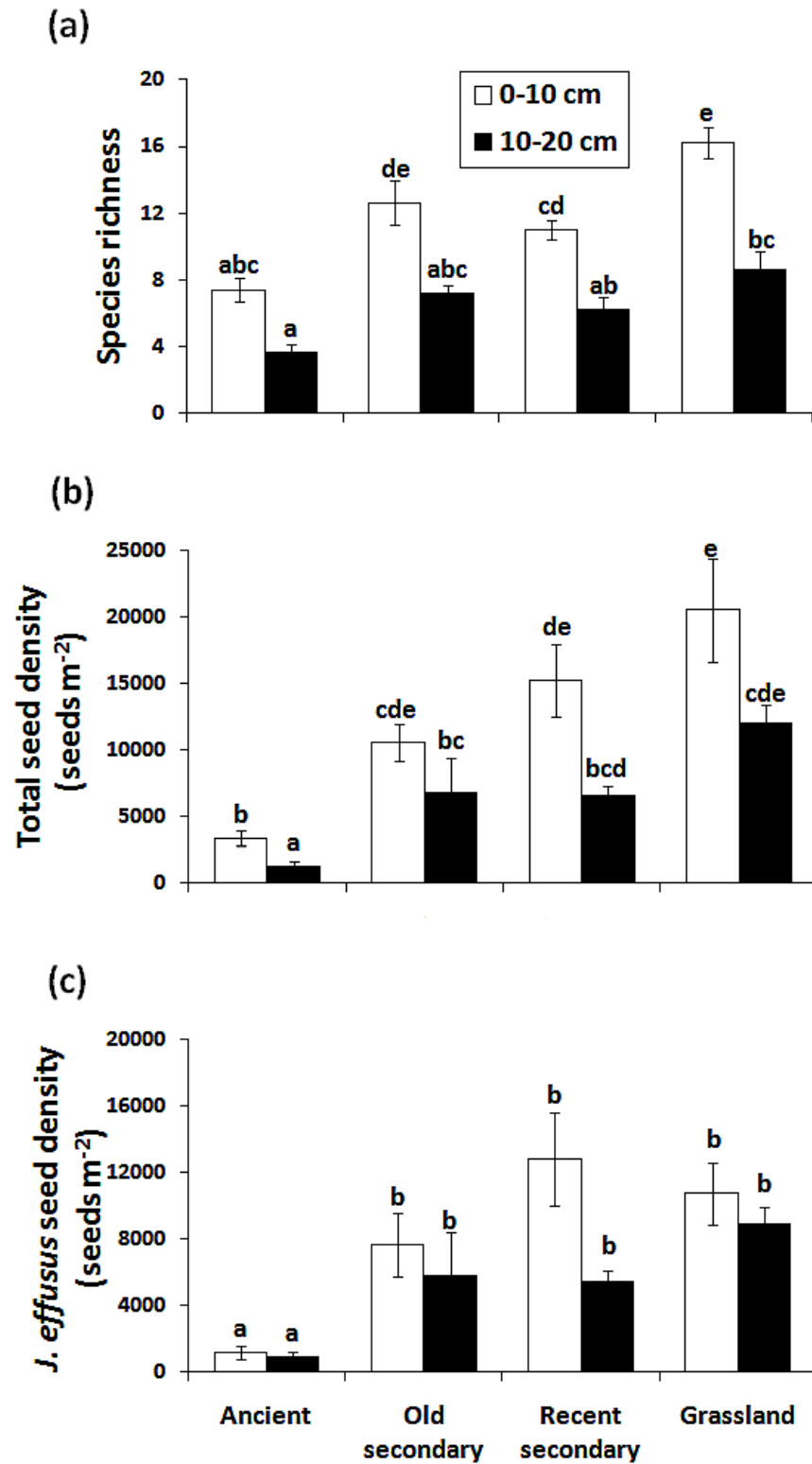


Fig. 5.4 Characteristics of the seed bank data for the four habitat types in the Gearagh per depth layer, showing (a) species richness, (b) total seed density, and (c) density of *Juncus effusus* seeds. Mean values \pm standard error are shown. Significant differences between the treatments are indicated with different letters above the bars; any bars with a common letter are not significantly different using Tukey's honestly significant difference test ($P > 0.05$).

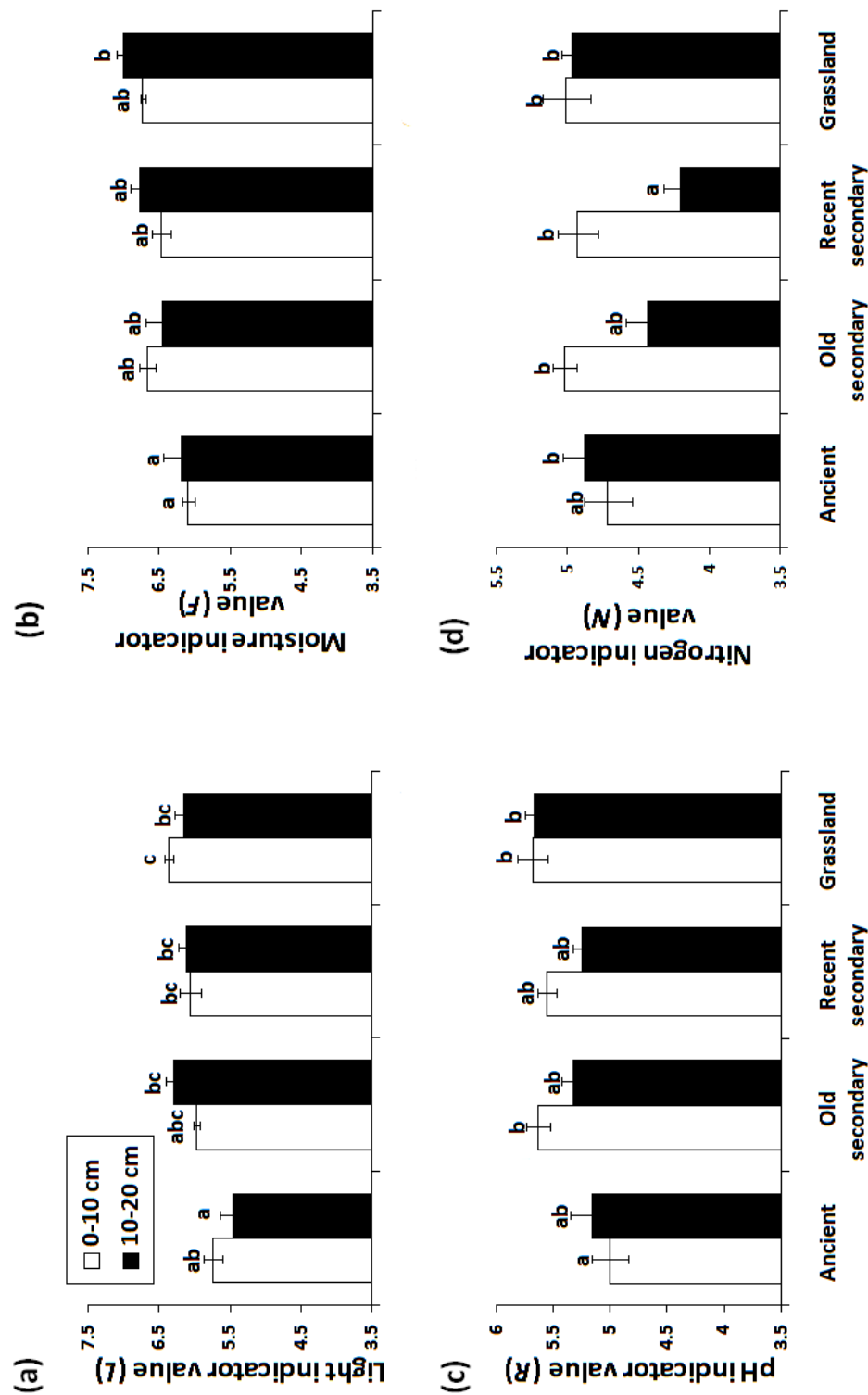


Fig. 5.5 Mean (\pm standard error) Ellenberg indicator values for (a) light, (b) moisture, (c) soil pH, and (d) nitrogen of seed bank species for each of the four habitat types of the Gearagh per soil layer. Significant differences between the treatments are indicated with different letters above the bars; any bars with a common letter are not significantly different using Tukey's honestly significant difference test ($P > 0.05$).

Mean Ellenberg indicator values for light, moisture and soil pH were all lowest in the ancient woodland, increased significantly in the secondary, and were highest in the grassland (Fig. 5.5). The values for nitrogen did not differ significantly between in the habitats in the 0-10 cm layer. However, in the 10-20 cm layer, nitrogen values were greatest in the ancient and grassland habitats and decreased in both secondary habitats. The relative abundance of small and large seeded species did not differ significantly between the habitats or between the two soil depths.

PERMANOVA analysis confirmed that habitat and soil depth were both significant factors driving differences in seed bank communities (Table 5.4). There was, however, no significant interaction between habitat and depth. Pair-wise *a posteriori* comparison on the habitat types showed that the seed bank composition of the ancient woodland was significantly different to those in all other habitats. Although the seed bank of the grassland habitat differed to all of the woodland habitats, it was most similar to the recent secondary woodland. There was no significant difference in the seed bank composition between the two secondary woodlands.

Table 5.4 Results of two-way PERMANOVA testing the effects of Habitat and Depth on Sørensen (Bray-Curtis) distances for the composition and relative abundance of soil seed banks collected in the Gearagh.

Source of variation	<i>df</i>	SS	MS	<i>F</i>	<i>P</i>
Habitat	3	3.098	1.033	8.752	< 0.001
Depth	1	0.425	0.425	3.598	< 0.01
Habitat x Depth	3	0.54	0.18	1.526	0.106
Residual	32	3.776	0.118		
Total	39	7.839			

Comparison *	<i>t</i>	<i>P</i>
Ancient versus old secondary	2.73	< 0.001
Ancient versus recent secondary	3.814	< 0.001
Ancient versus grassland	4.044	< 0.001
Old secondary versus recent secondary	0.965	> 0.05
Old secondary versus grassland	2.002	< 0.01
Recent secondary versus grassland	1.85	< 0.05

* Pair-wise *a posteriori* tests among the four different habitat treatments.

The indicator seed species identified from the seed bank from each of the four habitat types are shown in Table 5.5. Although 10 species were associated with the ancient woodland, most have low indicator values and only one species, *Betula pubescens*, is actually a significant indicator of ancient seed banks. While 11 species were affiliated with the old secondary woodland, three were significant indicators (*Lysmachia nummularia*, *Rubus fruticosus* and *Glechoma hederacea*). In the recent secondary woodland, only four seed species were identified, of which only one was a significant indicator (*Ulex europaeus*). The grassland seed bank had by far the greatest number of indicator species (25), twelve of which were significantly associated with that habitat.

As in many woodland seed bank studies, the lack of similarity between seed bank and vegetation was confirmed; the Sørensen's similarity index values were very low for the woodland habitats (Fig. 5.6). Over all the plots, only 26 out of a total of 94 species occurred in both the seed bank and vegetation, compared to 24 which were restricted to the seed bank, while 44 species were confined to the vegetation. Only 7, 8, and 7 species were common to the vegetation and seed bank of the ancient, old secondary, and recent secondary woodlands, respectively, while the grassland sites contained 15 species that occurred in both the vegetation and seed bank. These results are reflected by the Sørensen's similarity index (Fig. 5.6), which differed significantly between the grassland and the three woodland habitats ($F = 29.727$; $d.f. = 3,16$; $P < 0.001$). Although *post hoc* tests did not indicate a significant difference between the woodland habitats, the Sørensen's similarity index was noticeably greater in the recent secondary woodland. A list of the species found in the seed bank and the aboveground vegetation and their frequency in the study sites is shown in Table 5.5.

5.4.2 Seed germination and survival

Germination of seeds in the experimental plots was generally low. In total, 109 *A. nemorosa* seedlings (5%), 140 *P. vulgaris* seedlings (6%), and 261 *H. non-scripta* seedlings (12%) emerged across all sites. Nonetheless, the number of seedlings of each species that were recorded at any one time often varied between the habitats

Table 5.5 Species occurring in the seed bank in each habitat type of the Gearagh. Species are listed according to Indicator Value (IV). Species with a significant indicator value ($P \leq 0.05$) are shown in bold. Significance of Monte-Carlo tests: * $0.01 < P \leq 0.05$; ** $0.001 < P \leq 0.01$; *** $P \leq 0.001$. The percentage frequency of occurrence of each species in the seed bank, the ground flora vegetation, and the canopy layer in the four different habitat types of the Gearagh is also given.

Indicator species	Ancient woodland			Old secondary woodland			Recent secondary woodland			Grassland		
	IV	Seed bank	Ground flora	Canopy	IV	Seed bank	Ground flora	Canopy	IV	Seed bank	Ground flora	Canopy
Ancient woodland												
<i>Betula pubescens</i>	35**	23	0	60	4	10	2	100	1	3	0	100
<i>Lysimachia nemorum</i>	13	7	0	0	0	0	2	0	0	0	0	0
<i>Digitalis purpurea</i>	7	7	0	0	0	0	0	0	0	0	0	0
<i>Euphorbia hyberna</i>	7	3	58	0	0	0	11	0	0	0	2	0
<i>Primula vulgaris</i>	7	3	9	0	0	0	27	0	0	0	4	0
<i>Sanicula europaea</i>	7	3	29	0	0	0	16	0	0	0	13	0
<i>Oxalis acetosella</i>	5	7	0	0	3	3	0	0	1	3	0	0
<i>Potentilla sterilis</i>	5	3	0	0	1	3	0	0	0	0	0	0
<i>Geum urbanum</i>	3	3	7	0	2	3	36	0	2	3	42	0
<i>Mentha aquatica</i>	3	3	0	0	2	3	0	0	0	0	0	0
Old secondary woodland												
<i>Lysimachia nummularia</i>	9	20	0	0	36**	30	0	0	1	7	0	0
<i>Rubus fruticosus</i>	7	23	51	0	31*	43	11	0	12	27	20	0
<i>Glechoma hederacea</i>	0	0	0	0	27**	13	0	0	0	0	0	0
<i>Veronica montana</i>	6	10	18	0	21	20	53	0	1	7	16	0
<i>Myosotis scorpioides</i>	0	0	0	0	13	7	0	0	0	0	0	0
<i>Hypericum pulchrum</i>	3	7	0	0	10	13	0	0	2	7	0	0

Table 5.5 continued

Indicator species	Ancient woodland				Old secondary woodland				Recent secondary woodland				Grassland			
	IV	Seed bank	Ground flora	Canopy	IV	Seed bank	Ground flora	Canopy	IV	Seed bank	Ground flora	Canopy	IV	Seed bank	Ground flora	Canopy
Old secondary woodland																
<i>Cerastium fontanum</i>	0	0	0	0	7	3	0	0	0	0	0	0	0	0	0	0
<i>Isoplepis setacea</i>	0	0	0	0	7	3	0	0	0	0	0	0	0	0	0	0
<i>Salix cinerea</i> spp. <i>aleifolia</i>	0	0	0	0	7	3	0	40	0	0	0	40	0	0	0	0
<i>Crepis capillaris</i>	1	3	0	0	5	7	0	0	0	0	0	0	5	7	0	0
<i>Trifolium repens</i>	0	0	0	0	5	7	0	0	5	7	0	0	1	3	2	0
Recent secondary woodland																
<i>Ulex europaeus</i>	0	0	0	0	12	27	0	0	25*	30	0	0	1	7	2	0
<i>Carex paniculata</i>	0	0	0	0	0	0	0	0	7	3	0	0	0	0	0	0
<i>Festuca altissima</i>	0	0	0	0	0	0	0	0	7	3	0	0	0	0	0	0
<i>Hydrocotyle vulgaris</i>	0	0	0	0	1	3	0	0	4	7	0	0	3	3	0	0
Grassland																
<i>Poa trivialis</i>	1	7	9	0	1	10	27	0	5	20	44	0	68***	67	58	0
<i>Juncus articulatus</i>	0	0	0	0	7	37	0	0	8	37	0	0	65***	73	0	0
<i>Ranunculus repens</i>	0	0	0	0	1	3	0	0	6	13	0	0	51***	47	20	0
<i>Brachypodium sylvaticum</i>	0	0	0	0	0	0	0	0	1	3	0	0	49***	27	20	0
<i>Carex remota</i>	0	0	0	0	10	43	2	0	10	40	38	0	47*	53	0	0
<i>Ranunculus flammula</i>	0	0	0	0	0	0	0	0	0	0	0	0	47***	37	20	0
<i>Deschampsia caespitosa</i>	4	10	11	0	1	3	27	0	1	7	47	0	38**	33	56	0
<i>Juncus effusus</i>	3	67	0	0	25	93	0	0	34	90	0	0	37*	97	53	0

Table 5.5 continued

Indicator species	Ancient woodland				Old secondary woodland				Recent secondary woodland				Grassland			
	IV	Seed bank	Ground flora	Canopy	IV	Seed bank	Ground flora	Canopy	IV	Seed bank	Ground flora	Canopy	IV	Seed bank	Ground flora	Canopy
Grassland																
<i>Galium palustre</i>	0	0	0	0	1	7	0	0	0	0	20	0	31**	23	4	0
<i>Carex sylvatica</i>	5	27	0	0	15	40	0	0	28	63	0	0	29	60	0	0
<i>Agrostis stolonifera</i>	0	0	0	0	2	13	0	0	7	17	9	0	29*	27	100	0
<i>Chrysosplenium oppositifolium</i>	0	0	0	0	0	0	9	0	0	0	7	0	27*	13	0	0
<i>Urtica dioica</i>	1	3	0	0	1	7	0	0	0	0	0	0	25*	17	44	0
<i>Filipendula ulmaria</i>	0	0	53	0	1	3	60	0	0	0	76	0	21	13	71	0
<i>Plantago major</i>	0	0	0	0	0	0	0	0	0	0	0	0	20	13	0	0
<i>Hypericum humifusum</i>	2	3	0	0	5	23	0	0	6	33	0	0	16	23	0	0
<i>Stachys sylvatica</i>	0	0	0	0	0	0	0	0	0	0	0	0	13	7	0	0
<i>Rumex conglomerates</i>	0	0	0	0	0	0	0	0	1	3	0	0	12	10	18	0
<i>Bromus mollis</i>	0	0	0	0	0	0	0	0	0	0	0	0	7	3	0	0
<i>Melampyrum pratense</i>	0	0	0	0	0	0	0	0	0	0	0	0	7	3	0	0
<i>Oenanthe crocata</i>	0	0	0	0	0	0	0	0	0	0	0	0	7	3	0	0
<i>Potentilla anserina</i>	0	0	0	0	0	0	0	0	0	0	0	0	7	3	0	0
<i>Stellaria media</i>	0	0	0	0	0	0	0	0	0	0	0	0	7	3	0	0
<i>Veronica chamaedrys</i>	0	0	0	0	0	0	4	0	0	0	2	0	7	3	20	0
<i>Luzula sylvatica</i>	2	3	0	0	0	0	0	0	0	0	0	0	4	3	0	0

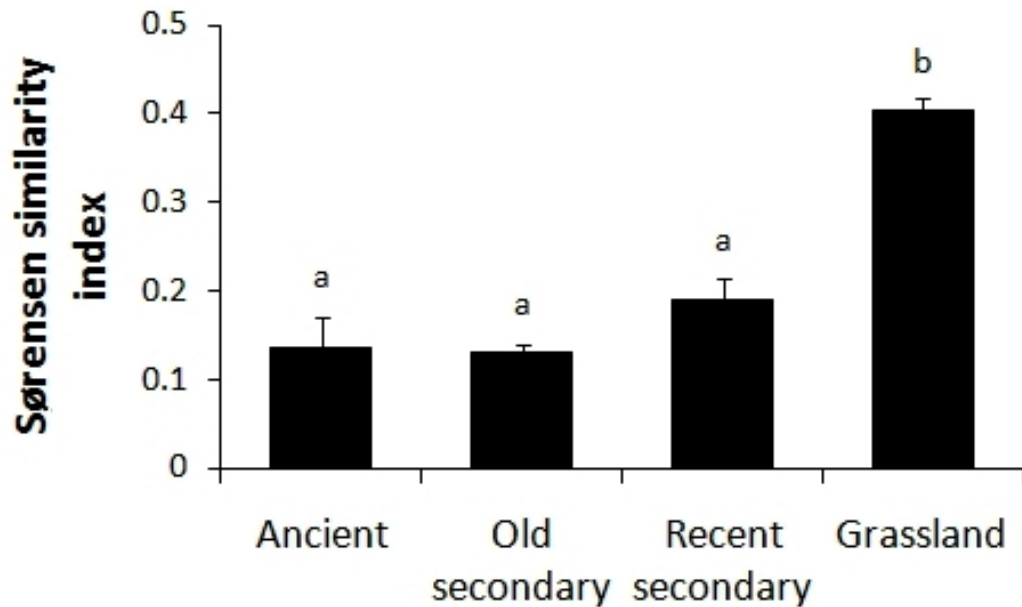


Fig. 5.6 Mean (\pm standard error) Sørensen's similarity index between seed bank and vegetation composition for the total sample depth (0-20 cm) per habitat type in the Gearagh. Letters above each bar signify Tukey's honestly significant differences between the habitat types ($P > 0.05$) after testing with ANOVA; any two bars with a common letter are not significantly different.

and fluctuated over time. The clearest difference in the numbers of seedlings that emerged between habitats was observed for *P. vulgaris* (Fig. 5.7, c). After 40 days, the number of seedlings in the ancient woodland began to increase, while seedling numbers in both the old secondary and recent secondary remained low. The number of *P. vulgaris* seedlings in the ancient woodland showed a marginal decrease in year 2 (days 350-400). However, seedling emergence was still greater than in either of the secondary habitats. In contrast, similar numbers of *H. non-scripta* seedlings were recorded in each of the three woodland habitats throughout the sampling period (Fig. 5.7, b). At the beginning of each year, the numbers of *H. non-scripta* seedlings were low, but they gradually increased over time. However, the numbers of *A. nemorosa* seedlings, which die back in summer, showed greater fluctuation over time (Fig. 5.7, a). This variation means that differences between the habitats for *A. nemorosa* seedlings are less apparent, although more seedlings were recorded in the ancient woodland than in either of the secondary woodlands

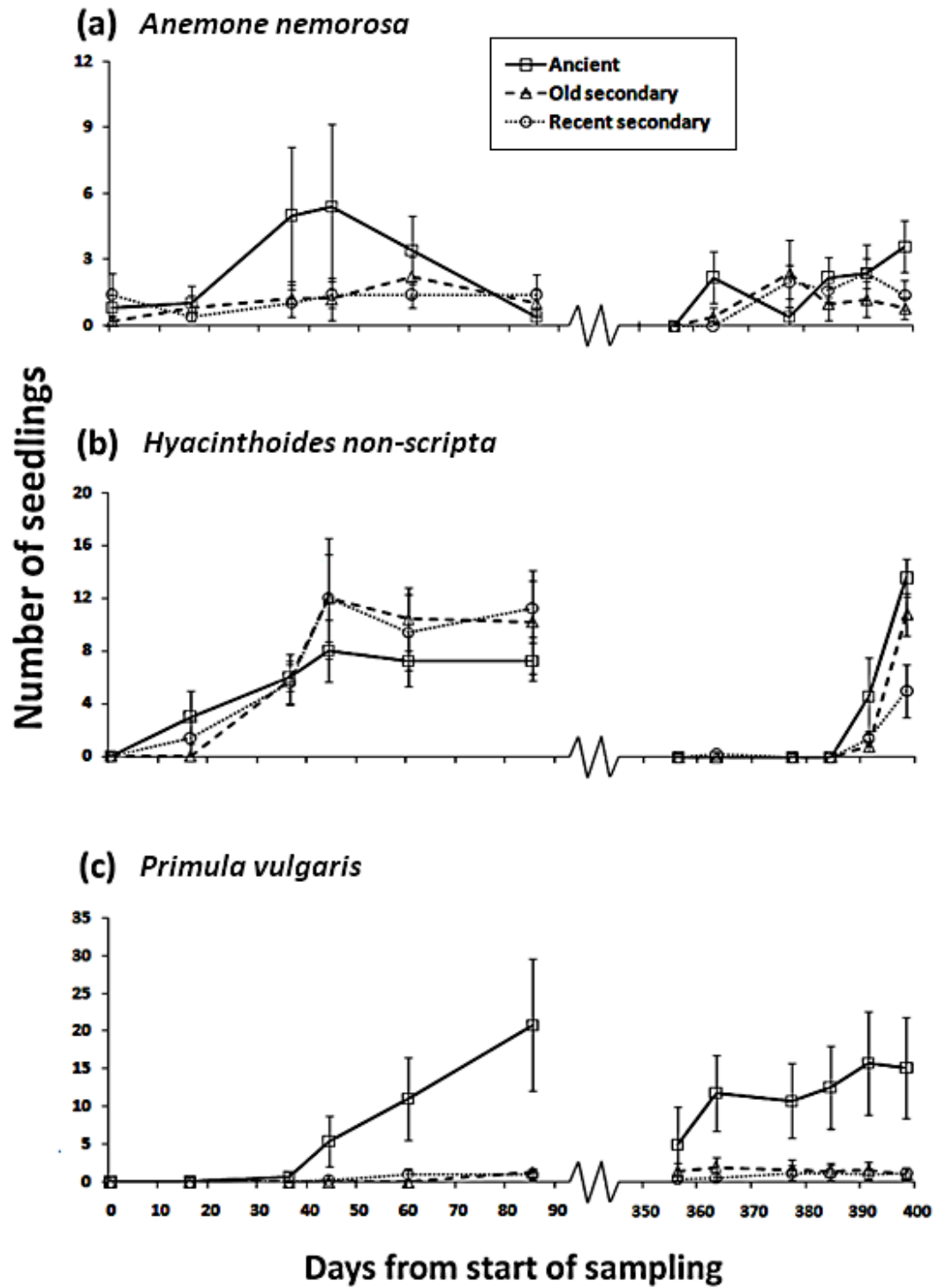


Fig. 5.7 Mean (\pm standard error) numbers of (a) *Anemone nemorosa*, (b) *H. non-scripta*, and (c) *P. vulgaris* seedlings recorded per 150 seeds sown over the sampling period in each of the three woodland habitats of the Gearagh.

Table 5.6. Results of a two-way ANOVA on the effect of woodland habitat and year on the maximum number of seedlings that emerged in each year of the three study species. Data that were log transformed are indicated with *.

Species	Source of variation	df	MS	F	P
<i>Anemone nemorosa</i> *					
	Corrected model	5	0.986	2.497	0.059
	Habitat	2	2.088	5.288	< 0.05
	Year	1	0.295	0.747	> 0.05
	Habitat × Year	2	0.230	0.582	> 0.05
	Error	24	0.395		
<i>Hyacinthoides non-scripta</i>					
	Corrected model	5	55.313	1.810	> 0.05
	Habitat	2	29.033	0.950	> 0.05
	Year	1	56.033	1.833	> 0.05
	Habitat × Year	2	81.233	2.658	0.091
	Error	24	30.567		
<i>Primula vulgaris</i> *					
	Corrected model	5	3.228	2.563	0.054
	Habitat	2	7.525	5.974	< 0.01
	Year	1	0.063	0.050	> 0.05
	Habitat × Year	2	0.513	0.407	> 0.05
	Error	24	1.260		

on most sampling dates. The frequently large error bars, particularly for *P. vulgaris* in the ancient woodland, indicate that there can be considerable variation in seedling germination within habitats.

The results of the two-way ANOVA on the maximum numbers of seedlings recorded for each species in both years 1 and 2 (Table 5.6) corroborate the patterns of seedling abundance observed over time. The effect of habitat was significant for both *P. vulgaris* and *A. nemorosa*, confirming that significantly greater numbers of these seeds germinated in the ancient woodland than the secondary woodlands. However, there was no significant difference in the number of *H. non-scripta* seedlings between the habitats. None of the three species showed a significant difference between year 1 and year 2.

5.5 Discussion

5.5.1 Seed bank composition

The clear differences in seed bank composition and density between the ancient woodland and the two secondary woodland sites confirmed both the current and historical differences between sites, and also revealed important aspects of woodland ecology that are critical for the understanding and management of ancient woodland.

Although the value of ancient woodland has long been recognised, it is often difficult to unequivocally verify the historical continuity of a site. In the Gearagh, few vascular plant species were confined solely to the ancient woodland, so that floristic differences between the ancient and secondary habitats were subtle (Chapter 4). This reflects the difficulties in the use of ancient woodland indicator species to identify ancient woodland sites in Ireland. This is partly due to the depauperate nature of the Irish flora (Webb, 1983), as many true woodland specialists are absent in Ireland (e.g. *Paris quadrifolia*), while other species (e.g. *Hedera helix*, *Lonicera periclymenum*) occupy a broader niche than they do elsewhere in Europe (Kelly, 2004). Ancient woodlands are thus usually identified from a combination of historical maps and documents, archaeology, and topographical evidence (Perrin & Daly, 2010). However, these sources have their limitations and the confirmation of ancient status is often problematic. While other work in the Gearagh has demonstrated that both soil properties and the communities of soil and ground-dwelling invertebrates can also indicate differences between stands of contrasting land-use history (Chapters 3 and 6), these are often difficult to sample and analyse. Soil types in particular are often region-specific, and undisturbed ancient soils may not exist in many cases.

However, the results of this study suggest that the determination of woodland age, and hence conservation status, may readily be determined by examining the seed bank. The presence of many open-habitat species in the seed bank may be an indicator of previous disturbed conditions in the woodland, as many of these species can persist in the soil for tens and even hundreds of years. Equally, the lack of many species in the seed bank, particularly species such as *Juncus effusus*, may

help to confirm the ancient nature of a woodland. In this study, the mean seed density of the ancient woodland (4,625 seeds m⁻²) was lower than both the old secondary (17,369 seeds m⁻²) and recent secondary woodlands (21,794 seeds m⁻²). This corroborates the findings of other studies which have shown that older woodlands frequently differ from younger woodlands in terms of their seed density and seed bank composition (Bossuyt *et al.*, 2002; Plue *et al.*, 2010b).

The composition of the seed bank can also provide important information on the vegetation dynamics of a habitat. The marked dissimilarity between seed bank and aboveground vegetation communities (Chapter 4) observed in the Gearagh has also been found in several other studies (Hopfensperger, 2007; Bossuyt & Honnay, 2008; Erenler *et al.*, 2010), and indicates that the existing plant community composition of a woodland habitat plays only a minor role in determining seed bank composition (Schmidt *et al.*, 2009; Plue *et al.*, 2010a). In our study, the greatest similarity between plants and seeds was seen in the grassland, indicating that plants of open habitats tend to form persistent seeds more than do plants of woodland habitats.

Typical woodland species, as well as tree species, were rare components of the seed bank, with the exception of *Veronica montana*, *Lysimachia nemorum* and *Lysimachia nummularia*, all of which are common in Irish woods. The one notable tree species found in the ancient woodland seed bank was *Betula pubescens*, which produces seed every year and forms an important part of the normal cycles of regeneration in woodland (Leckie *et al.*, 2000; Bossuyt & Hermy, 2001). Many of the plant species that are typically abundant in woodland are clonal and reproduce chiefly by vegetative propagation (e.g. stolons, rhizomes, bulbs), or produce only short-lived seeds that are rarely found in the seed bank (Brown & Oosterhuist, 1981). In fact, the seeds of most woodland plants die unless they germinate within a year after dispersal (Brown & Oosterhuist, 1981; Bossuyt & Hermy, 2001; Decocq *et al.*, 2004), an adaptation to a highly stressful but low disturbance environment (Hermy *et al.*, 1999). This inability of most woodland species to form a persistent seed bank means however that they are vulnerable to disturbance, particularly woodland clearance and conversion to agriculture.

The ancient woodland soils not only contained few seeds of woodland-associated species, but they also contained few seeds of open-habitat species. This was reflected in the Ellenberg scores, which showed that the few seeds that germinated from ancient woodland soil tended to be of species with a preference for woodland rather than open habitats. The scarcity of species associated with open-habitat condition in the ancient woodland is consistent with previous findings from ancient woodland seed banks (Leckie *et al.*, 2000; Wang *et al.*, 2009). Plant species from the surrounding open habitat landscape therefore appear to be unable to successfully colonise the ancient woodland seed bank, despite the close proximity of grassland habitats. Several possible factors may account for this finding. Firstly, ancient woodland edges may act as an extensive barrier to the dispersal of seeds of species from the surrounding habitat (Devlaeminck *et al.*, 2005). Even if some seeds do penetrate into the woodland, the deeper litter layer in the ancient woodland may physically impede small-seeded species, preventing them from reaching the soil layer and becoming part of the seed bank (Eriksson, 1995; Dzwonko & Gawroński, 2002). Light levels at the soil surface may also be much lower, given the denser, more complex shrub and ground layer of ancient woodlands (Jankowska-Błaszczuk *et al.*, 1998). Other open-habitat species may require burial by earthworms in order to germinate (Thompson *et al.*, 1993). The low abundance of earthworms in the ancient woodland (see Chapter 6) means that these seeds are more likely to remain on the surface where they would be more vulnerable to predators (Thompson, 1987).

In contrast, the high seed densities of open-habitat species recorded in the secondary woodlands are most likely due to the effects of past land-use and former management on seed bank composition (Bossuyt & Hermy, 2001; Plue *et al.*, 2008; Erenler *et al.*, 2010; Plue *et al.*, 2010b). Many of the species of open-habitat conditions are very competitive and are able to produce large amounts of long-lived seeds (Kjellsson, 1992; Warr *et al.*, 1994; Brunet & Von Oheimb, 1998). For example, high densities of *J. effusus* were found in the grassland and both secondary woodlands, but relatively few seeds were buried in the soil of the ancient woodland. *J. effusus* has a particularly high reproductive output and its

seeds have been found to survive for up to 200 years before germinating (Kjellsson, 1992). The exceptional long life-span of these seeds means that their presence in the soil seed bank can easily be maintained, even once all the parent plants have disappeared (Decocq *et al.*, 2004). Some studies suggest that certain characteristics of the former land-use will continue to persist in the seed bank even after 150 years (Plue *et al.*, 2010b).

Furthermore, while it appears that the ancient woodland is generally resistant to colonisation by non-woodland species, conditions in the secondary woodland may be more suitable for the germination and persistence of these species. Reductions in the litter layer, increased earthworm activity (see Chapter 6), and altered soil conditions (Chapter 3) may all promote the recruitment of many of these species (Dzwonko & Gawroński, 2002; Jankowska-Błaszczuk & Grubb, 2006), thereby reinforcing their presence in the seed bank. The seed banks of the secondary woodland may therefore potentially have a negative effect on the aboveground vegetation by sustaining undesirable competitive species, including those that originated from the former grasslands (Bossuyt *et al.*, 2002). This may have important implications for woodland management, particularly practices such as coppicing and gap creation. By reducing shade in the woodland, these procedures may enable the germination of even greater numbers of these open-habitat species in secondary woodlands (Plue *et al.*, 2010b). If these develop into adult plants, they have the potential to disperse even more seeds into the seed bank (Van Calster *et al.*, 2008). These species would therefore continue to persist both in the woodland ground vegetation and the seed bank, most likely at the expense of other poorly-competitive woodland plant species. The results of this study show that even without active management or significant disturbance, these seeds can persist in the soil for at least 170 years. Management practices such as coppicing should therefore be practiced with caution, particularly if the history of the woodland is poorly known.

In addition, altered environmental conditions may make secondary woodlands more vulnerable to colonisation by invasive plant species. In North America, altered soil properties and increased earthworm activity has facilitated the spread of exotic

plant species, often at the expense of native plant species (Frelich *et al.*, 2006). In Ireland, the seed banks of disturbed sites that are dominated by large invasive species (e.g. *Fallopia japonica*, *Gunnera tinctoria*) mostly contain seeds of agricultural weeds and open-habitat species (Gioria & Osborne, 2010). This suggests that abandoned agricultural land and disturbed habitats may be more susceptible to colonisation by large invasive species, possibly as a result of altered habitat conditions. It is important therefore to consider land-use history in ecological studies, including those relating to soil seed banks and plant establishment process.

The results of this study also have important implications for the restoration of ancient woodland. Many ancient woodlands have been subject to a variety of management practices in the past that can result in the long-term suppression of adult woodland plants (e.g. through the planting of conifer species or over-grazing). Because many woodland plants do not form a persistent seed bank, it can be very difficult for these species to re-establish once most of the adult plants have been lost. In order to restore the woodland to its original state, many management guidelines advocate the removal of the initial disturbance (e.g. by felling all remaining conifers), with the expectation that this will also result in the rapid re-colonisation of the woodland ground flora (Ferris & Simmons, 2000; Thompson *et al.*, 2003; The Woodland Trust, 2005). However, these results show that the re-establishment of an ancient woodland ground flora may be difficult even once the original woodland canopy is restored, and may only occur gradually over hundreds of years.

5.5.2 Seed germination and survival

The proportion of introduced seeds of the three woodland plant species that germinated successfully was often lower than 5%, indicating that post-dispersal abiotic and biotic factors act to further limit seedling recruitment (Verheyen *et al.*, 2003; Baeten *et al.*, 2009b). This suggests that the critical stage for seed recruitment occurs between when seeds arrive and when seedlings first emerge. Processes that affect seed survival during this period therefore can act as a crucial bottleneck for plant populations (Clark *et al.*, 2007).

The seed germination experiment also showed that certain woodland species may be particularly sensitive to changes in site conditions that have arisen as a result of past land-use. Both *P. vulgaris* and *A. nemorosa* germinated more successfully in the ancient woodland. Factors that may influence seed germination include soil pH (Thomaes *et al.*, 2011), phosphorus availability (Baeten *et al.*, 2009a), and interactions with mycorrhizal fungi, herbivores, pollinators and pathogens (Verheyen & Hermy, 2004; Flinn & Vellend, 2005), most of which remain poorly studied.

The soils of the secondary woodland have a higher moisture content and lower pH than those of the ancient woodland (Chapter 3). *P. vulgaris* does not always germinate well under these conditions (Jacquemyn *et al.*, 2009), and this may have affected seed germination in these habitats. Increased earthworm abundance and activity in the secondary woodland (see Chapter 6 for further details) may also have a negative impact on the germination of small-seeded species such as *P. vulgaris*. Previous studies have shown that ingestion and deep burial of seeds by earthworms may act to reduce the viability of seeds, thereby limiting the establishment of woodland plants (Willems & Huijsmans, 1994; Frelich *et al.*, 2006; Milcu *et al.*, 2006). Indeed, the high numbers of seeds in the 10-20 cm soil layer of the secondary woodland habitats is likely due to the relatively high earthworm density in these soils (Schmidt *et al.*, 2009). Earthworms may also have an indirect effect on seed germination by acting to reduce the depth of the litter layer (Leck *et al.*, 1993). The low quantity of litter in the secondary woodland may be due to the greater abundance of earthworms in that soil (see Chapter 6). A smaller litter layer can lead to greater seed mortality due to the increased risk of freezing, desiccation, and predation (Cothrel *et al.*, 1997). In contrast, the often deeper litter layer in the ancient woodland may act to reduce the exposure of seeds to these threats.

The more successful germination of *A. nemorosa* in the ancient woodland soil contrasts with the finding of Verheyen and Hermy (2004) that the germination of this woodland species was not affected by former land-use. However, a re-evaluation of the experiment after eight growing seasons showed that the experimental populations had declined considerably in secondary woodland sites,

but were still present in the ancient sites (Baeten *et al.*, 2009a). A longer-term study across multiple life-stages may be necessary to fully determine the importance of environmental limitation as a result of past land use on woodland species such as *A. nemorosa* (Baeten *et al.*, 2009a).

H. non-scripta was able to germinate equally well in all three of the woodland habitats, regardless of changes in microhabitat conditions due to past land-use. Germination success across all three soil types may be partly related to seed size (Turnbull *et al.*, 1999; Coomes & Grubb, 2003; Moles & Westoby, 2004). *P. vulgaris* had the smallest seed size of all of the study species, and had the most restricted germination success, being largely confined to ancient woodland. *H. non-scripta* in contrast had the largest seeds and germinated equally successfully in the three soil types. Most woodland plants have large seeds which contain greater reserves for initial growth of roots and shoots, making them better able to withstand adverse microsite conditions (Moles & Westoby, 2004). Large-seeded species are also less affected by earthworm burial than are small-seeded species. This is due to lower ingestion and digestion rates by earthworms and the ability of seedlings from large seeds to emerge from greater depths (Milcu *et al.*, 2006). However, this competitive advantage may decrease as plants enter post-seedling stages (Dalling & Hubbell, 2002). Indeed, the long-term growth and survival of *H. non-scripta* can be adversely affected by disturbances such as trampling and grazing (Van der Veken *et al.*, 2007).

The results of this experiment have shown that the recruitment success of woodland plants may be due as much to soil conditions as to dispersal limitation or the physical and biological conditions of the above-ground woodland community. Other work from the Gearagh (Chapters 3 and 6) has shown that the soils of the ancient woodland are markedly different biologically and physically to the secondary woodlands. The ancient woodland soil is less acidic than the secondary woodland soil, has a high organic matter content, a low bulk density, and is extremely well-drained. These differences are partly related to the soil decomposer communities; the ancient woodland soil has a large enchytraeid population but few earthworms, and is also associated with many fungal-feeding organisms (Chapter

6). These ancient soils will have developed without disturbance for many centuries, and date from at least medieval times (Brown, 1999). Secondary woodland soils are more poorly-drained, show signs of podzolisation, have lower pH, and have a very different soil microbial and faunal community. The seed bank community clearly showed that secondary woodlands must have resembled the grassland until abandonment, but also have not yet returned to its pre-disturbance state. Studies in North America have shown how disturbances in the form of invasive earthworm species can significantly alter soil structure (e.g. through increased mixing of organic and mineral materials) (Frelich *et al.*, 2006). Such changes in soil conditions can increase seed mortality through increased exposure to desiccation and predation, ultimately resulting in reduced plant regeneration and a reduction in the abundance and diversity of woodland plant species (Bohlen *et al.*, 2004). There have been relatively few investigations in Europe into how previous woodland soil disturbance may impact on seedling recruitment and success of sensitive woodland species (Eriksson & Ehrlén, 1992; Verheyen & Hermy, 2004; Baeten *et al.*, 2009a). Our results show that much more attention in future should be placed on soil conditions in the management of woodland biodiversity, rather than the current emphasis on seed source proximity or creating conditions suitable for adult plants.

5.6 Conclusions

The seed bank survey together with the germination study show that secondary woodland can remain distinct from undisturbed ancient woodland for over 150 years after woodland regrowth. While the secondary woodland may undergo a partial recovery over time, differences in plant communities between these woodland habitats can be maintained by changes in the seed bank composition and by limitations imposed on the colonisation capacity of woodland species as a result of land-use legacies. Woodland species respond differently to the legacies of former agricultural use. Species with small seeds may be particularly vulnerable to altered microhabitat conditions, while other woodland species with larger seeds may be initially less susceptible to these changes. The lack of disturbance in the ancient woodland also means that it is less likely to be colonised by species from the surrounding agricultural environment.

5.7 References

- Anderson, M. (2001) A new method for non parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32-46.
- Baeten, L., Hermy, M. & Verheyen, K. (2009a) Environmental limitation contributes to the differential colonization capacity of two forest herbs. *Journal of Vegetation Science*, **20**, 209-223.
- Baeten, L., Jacquemyn, H., Van Calster, H., Van Beek, E., Devlaeminck, R., Verheyen, K. & Hermy, M. (2009b) Low recruitment across life stages partly accounts for the slow colonization of forest herbs. *Journal of Ecology*, **97**, 109-117.
- Baeten, L., Vanhellemont, M., De Frenne, P., De Schrijver, A., Hermy, M. & Verheyen, K. (2010) Plasticity in response to phosphorus and light availability in four forest herbs. *Oecologia*, **163**, 1021-1032.
- Baskin, C.C. & Baskin, J.M. (2001) *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, London, UK, pp. 666.
- Bekker, R.M., Bakker, J.P., Grandin, U., Kalamees, R., Milberg, P., Poschlod, P., Thompson, K. & Willems, J.H. (1998) Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Functional Ecology*, **12**, 834-842.
- Bohlen, P.J., Scheu, S., Hale, C.M., McLean, M.A., Migge, S., Groffman, P.M. & Parkinson, D. (2004) Non-native invasive earthworms as agents of change in northern temperate forests. *Frontiers in Ecology and the Environment*, **2**, 427-435.
- Bossuyt, B. & Hermy, M. (2001) Influence of land use history on seed banks in European temperate forest ecosystems: a review. *Ecography*, **24**, 225-238.
- Bossuyt, B., Hermy, M. & Deckers, J. (1999) Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. *Journal of Ecology*, **87**, 628-638.
- Bossuyt, B., Heyn, M. & Hermy, M. (2002) Seed bank and vegetation composition of forest stands of varying age in central Belgium: consequences for regeneration of ancient forest vegetation. *Plant Ecology*, **162**, 33-48.

- Bossuyt, B. & Honnay, O. (2008) Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. *Journal of Vegetation Science*, **19**, 875-884.
- Bradshaw, R.H.W. (2004) Past anthropogenic influence on European forests and some possible genetic consequences. *Forest Ecology and Management*, **197**, 203-212.
- Brown, A.G. (1999) Biodiversity and pollen analysis: modern pollen studies and the recent history of a floodplain woodland in S. W. Ireland. *Journal of Biogeography*, **26**, 19-32.
- Brown, A.H.F. & Oosterhuist, L. (1981) The role of buried seed in coppicewoods. *Biological Conservation*, **21**, 19-38.
- Brunet, J. & Von Oheimb, G. (1998) Migration of vascular plants to secondary woodlands in southern Sweden. *Journal of Ecology*, **86**, 429-438.
- Clark, C., Poulsen, J., Levey, D. & Osenberg, C. (2007) Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *American Naturalist*, **170**, 128-142.
- Coomes, D.A. & Grubb, P.J. (2003) Colonization, tolerance, competition and seed-size variation within functional groups. *Trends in Ecology & Evolution*, **18**, 283-291.
- Cothrel, S.R., Vimmerstedt, J.P. & Kost, D.A. (1997) In situ recycling of urban deciduous litter. *Soil Biology and Biochemistry*, **29**, 295-298.
- Dalling, J.W. & Hubbell, S.P. (2002) Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *Journal of Ecology*, **90**, 557-568.
- De Frenne, P., Graae, B.J., Kolb, A., Brunet, J., Chabrierie, O., Cousins, S.A.O., Decocq, G., Dhondt, R., Diekmann, M., Eriksson, O., Heinken, T., Hermy, M., Jögar, Ü., Saguez, R., Shevtsova, A., Stanton, S., Zindel, R., Zobel, M. & Verheyen, K. (2010) Significant effects of temperature on the reproductive output of the forest herb *Anemone nemorosa* L. *Forest Ecology and Management*, **259**, 809-817.

- Decocq, G., Valentin, B., Toussaint, B., Hendoux, F., Saguez, R. & Bardat, J. (2004) Soil seed bank composition and diversity in a managed temperate deciduous forest. *Biodiversity and Conservation*, **13**, 2485-2509.
- Devlaeminck, R., Bossuyt, B. & Hermy, M. (2005) Inflow of seeds through the forest edge: evidence from seed bank and vegetation patterns. *Plant Ecology*, **176**, 1-17.
- Dufrene, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345-366.
- Dzwonko, Z. & Gawroński, S. (2002) Influence of litter and weather on seedling recruitment in a mixed oak–pine woodland. *Annals of Botany*, **90**, 245-251.
- Endels, P., Adriaens, D., Verheyen, K. & Hermy, M. (2004) Population structure and adult plant performance of forest herbs in three contrasting habitats. *Ecography*, **27**, 225-241.
- Erenler, H., Ashton, P., Gillman, M. & Ollerton, J. (2010) Factors determining species richness of soil seed banks in lowland ancient woodlands. *Biodiversity and Conservation*, **19**, 1631-1648.
- Eriksson, O. (1995) Seedling recruitment in deciduous forest herbs - the effects of litter, soil chemistry and seed bank. *Flora*, **190**, 65-70.
- Eriksson, O. & Ehrlén, J. (1992) Seed and microsite limitation of recruitment in plant populations. *Oecologia*, **91**, 360-364.
- Ferris, R. & Simmons, E. (2000) *Plant Communities and Soil Seedbanks in Broadleaved-Conifer Mixtures on Ancient Woodland Sites in Lowland Britain*. Forestry Commission, Edinburgh, UK, pp. 8.
- Fitter, A. & Peat, H. (1994) The ecological flora database. *Journal of Ecology*, **82**, 415-425.
- Flinn, K.M. (2007) Microsite-limited recruitment controls fern colonization of post-agricultural forests. *Ecology*, **88**, 3103-3114.
- Flinn, K.M. & Vellend, M. (2005) Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and the Environment*, **3**, 243-250.

- Fraterrigo, J.M., Pearson, S.M. & Turner, M.G. (2009) The response of understory herbaceous plants to nitrogen fertilization in forests of different land-use history. *Forest Ecology and Management*, **257**, 2182-2188.
- Frelich, L., Hale, C., Scheu, S., Holdsworth, A., Heneghan, L., Bohlen, P. & Reich, P. (2006) Earthworm invasion into previously earthworm-free temperate and boreal forests. *Biological Invasions*, **8**, 1235-1245.
- Gioria, M. & Osborne, B. (2009) Assessing the impact of plant invasions on soil seed bank communities: use of univariate and multivariate statistical approaches. *Journal of Vegetation Science*, **20**, 547-556.
- Gioria, M. & Osborne, B. (2010) Similarities in the impact of three large invasive plant species on soil seed bank communities. *Biological Invasions*, **12**, 1671-1683.
- Hermý, M., Honnay, O., Firbank, L., Grashof-Bokdam, C. & Lawesson, J.E. (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation*, **91**, 9-22.
- Hermý, M. & Verheyen, K. (2007) Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. *Ecological Research*, **22**, 361-371.
- Hill, M.O., Mountford, J.O., Roy, D.B. & Bunce, R.G.H. (1999) *ECOFAC 2a Technical Annex - Ellenberg's Indicator Values for British Plants*. Department of the Environment, Transport and the Regions (DETR), Norwich, UK, pp. 47.
- Hodkinson, D.J., Askew, A.P., Thompson, K., Hodgson, J.G., Bakker, J.P. & Bekker, R.M. (1998) Ecological correlates of seed size in the British flora. *Functional Ecology*, **12**, 762-766.
- Honnay, O., Hermý, M. & Coppin, P. (1999) Impact of habitat quality on forest plant species colonization. *Forest Ecology and Management*, **115**, 157-170.
- Hopfensperger, K.N. (2007) A review of similarity between seed bank and standing vegetation across ecosystems. *Oikos*, **116**, 1438-1448.
- Jacquemyn, H., Endels, P., Brys, R., Hermý, M. & Woodell, S.R.J. (2009) Biological flora of the British Isles: *Primula vulgaris* Huds. (*P. acaulis* (L.) Hill). *Journal of Ecology*, **97**, 812-833.

- Jankowska-Blaszczuk, M. & Grubb, P.J. (2006) Changing perspectives on the role of the soil seed bank in northern temperate deciduous forests and in tropical lowland rain forests: parallels and contrasts. *Perspectives in Plant Ecology, Evolution and Systematics*, **8**, 3-21.
- Jankowska-Blaszczuk, M., Kwiatkowska, A.J., Panufnik, D. & Tanner, E. (1998) The size and diversity of the soil seed banks and the light requirements of the species in sunny and shady natural communities of the Bialowieza Primeval Forest. *Plant Ecology*, **136**, 105-118.
- Kelly, D.L. (2004) Irish native woodland plant communities. In: *Ireland's Native Woodlands* (eds C. Doyle & D. Little), pp. 91-100. Woodlands of Ireland, Galway, Ireland.
- Kjellsson, G. (1992) Seed banks in Danish deciduous forests: species composition, seed influx and distribution pattern in soil. *Ecography*, **15**, 86-100.
- Leck, M.A., Parker, T. & Simpson, R.L. (1993) *Ecology of Soil Seed Banks*. Academic Press, London, UK, pp. 462.
- Leckie, S., Vellend, M., Bell, G., Waterway, M.J. & Lechowicz, M.J. (2000) The seed bank in an old-growth, temperate deciduous forest. *Canadian Journal of Botany*, **78**, 181-192.
- Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell Publishing, Malden, USA, pp. 256.
- Matlack, G.R. (1994) Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology*, **75**, 1491-1502.
- McCune, B. & Grace, J.B. (2002) *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, USA, pp. 300.
- McCune, B. & Mefford, M.J. (2006) *PC-ORD: Multivariate Analysis of Ecological Data, Version 5*. MjM Software Design, Gleneden Beach, USA.
- Milcu, A., Schumacher, J. & Scheu, S. (2006) Earthworms (*Lumbricus terrestris*) affect plant seedling recruitment and microhabitat heterogeneity. *Functional Ecology*, **20**, 261-268.
- Moles, A.T. & Westoby, M. (2004) Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology*, **92**, 372-383.

- Perrin, P.M. & Daly, O.H. (2010) *A Provisional Inventory of Ancient and Long-Established Woodland in Ireland*. Irish Wildlife Manuals, No. 46. National Parks and Wildlife Service, Department of the Environment, Heritage and Local Government, Dublin, Ireland, pp. 71.
- Peterken, G.F. & Game, M. (1984) Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *The Journal of Ecology*, **72**, 155-182.
- Plue, J., Dupouey, J.-L., Verheyen, K. & Hermy, M. (2009) Forest seed banks along an intensity gradient of ancient agriculture. *Seed Science Research*, **19**, 103-114.
- Plue, J., Hermy, M., Verheyen, K., Thuillier, P., Saguez, R. & Decocq, G. (2008) Persistent changes in forest vegetation and seed bank 1,600 years after human occupation. *Landscape Ecology*, **23**, 673-688.
- Plue, J., Van Gils, B., Peppler-Lisbach, C., De Schrijver, A., Verheyen, K. & Hermy, M. (2010a) Seed-bank convergence under different tree species during forest development. *Perspectives in Plant Ecology, Evolution and Systematics*, **12**, 211-218.
- Plue, J., Verheyen, K., Van Calster, H., Marage, D., Thompson, K., Kalamees, R., Jankowska-Blaszczuk, M., Bossuyt, B. & Hermy, M. (2010b) Seed banks of temperate deciduous forests during secondary succession. *Journal of Vegetation Science*, **21**, 965-978.
- Reader, R.J. (1993) Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. *Journal of Ecology*, **81**, 169-175.
- Schmidt, I., Leuschner, C., Mölder, A. & Schmidt, W. (2009) Structure and composition of the seed bank in monospecific and tree species-rich temperate broad-leaved forests. *Forest Ecology and Management*, **257**, 695-702.
- Ter Heerdt, G.N.J., Verweij, G.L., Bekker, R.M. & Bakker, J.P. (1996) An improved method for seed-bank analysis: seedling emergence after removing the soil by sieving. *Functional Ecology*, **10**, 144-151.

- The Woodland Trust (2005) *The Conservation and Restoration of Plantations on Ancient Woodland Sites: A Guide for Woodland Owners and Managers*. The Woodland Trust, Grantham, UK, pp. 11.
- Thomaes, A., De Keersmaecker, L., De Schrijver, A., Vandekerckhove, K., Verschelde, P. & Verheyen, K. (2011) Can tree species choice influence recruitment of ancient forest species in post-agricultural forest? *Plant Ecology*, **212**, 573-584.
- Thompson, K. (1987) Seeds and seed banks. *New Phytologist*, **106**, 23-34.
- Thompson, K., Bakker, J.P., Bekker, R.M. & Hodgson, J.G. (1998) Ecological correlates of seed persistence in soil in the north-west European flora. *The Journal of Ecology*, **86**, 163-169.
- Thompson, K., Band, S.R. & Hodgson, J.G. (1993) Seed size and shape predict persistence in soil. *Functional Ecology*, **7**, 236-241.
- Thompson, R., Humphrey, J., Harmer, R. & Ferris, R. (2003) *Restoration of Native Woodland on Ancient Woodland Sites*. Forestry Commission, Edinburgh, UK, pp. 58.
- Turnbull, L.A., Rees, M. & Crawley, M.J. (1999) Seed mass and the competition/colonization trade off: a sowing experiment. *Journal of Ecology*, **87**, 899-912.
- Van Calster, H., Chevalier, R., Van Wyngene, B., Archaux, F., Verheyen, K. & Hermy, M. (2008) Long-term seed bank dynamics in a temperate forest under conversion from coppice-with-standards to high forest management. *Applied Vegetation Science*, **11**, 251-260.
- Van der Veken, S., Rogister, J., Verheyen, K., Hermy, M. & Nathan, R. (2007) Over the (range) edge: a 45-year transplant experiment with the perennial forest herb *Hyacinthoides non-scripta*. *Journal of Ecology*, **95**, 343-351.
- Vellend, M. (2005) Land-use history and plant performance in populations of *Trillium grandiflorum*. *Biological Conservation*, **124**, 217-224.
- Verheyen, K. & Hermy, M. (2001) The relative importance of dispersal limitation of vascular plants in secondary forest succession in Muizen Forest, Belgium. *Journal of Ecology*, **89**, 829-840.

- Verheyen, K. & Hermy, M. (2004) Recruitment and growth of herb-layer species with different colonizing capacities in ancient and recent forests. *Journal of Vegetation Science*, **15**, 125-134.
- Verheyen, K., Honnay, O., Motzkin, G., Hermy, M. & Foster, D.R. (2003) Response of forest plant species to land-use change: a life-history trait-based approach. *Journal of Ecology*, **91**, 563-577.
- Wang, J., Ren, H., Yang, L., Li, D. & Guo, Q. (2009) Soil seed banks in four 22-year-old plantations in South China: Implications for restoration. *Forest Ecology and Management*, **258**, 2000-2006.
- Warr, S.J., Kent, M. & Thompson, K. (1994) Seed bank composition and variability in five woodlands in south-west England. *Journal of Biogeography*, **21**, 151-168.
- Webb, D. (1983) The flora of Ireland in its European context. *Journal of Life Sciences of the Royal Dublin Society*, **4**, 143-160.
- Willems, J.H. & Huijsmans, K.G.A. (1994) Vertical seed dispersal by earthworms: a quantitative approach. *Ecography*, **17**, 124-130.

CHAPTER 6

THE IMPACTS OF LAND-USE HISTORY ON WOODLAND DECOMPOSER POPULATION AND DECOMPOSITION DYNAMICS IN THE GEARAGH

6.1 Abstract

The aim of this study was to compare the soil and surface decomposer community as well as the decomposition dynamics of an ancient woodland with adjacent stands of old secondary woodland, recent secondary woodland, and grassland. Investigations were made into: (i) the ground- and litter-dwelling (non-oligochaete) invertebrate communities using pitfall traps; (ii) the oligochaete communities using the liquid-mustard extraction method; (iii) the bacterial communities using microbial community-level physiological profiling with Biolog EcoPlates™; and (iv) decomposition dynamics by measuring the percentage mass loss of leaf litter in coarse, medium, and fine mesh litterbags. The decomposer communities, soil bacteria, and decomposition processes were markedly different in the ancient woodland, secondary woodland, and grassland sites. The ancient woodland communities were dominated by detritivores, had high abundances of enchytraeid worms, but relatively low densities of earthworms. The secondary woodland sites had greater activity and diversity of bacteria, low abundances of enchytraeids, and high densities of earthworms compared to ancient woodland. The results suggest that fungi, fungal-feeding organisms and their predators are more abundant in the ancient woodland, while the secondary woodland has become a more bacterial-dominated system. Past woodland clearance and conversion to agriculture has modified several abiotic and biotic factors which have resulted in an altered community structure and functioning in the secondary woodland sites.

6.2 Introduction

The soil and surface faunal community of woodland ecosystems is generally acknowledged to be remarkably abundant and diverse (Petersen and Luxton, 1982). The high diversity of these communities is thought to be related to the complex spatial heterogeneity of the soil and litter microhabitats (Giller, 1996; Bardgett, 2002). In addition, the large annual influx of organic material through litterfall provides an abundant source of energy and nutrients for most organisms in woodland food webs (Moore *et al.*, 2004). These organisms play a key role in the decomposition of this material (Seastedt, 1984), and also influence important processes such as nutrient cycling, soil structure, and soil organic matter turnover.

Fungi and bacteria are directly responsible for most of the decomposition of organic matter in temperate woodlands. Indeed, decomposition often increases with greater fungal diversity (Setälä and McLean, 2004; Tiunov and Scheu, 2005). Many invertebrate species are unable to digest complex recalcitrant materials in leaf litter themselves, and so depend on bacteria and fungi to process the material for them. Collembolans and mites, for example, not only directly consume detritus, but also consume the bacterial and fungal populations in the soil and litter layers and in fact regulate populations of these microbes (Hattenschwiler *et al.*, 2005).

Enchytraeid worms ('pot worms') are a group of small unpigmented oligochaetes found in marine, freshwater and terrestrial habitats, and commonly found in moist woodland soils rich in organic matter (Coleman *et al.*, 2004). Enchytraeids mix organic material into the soil and can influence soil structure through their burrowing activity (Van Vliet *et al.*, 1995). Macrofauna (invertebrates > 10mm length) such as diplopods, isopods, and earthworms, fragment and consume larger amounts of litter and distribute it as faecal pellets elsewhere in the soil (Coleman *et al.*, 2004). Their actions further impact on the activity and composition of microbial decomposers, as well as other microfauna (invertebrates < 0.2mm in length; mesofauna are invertebrates between 0.2 mm and 10 mm in length) (Seastedt, 1984). Finally, predators, such as carabid beetles, can regulate the activity of these detritivore populations.

Considerable differences in the soil and ground faunal community can exist between different types of woodland and forest. For instance, coniferous forest soils, which typically have a low pH, are generally dominated by enchytraeids and other microfauna such as mites and collembolans, while deciduous woodlands tend to have greater abundances of macrofauna such as diplopods, isopods, and earthworms (Petersen and Luxton, 1982). The abundance and diversity of carabid beetles has also been found to vary between natural deciduous woodlands and conifer plantations (Day *et al.*, 1993; Koivula *et al.*, 2002; Yu *et al.*, 2008). Studies have even found different soil types within woodlands to possess distinct soil fauna communities, including beech (Schaefer and Schauer mann, 1990; David *et al.*, 1993), pine (Tueben and Smidt, 1992), and oak woodlands (Little *et al.*, 2001).

Differences in previous land-use (Huhta, 2002) and replanting forest stands with a new tree species (Scheu *et al.*, 2003; Cassagne *et al.*, 2004) can also affect the abundance and biomass of soil macrofauna by altering environmental conditions (e.g. nutrient availability, soil structure, microhabitat availability) and soil food web structure. Even differences in management practices between similar types of woodland can alter collembolan communities, as many collembolan species are highly sensitive to increases in soil disturbance (Cassagne *et al.*, 2006). Other studies have tracked changes in macrofauna in boreal forests after a major disturbance event (Paquin and Coderre, 1997). These studies show that soil and ground faunal communities are often very sensitive to environmental variations, and that community composition may be considerably altered by disturbance events (Bardgett, 2002).

The recovery trajectory of faunal communities after woodland clearance for agriculture can influence subsequent ecosystem functioning in secondary woodlands. Indeed, site history can continue to affect soil faunal communities in various ways, even decades after woodland recovery (Goßner *et al.*, 2008). Few studies, however, have made a direct comparison between the soil and ground faunal communities in regenerating secondary woodlands and undisturbed ancient woodlands; most have tended to concentrate only on the vegetation composition (Chapter 4). This is despite the fact that the availability of old-growth habitats is essential for many soil-dwelling arthropod species (Grove, 2002). Previous investigations comparing soil invertebrate communities in old-growth and managed woodlands are restricted to Fennoscandia (Huhta, 2002), and central Europe (Chumak *et al.*, 2005). Some other studies have focused solely on carabid beetles; these have found species richness and abundance to be greater in ancient woodlands than in regenerating stands (Terrell-Nield, 1990; Spence *et al.*, 1996; Assmann, 1999). A number of studies have also reported earthworms to be scarce or absent in old-growth woodlands (Harris and Hill, 1995; Rätty and Huhta, 2004), even though deciduous woodlands are generally regarded as being favourable habitats for earthworms (Lee, 1985). Ancient woodland stands have also been found to differ in terms of their microbial community; indications are that ancient

woodlands have a higher relative abundance of fungi and a lower abundance of bacteria compared with secondary woodlands (Harris and Hill, 1995; Fraterrigo *et al.*, 2006).

Disturbances to the soil as a result of agricultural use (both directly through physical alteration of soil structure and indirectly from effects on the above-ground plant community) can greatly modify environmental conditions even on a small scale, thereby affecting the abundance of many microbial species (Kang and Mills, 2004; Fraterrigo *et al.*, 2006). Fungal organisms are generally more vulnerable to these disturbance events than are bacteria (Hedlund *et al.*, 2004), potentially leading to reduced fungal abundance and diversity in post-agricultural woodlands. The enduring effects of past land-use on soil properties may lead to lasting changes in microbial community composition and activity (Compton and Boone, 2002).

Changes in soil properties may also be related to the activity of burrowing earthworms that consume litter and mix it with the mineral soil (Huhta, 2002). Agricultural land is frequently improved by liming, which can have the effect of enhancing earthworm populations and reducing the abundance of more acid-tolerant microbial species (Pawlett *et al.*, 2009). Other effects of past land-use include changes in site hydrology and altered litter inputs; most organisms in the soil food web depend on litter and other detritus as a source of energy and nutrients (Moore *et al.*, 2004). A reduction in litter quantity as a result of woodland clearance may therefore have a negative impact on microorganisms and other organisms that consume them. Even carabid beetles have been shown to be sensitive to such changes on the woodland floor (Day *et al.*, 1993; Poole *et al.*, 2003). Disturbances can also arise indirectly via effects on the plant community (Hedlund *et al.*, 2004; Kang and Mills, 2004; Goßner *et al.*, 2008). Ultimately, the numbers of species that can recolonise new woodland within a given time is determined by their dispersal ability, although this remains unclear for many groups of organisms (Ojala and Huhta, 2001; Rantalainen *et al.*, 2004).

Any changes in the diversity or abundance of soil and litter communities are likely to affect decomposition rates of organic matter (Hattenschwiler *et al.*, 2005).

Changes in the feeding activities of microfauna can stimulate or reduce the microbial communities that are responsible for the majority of litter decomposition (Seastedt and Crossley, 1984). In addition, the presence of certain keystone taxa, particularly earthworms, is central for decomposition processes (Bohlen *et al.*, 2004). Earthworms can alter the physical and chemical environment of the soil, modify microbial activity, and aid in the dispersal of microorganisms (McLean *et al.*, 2006). Even increases in predator abundance can indirectly affect microbial populations, for instance by alleviating the negative effect of fungivores on fungal biomass (Lenoir *et al.*, 2006).

An assessment of the diversity and functioning of woodland decomposers is central to understanding how communities and ecosystems respond to past disturbance events. The aim of this study therefore is to compare the soil and ground decomposer communities and the decomposition dynamics of ancient woodland stands with adjacent stands of secondary woodland and grassland. This is investigated by focusing on four aspects relating to woodland biodiversity and function across all study sites: (i) ground- and litter-dwelling invertebrates, (ii) oligochaete communities, (iii) soil bacterial communities, and (iv) the decomposition rates of leaf litter.

6.3 Materials and methods

6.3.1 Ground- and litter-dwelling invertebrates

Information on study site and site selection can be found in previous chapters (see Sections 3.3.1 and 3.3.2). Pitfall traps were used to sample the ground- and litter-dwelling invertebrates in late spring to early summer (April and May). Most invertebrates in the Gearagh have emerged and are active on the woodland floor by this date (McLaughlin *et al.*, 2010). Sampling consisted of a grid of six pitfall traps spaced at least 5 m apart, in each of the replicate sites in the four habitat types (Fig. 6.1). Pitfall traps consisted of plastic cups (7 cm diameter, 9 cm depth) with two drainage holes cut 1 cm from the top of the cup. Each trap was filled with 25 % (v/v) aqueous solution of ethylene glycol to a depth of 1 cm to act as a preserving agent. Liquid detergent was also added to reduce surface tension. Traps were protected

from interference by small mammals and birds with a cover that was raised 2 cm above ground level. Traps were left open for a period of 14 days. All specimens collected in the pitfall traps were preserved in 70 % (v/v) ethanol. Invertebrates were identified to family level when possible, except for carabid beetles, which were identified to species level. A collection of published keys was used for the identification of various taxa, including Acarina (Krantz, 1978), Diplopoda (Blower, 1985), Coleoptera (Unwin, 1988; Luff, 2007), Gastropoda (Cameron *et al.*, 1983; Cameron, 2003), Opiliones (Hillyard, 2005), Collembola (Hopkin, 2007), Diptera (Oosterbroek, 2007), and other ground invertebrates (Tilling, 1987). Specimens collected from the six traps within a site were pooled for the analysis; results are calculated per sampling site.

6.3.2 Oligochaete communities

Earthworms were extracted from 25 × 25 cm plots. Six plots were established randomly in each of the replicate sampling sites (Fig. 6.1). Earthworms were sampled using the liquid-mustard extraction method (Lawrence and Bowers, 2002). Mustard powder (60 g) was dissolved in 6 l of water and the solution was carefully applied to the sample plot. As the liquid-mustard extraction method also stimulates enchytraeid worms to come to the soil surface, these were also included in the sampling procedure. All worms were collected and the earthworms were identified to species level, except for immature earthworms which were labelled as juveniles. Identification and nomenclature follows Sims and Gerard (1999).

6.3.3 Bacterial community-level physiological profiling

The bacterial community-level physiological profile was assessed using Biolog EcoPlates™ (Insam, 1997). Each plate contains a total of 96 wells, consisting of three replicate sets, each of 31 different carbon sources and one control well per set. A tetrazolium dye in each well develops a purple colour in response to carbon utilisation. Soil samples, bulked from six subsamples from each replicate site (Fig. 6.1), were taken from a depth of 0-10 cm using a stainless steel corer (3.5 cm diameter). Samples were stored at 4 ° C for no longer than 24 hours before the soil was extracted for analysis. Five 10 g subsamples were taken from each fresh soil sample, resulting in five subsamples for each sampling site. Each 10 g subsample

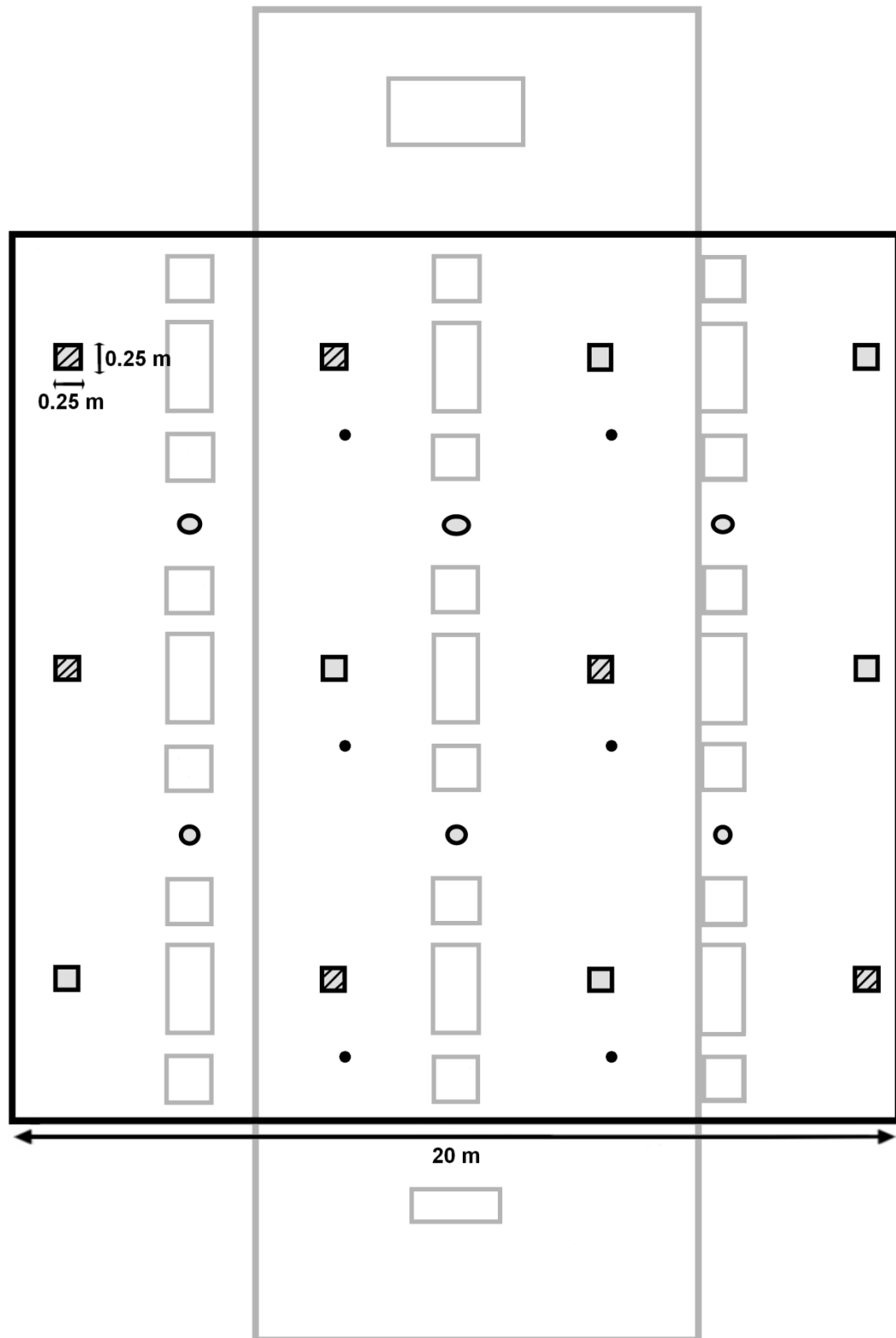


Fig. 6.1 Design of one sampling site, i.e. one of the replicate study sites, with the location of the pitfall traps (grey circles), earthworm sampling plots (grey plots), and soil cores for the bacterial community-level physiological profiling (black dots) outlined in black. The sampling designs used in other sections of the thesis are outlined in grey; see Figs. 3.2, 4.1, and 5.2 for further details. Six of the twelve 0.25 m × 0.25 m plots were randomly selected for earthworm sampling (hatched plots).

was added to 20 ml half-strength Ringer's solution; this was then diluted to a ratio of 1:5000 with Ringer's solution. A 150 μ l aliquot of each subsample was added to each well of a Biolog EcoPlate™. Plates were incubated in darkness at 20 °C and absorbance readings were taken every 24 hours for 3 days at 600 nm using a microplate reader (Model 680 microplate reader; Bio-Rad, Hertfordshire). The single time point absorbance at 72 h was used to quantify carbon source utilisation (Zak *et al.*, 1994).

6.3.4 Decomposition dynamics

Litterbags were used to compare organic matter decomposition rates between ancient, secondary and grassland sites. The old and recent secondary stands were pooled into a single secondary habitat, as there were not enough litterbags constructed by the beginning of the experimental period to use all available sites. Fresh hazel leaf litter (*Corylus avellana*) was collected from the woodland floor and dried in an oven at 40 °C to a constant weight for 3-4 days. Litterbags with one of three different mesh sizes were used: (i) fine mesh (500 μ m), permitting entry of microfauna only; (ii) medium mesh (2 mm), permitting entry of both micro- and mesofauna; and (iii) coarse mesh (10 mm), permitting entry of all micro-, meso-, and macrofauna. All mesh sizes permitted entry of bacteria and fungi. Each of the three different types of litterbags was filled with 4 g of the oven-dried hazel leaves. The litterbags were placed in three different positions in the field: (i) on the soil surface, in contact with the litter layer; (ii) buried 5 cm beneath the soil surface; and (iii) buried 20 cm beneath the soil surface. Five replicates of each treatment were placed in each habitat, giving a total of 45 litterbags at each of the three habitats. Surface litterbags were held in place by a wooden stake. The litterbags were harvested after a period of 120 days in the field. Once retrieved from the field, the litterbags were carefully cleaned to remove major contaminants, mainly soil, and were placed in a drying oven at 40 °C for 48 hours. The leaf material was then weighed in order to determine the percentage mass loss due to decomposition.

Litter on the woodland floor was collected from within four $0.25 \times 0.25 \text{ m}^2$ quadrats randomly located in each of the replicate sites in the three woodland habitats. The

depth of the loose litter was also measured prior to removal. The collected litter was oven-dried at 40 °C for 48 hours and weighed.

Litterfall biomass was assessed using a litter trap design. 10 litter traps were randomly placed in each of the three woodland habitats. The traps used were plastic buckets, 270 mm in diameter and 250 mm high, which were dug into the ground and secured in place with large stones. Litter was collected and processed from all traps every month over a 12 month period. Litter was oven-dried at 40 °C for 48 hours and sorted into leaves of *Quercus robur*, *Fraxinus excelsior*, *Betula pubescens*, *Corylus avellana*, and other litterfall components (leaves of other species, fruits, bark, and twigs).

6.3.5 Data analysis

Ground- and litter-dwelling invertebrates

Macrofauna collected from the pitfalls were classified into principal taxon groups, generally Class or Order (e.g. Coleoptera, Diptera, Gastropoda, etc). The total frequencies in each of the four habitat types were assessed using a one-way chi-squared test for each individual taxon group. Total pitfall data (to family and species level) were also analysed for taxon richness (the total number of taxa in the community), Pielou's evenness, and Shannon-Wiener diversity (Magurran, 2004). Data were analysed with analysis of variance (ANOVA) with Tukey's HSD *post hoc* test, after testing for normality and homogeneity of variance.

Non-metric multidimensional scaling (NMS) (Kruskal, 1964) was used to examine the total ground-dwelling invertebrate assemblages across the habitat types with PC-ORD (McCune and Mefford, 2006). It was run in the autopilot mode using the 'slow and thorough' setting, with the Sørensen (Bray-Curtis) index as a distance measure. The taxon data were log transformed prior to analysis and rare taxa that occurred in fewer than two samples were deleted. The microfauna (mites and collembolans) were examined in greater detail. Each group was analysed with Kruskal-Wallis tests to determine if there were any differences in abundances between the different habitat types. Indicator species analysis (ISA) was used to determine ground-dwelling invertebrate taxa which were affiliated with particular

habitats (Dufrene and Legendre, 1997). An indicator value, ranging from zero (no indication) to 100 (perfect indication) was calculated for each taxon in each habitat type. The statistical significance of the indicator values was evaluated by a Monte-Carlo method with 1000 randomisations. The feeding preference of each group (herbivore, macrodetritivore, microdetritivore, predator, or omnivore) was assigned based on information from the keys (Krantz, 1978; Blower, 1985; Cameron, 2003; Hillyard, 2005; Hopkin, 2007; Oosterbroek, 2007). The total abundances of individuals in each habitat type were assessed using a one-way chi-squared test for each individual feeding preference group.

The carabid species data were treated separately and used to calculate carabid species richness, Pielou's evenness, and Shannon-Wiener diversity (Magurran, 2004); these parameters were analysed using analysis of variance (ANOVA) with Tukey's HSD *post hoc* test. Species traits were also classified according to broad habitat associations (woodland, generalist or open habitat) and microhabitat associations (moist, eurytopic or dry), based on information from Luff (2007). Community ordinations of the carabid data was carried out using non-metric multidimensional scaling (NMS) (Kruskal, 1964) with PC-ORD (McCune and Mefford, 2006). The ordination was run using the 'slow and thorough' setting in the autopilot mode, with the Sørensen (Bray-Curtis) index as a distance measure.

Oligochaete communities

The earthworm and enchytraeid abundances for each sample were calculated per square metre. Differences in population densities between the habitat types were examined using an analysis of variance (ANOVA). All data was log transformed prior to analysis in order to approximate to normality and homogeneity of variance. Tukey's HSD *post hoc* test was used to identify significant differences between habitat types. Species data were examined using Kruskal-Wallis tests, as the data for several individual species contained many zeros and could not conform to the assumptions of a parametric test. Earthworm species were also pooled into ecological groups (Bouché, 1977): epigeic species, which live and feed in the litter layer; endogeic species, which live and feed in the mineral soil horizon; and anecic species, which feed on surface litter, but burrow deeply. The abundance of

earthworms was then analysed with a two-way analysis of variance, with ecological category (epigeic, endogeic, or anecic) and habitat (ancient, old secondary, recent secondary, or grassland) as factors.

Bacterial community-level physiological profiling

The data from the Biolog EcoPlatesTM were used to assess the functional diversity of the samples. The triplicate samples were used to calculate the average absorbance values for each carbon source for every plate. The average well colour development minus the control blank wells (AWCD) is a measure of bacterial activity (Garland and Mills, 1991). The functional diversity (substrate diversity) was calculated as the Shannon index for diversity (H'). Substrate richness (S) is a measure of the number of different carbon substrates utilised and is a reflection of the number of different groups of microorganisms found in the sample. Shannon evenness (E) is the equitability of activities across all utilised substrates. Differences in AWCD, Shannon diversity, richness, and evenness were analysed using Kruskal-Wallis tests.

Principal components analysis (PCA) ordination was performed on the Biolog EcoPlate data to characterise the microbial ecology of the soil in the Gearagh using PC-ORD (McCune and Mefford, 2006). The data were first corrected using the control wells, and then separately divided by the respective plate's average well colour development (AWCD). The resulting data were then subject to a logarithmic transformation. Analysis was performed based on the utilisation of all of the individual substrates of a plate.

Decomposition dynamics

Differences in leaf litter mass loss due to decomposition were analysed using a parametric three-way analysis of variance (ANOVA) with site (ancient, secondary or grassland), mesh size (coarse, medium or fine) and position (surface, 5 cm depth or 20 cm depth) as independent fixed factors. All data were log transformed prior to analysis to approximate to normality and homogeneity of variance among treatments.

The depth and quantity of leaf litter on the woodland floor was analysed using a one-way analysis of variance (ANOVA). A one-way analysis of variance (ANOVA) was

also used to compare the total annual litterfall biomass in each of the three woodland habitats, as well as the total biomass of each of the measured litterfall components (*Quercus robur*, *Fraxinus excelsior*, *Betula pubescens*, and *Corylus avellana* leaves). Data were log transformed when necessary to meet statistical assumptions.

6.4 Results

6.4.1 Ground- and litter-dwelling invertebrates

A total of 30,222 invertebrates from 92 taxa were collected and identified from the pitfall traps. Microarthropods (Collembola and Acarina) accounted for the majority of these individuals, with 24,416 individuals identified from the Collembola alone. Coleoptera were the most abundant macrofaunal group, with 1,409 collected from 15 different families. Other notable macrofaunal groups that were collected included Diptera (22 % of macrofauna), Gastropoda (10 %), Diplopoda (9 %), Hemiptera (8 %), and Opiliones (7 %) (see Table 6.1).

Although the total abundance of macrofauna was similar between all habitats, certain taxonomic groups showed considerable differences between habitats (Table 6.1). Gastropoda appeared to be far more abundant in the ancient woodland than in any of the other sites, while Opiliones were most abundant in the ancient and old secondary woodlands. However, Hemiptera and Hymenoptera were more abundant in the grassland habitat. Coleoptera were the most abundant group in each of the woodland habitats, but were only the third most abundant group in the grassland after Hemiptera and Diptera.

There was little difference in taxon richness between the sites (Table 6.2). However, the greatest diversity was found in the ancient woodland. Diversity decreased as time since agricultural abandonment decreased, so that the recent secondary had the lowest diversity of the woodland sites and the grassland the lowest of all sites. A similar trend was shown by the evenness index, which quantifies the similarity in abundance of each taxonomic group in a community; the higher values in the

Table 6.1 Total number of individuals and relative abundance of each macrofaunal taxon group from the four habitat types of the Gearagh (excluding microfauna: Acarina and Collembola) from the total pitfall sampling effort. Significance of a one-way chi-squared test on the number of individuals per habitat type in each taxon group is given.

Taxonomic group	Ancient woodland		Old secondary woodland		Recent secondary woodland		Grassland		p
	No.	%	No.	%	No.	%	No.	%	
Aranae	2	0.18	4	0.39	1	0.09	9	0.79	< 0.05
Coleoptera	316	27.94	484	47.59	396	37.29	251	21.92	< 0.001
Diplopoda	131	11.58	45	4.42	88	8.29	139	12.14	< 0.001
Diptera	212	18.74	236	23.21	327	30.79	262	22.88	< 0.001
Gastropoda	220	19.45	63	6.19	92	8.66	76	6.64	< 0.001
Hemiptera	44	3.89	35	3.44	19	1.79	271	23.67	< 0.001
Hirudinea	0	0	0	0	0	0	2	0.17	> 0.05
Hymenoptera	33	2.92	21	2.06	57	5.37	102	8.91	< 0.001
Isopoda	2	0.18	0	0	0	0	0	0	> 0.05
Lepidoptera	2	0.18	0	0	5	0.47	1	0.09	0.071
Oligochaeta	32	2.83	27	2.65	14	1.32	25	2.18	0.070
Opiliones	137	12.11	101	9.93	63	5.93	5	0.44	< 0.001
Thysanoptera	0	0	1	0.1	0	0	2	0.17	> 0.05
Total	1131		1017		1062		1145		< 0.05

Table 6.2 Mean (\pm standard error) values of total ground-dwelling invertebrate and carabid species diversity indices per sampling site in the four different habitat types of the Gearagh. Results of a one-way ANOVA are given. Significant differences between habitat types are indicated with different superscript letters; any two samples within a row with a common letter are not significantly different ($P \geq 0.05$).

	Ancient woodland	Old secondary woodland	Recent secondary woodland	Grassland	<i>P</i>
<i>Total invertebrates</i>					
Taxon richness	46.2 \pm 2.0	44.0 \pm 1.4	42.6 \pm 2.9	47.4 \pm 1.4	> 0.05
Evenness	0.61 \pm 0.03 ^b	0.57 \pm 0.03 ^b	0.51 \pm 0.02 ^{ab}	0.43 \pm 0.04 ^a	< 0.01
Diversity	2.33 \pm 0.09 ^b	2.15 \pm 0.12 ^b	1.91 \pm 0.08 ^{ab}	1.65 \pm 0.14 ^a	< 0.01
<i>Carabid beetles</i>					
Species richness	7.2 \pm 0.8	9.0 \pm 1.0	8.8 \pm 1.2	6.8 \pm 1.1	> 0.05
Evenness	0.78 \pm 0.01 ^{ab}	0.63 \pm 0.08 ^a	0.64 \pm 0.06 ^a	0.93 \pm 0.01 ^b	< 0.01
Diversity	1.52 \pm 0.09	1.35 \pm 0.16	1.35 \pm 0.10	1.72 \pm 0.14	> 0.05

ancient woodland indicate that there is less variation in taxon abundances in that community in comparison with the other habitats.

The microfauna also revealed a number of differences between the habitats (Table 6.3). Overall, significantly greater numbers of mites were found in the ancient woodland than in any of the other habitats. This is reflected in the abundance of oribatid mites, which were most numerous in the ancient woodland. A similar trend was shown for the Prostigmata; however, the Astigmata were significantly more abundant in the grassland sites. Trends in the Collembola were less obvious. Overall abundance was greatest in the grassland, followed by the recent secondary, ancient woodland, and the old secondary. The most abundant groups all had their greatest densities in the grassland sites: Sminthuridinae, Hypogastrurinae, and Dicyrtominae. However, there was no significant result for the latter due to high within-site variation. A number of the less common groups were most abundant in the ancient woodland, including Entomobryidae, Neanuridae, and Onychiuridae.

The NMS ordination of total ground-dwelling invertebrates represented 75 % of the variation, with a three-dimensional solution recommended (Fig. 6.2; only the first

Table 6.3 Average number of microfauna (Acarina and Collembola) per trap site in the four habitat types of the Gearagh. Results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different superscript letters; any two within a row with a common letter are not significantly different ($P > 0.05$).

Taxon group	Ancient woodland	Old secondary woodland	Recent secondary woodland	Grassland	<i>P</i>
<i>Acarina</i>					
Astigmata	4 ± 1.1 ^a	2 ± 0.6 ^a	6 ± 4.6 ^{ab}	14 ± 4.1 ^b	< 0.05
Mesostigmata	4 ± 1.3	3 ± 0.8	8 ± 7.0	7 ± 2.7	> 0.05
Oribatida	106 ± 19.0 ^b	31 ± 9.5 ^a	31 ± 8.1 ^a	27 ± 6.0 ^a	< 0.05
Prostigmata	13 ± 2.3 ^b	1 ± 0.7 ^a	2 ± 0.9 ^a	6 ± 2.1 ^a	< 0.01
Total	128 ± 22.0 ^b	36 ± 10.0 ^a	47 ± 12.5 ^a	53 ± 10.4 ^a	< 0.05
<i>Collembola</i>					
Dicyrtominae	146 ± 46.4	106 ± 23.9	362 ± 225.1	975 ± 531.5	> 0.05
Entomobryidae	16 ± 4.9 ^b	5 ± 1.3 ^a	5 ± 1.2 ^{ab}	1 ± 0.6 ^a	< 0.05
Hypogastrurinae	330 ± 110.3 ^{ab}	100 ± 30.2 ^a	399 ± 85.2 ^{ab}	581 ± 127.8 ^b	< 0.05
Isotomidae	2 ± 1.6	2 ± 0.4	3 ± 2.5	10 ± 5.3	> 0.05
Neanuridae	11 ± 8.0	1 ± 0.4	1 ± 0.4	1 ± 0.8	0.051
Onychiuridae	12 ± 1.8 ^a	5 ± 2.6 ^{ab}	4 ± 1.9 ^a	1 ± 0.7 ^a	< 0.05
Sminthurinae	166 ± 31.6	322 ± 83.5	274 ± 65.7	1042 ± 345.6	0.084
Total	683 ± 121.7	540 ± 78.1	1047 ± 269.9	2613 ± 909.4	0.082

two axes are shown). Across Axis 1 the grassland sites were separated clearly from the woodland sites; the five grassland sites form a relatively distinct, though rather scattered, group in one half of the ordination space. Axis two helped to further separate the woodland sites from each other; the separation between the ancient woodland and the two secondary woodland types is quite clear. The ancient woodland sites form a tight cluster in the top right hand sector of the diagram. However, the secondary woodland sites are grouped more widely apart, and there is a degree of overlap between the old secondary and the recent secondary woodland sites. The beetle family Carabidae was highly positively correlated with Axis 1 ($r = 0.70$, d.f. = 18, $P < 0.001$); thus, the woodland sites are likely to be highly favourable for carabid beetles, in comparison with the grassland. Axis 1 was also highly negatively correlated with family Aphididae ($r = -0.84$, d.f. = 18, $P < 0.001$), suggesting that aphids are an important component of the grassland sites. Harvestmen were positively correlated with Axis 2 ($r = 0.75$, d.f. = 18, $P < 0.01$

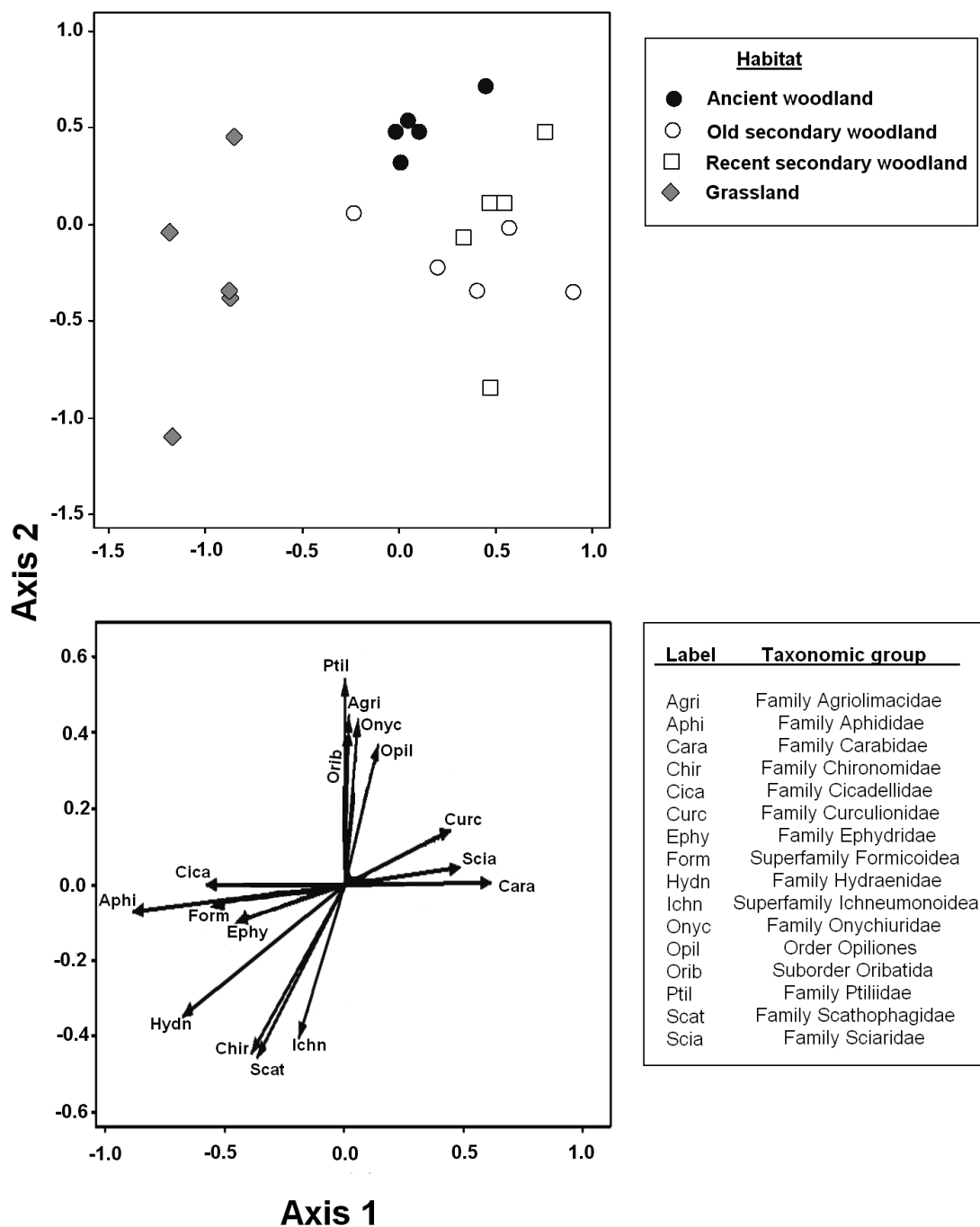


Fig. 6.2 NMS ordination of ground- and litter-dwelling invertebrates captured in pitfall traps. The upper panel shows axis 1 and axis 2 plots for all sites in the four habitat types of the Gearagh. The lower panel shows a joint plot between axes 1 and 2 and the 16 taxa selected by analysis as the most important (score greater than ± 0.3). Cumulative variation in the original dataset explained by the ordination is 51 %: Axis 1 = 43 %, Axis 2 = 8 %, Final Stress = 9.2; Final Instability = 0.00001.

A total of thirteen significant indicator taxa were identified by Indicator Species Analysis in the grassland sites, five of which were herbivores (Table 6.4). By contrast, only three taxa were significantly affiliated with the recent secondary (one herbivore), and only two with the old secondary (one herbivore). In the ancient woodland, nine taxa were identified as being significantly associated with the habitat, the majority of which were some form of detritivore. No herbivore was significantly identified as an indicator taxa in the ancient woodland. Taxa from Collembola, Acarina, Gastropoda, and Opiliones were all commonly identified in the ancient woodland, whereas a number of Coleoptera and Diptera families had a preference for the old and recent secondary woodlands. A species of dung-beetle, *Anoplotrupes stercorosus* (Coleoptera, Geotrupidae), was only found in the ancient woodland sites. The grassland habitat was associated with a wider range of taxonomic groups, including Hemiptera, Coleoptera, Collembola, Diptera, and Araneae.

The total abundance of individuals in each feeding preference group varied between the habitats (Fig. 6.3). Microdetritivores (invertebrates less than 1 mm in length that feed primarily on small detritus fragments and associated fungi) were significantly more abundant in the ancient woodland ($\chi^2 = 21.208$; $d.f. = 3$; $P < 0.001$), once the three most common groups of Collembola were excluded (Dicyrtominae, Hypogastrurinae, and Sminthuridinae). These were excluded in order to aid interpretation; these groups can occur in high density aggregations, which can pose problems for assessment of total pitfall catch abundances (Coleman *et al.*, 2004). Similarly, macrodetritivores (invertebrates more than 1 mm in length that feed primarily on large fragments of detritus and associated fungi) were caught more frequently in pitfall traps from the ancient woodland than in either of the secondary woodlands ($\chi^2 = 18.421$; $d.f. = 2$; $P < 0.001$). The abundance of herbivores on the woodland floor increased significantly from the ancient woodland to the secondary woodlands, and was greatest in the grassland ($\chi^2 = 30.665$; $d.f. = 3$; $P < 0.001$).

Table 6.4 Ground- and litter-dwelling invertebrates identified in each habitat type of the Gearagh by Indicator Species Analysis and their feeding preference. Taxa with a significant indicator value ($P \leq 0.05$) are shown in bold. Significance of Monte-Carlo tests: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$. See text (section 5.3.1) for a list of keys used to obtain information on feeding preference.

Indicator taxon	Taxonomic group	Indicator Value (%)				Feeding preference
		Ancient woodland	Old secondary woodland	Recent secondary woodland	Grassland	
Ancient woodland						
Family Neanuridae	Collembola	82 **	1	4	4	Microdetritivore
Family Entomobryidae	Collembola	58 *	17	20	3	Microdetritivore
Suborder Prostigmata	Acarina	58 **	4	8	26	Predator
Suborder Oribatida	Acarina	55 ***	16	16	14	Microdetritivore
Family Onychiuridae	Collembola	54 **	19	10	4	Microdetritivore
Family Agriolimacidae	Gastropoda	52 **	10	20	12	Macrodetritivore
Family Ptiliidae	Coleoptera	52 *	4	3	14	Microdetritivore
Lophopilio palpinalis	Opiliones	50 **	31	15	2	Predator
Family Limacidae	Gastropoda	50 **	14	25	10	Macrodetritivore
Family Polydesmidae	Diplopoda	45	4	16	2	Macrodetritivore
Leiobunum blackwalli	Opiliones	44	32	24	0	Predator
Family Zonitidae	Gastropoda	44	6	2	0	Macrodetritivore
Leiobunum rotundum	Opiliones	43	30	15	0	Predator
Family Phoridae	Diptera	41	19	24	13	Microdetritivore
Family Arionidae	Gastropoda	41	12	13	27	Macrodetritivore
Family Glomeridesmidae	Diplopoda	40	12	1	1	Macrodetritivore
Family Geotrupidae	Coleoptera	40	0	0	0	Macrodetritivore
Order Isopoda	Isopoda	40	0	0	0	Macrodetritivore
Family Curculionidae	Coleoptera	38	38	14	0	Herbivore
Family Lumbricidae	Oligochaeta	33	27	14	26	Macrodetritivore
Family Sphaeroceridae	Diptera	28	20	22	25	Microdetritivore
Family Delphacidae	Hemiptera	27	0	0	7	Herbivore
Family Pselaphidae	Coleoptera	24	24	9	11	Predator
Family Helicidae	Gastropoda	21	21	6	6	Macrodetritivore
Family Psychodidae	Diptera	21	14	19	11	Microdetritivore
Family Dytiscidae	Coleoptera	20	20	0	0	Predator
Family Anisopodidae	Diptera	11	11	6	3	Microdetritivore
Dicranopalpus ramosus	Opiliones	10	0	10	0	Predator
Family Fanniidae	Diptera	10	0	0	10	Microdetritivore
Old secondary woodland						
Family Elateridae	Coleoptera	0	79 **	0	16	Herbivore
Family Carabidae	Coleoptera	22	38 *	31	9	Predator
Family Limoniidae	Diptera	6	30	1	24	Omnivore
Family Tipulidae	Diptera	0	28	21	0	Herbivore
Platybunus triangularis	Opiliones	0	20	20	0	Predator
Family Silphidae	Coleoptera	0	20	0	0	Macrodetritivore
Phalangium opilio	Opiliones	0	20	0	0	Predator
Family Simuliidae	Diptera	0	20	0	0	Parasite
Family Camillidae	Diptera	0	20	0	0	Microdetritivore
Superfamily Apoidea	Hymenoptera	0	20	0	0	Herbivore
Family Lygaeidae	Hemiptera	0	20	0	0	Herbivore
Family Coccoidea	Hemiptera	0	20	0	0	Herbivore
Family Enchytraidae	Oligochaeta	4	16	4	4	Microdetritivore

Table 6.4 continued.

Indicator taxon	Taxonomic group	Indicator Value (%)				Feeding preference
		Ancient woodland	Old secondary woodland	Recent secondary woodland	Grassland	
Recent secondary woodland						
Order Psocoptera	Psocoptera	1	0	76 *	0	Microdetritivore
Family Sciaridae	Diptera	19	23	55 *	1	Herbivore
Family Anthomyiidae	Diptera	13	27	45	12	Herbivore
Superfamily Ceraphronoidea	Hymenoptera	27	7	41	1	Herbivore
Family Muscidae	Diptera	19	25	40	1	Omnivore
Family Hybotidae	Diptera	0	0	36	8	Predator
Family Staphylinidae	Coleoptera	24	19	34 *	23	Predator
Superfamily Chalcidoidea	Hymenoptera	10	8	32	23	Herbivore
Superfamily Cynipoidea	Hymenoptera	2	2	22	9	Herbivore
Family Empididae	Diptera	10	3	20	3	Predator
Family Rhizophagidae	Coleoptera	0	0	20	0	Predator
Family Opetiidae	Diptera	0	0	20	0	Microdetritivore
Family Clausiliidae	Gastropoda	0	0	20	0	Herbivore
Family Mycetophilidae	Diptera	0	0	10	10	Herbivore
Grassland						
Family Cicadellidae	Hemiptera	0	0	1	96 ***	Herbivore
Family Hydraenidae	Coleoptera	0	1	0	94 ***	Herbivore
Superfamily Formicoidea	Hymenoptera	0	0	0	80 ***	Macrodetritivore
Family Aphididae	Hemiptera	9	3	5	79 ***	Herbivore
Subfamily Dicyrtominae	Collembola	9	7	23	61	Microdetritivore
Family Byrrhidae	Coleoptera	3	0	3	60 *	Herbivore
Family Scydmaenidae	Coleoptera	0	0	0	60 *	Predator
Subfamily Sminthuridinae	Collembola	9	18	15	58 **	Microdetritivore
Family Cryptophagidae	Coleoptera	1	0	0	58 *	Macrodetritivore
Suborder Astigmata	Acarina	17	6	13	55 *	Microdetritivore
Family Chironomidae	Diptera	7	19	22	53 **	Herbivore
Family Linyphiidae	Araneae	5	16	1	53 *	Predator
Family Julidae	Diplopoda	7	11	26	52 **	Macrodetritivore
Family Cecidomyiidae	Diptera	3	7	6	51 *	Omnivore
Family Ephyridae	Diptera	3	0	0	50	Predator
Family Isotomidae	Collembola	4	8	12	48	Microdetritivore
Family Drosophilidae	Diptera	4	0	0	48	Microdetritivore
Family Hypogastrurinae	Collembola	23	7	28	41	Microdetritivore
Superfamily Proctotrupeoidea	Hymenoptera	8	13	24	41	Herbivore
Family Scathophagidae	Diptera	4	16	0	40	Predator
Subclass Hirudinea	Hirudinea	0	0	0	40	Predator
Superfamily Ichneumonoidea	Hymenoptera	8	2	20	37	Predator
Suborder Mesostigmata	Acarina	20	12	29	31	Predator
Family Calliphoridae	Diptera	5	0	0	30	Herbivore
Family Ceratopogonidae	Diptera	0	0	5	30	Predator
Family Aeolothripidae	Thysanoptera	0	7	0	27	Herbivore
Family Syrphidae	Diptera	0	7	0	27	Herbivore
Family Chrysomelidae	Coleoptera	0	0	0	20	Herbivore
Family Lycosidae	Araneae	0	0	0	20	Predator
Family Chloropidae	Diptera	0	0	0	20	Herbivore
Family Lonchopteridae	Diptera	0	0	0	20	Microdetritivore
Family Hydrometridae	Hemiptera	0	0	0	20	Predator
Family Saldidae	Hemiptera	0	0	0	20	Predator

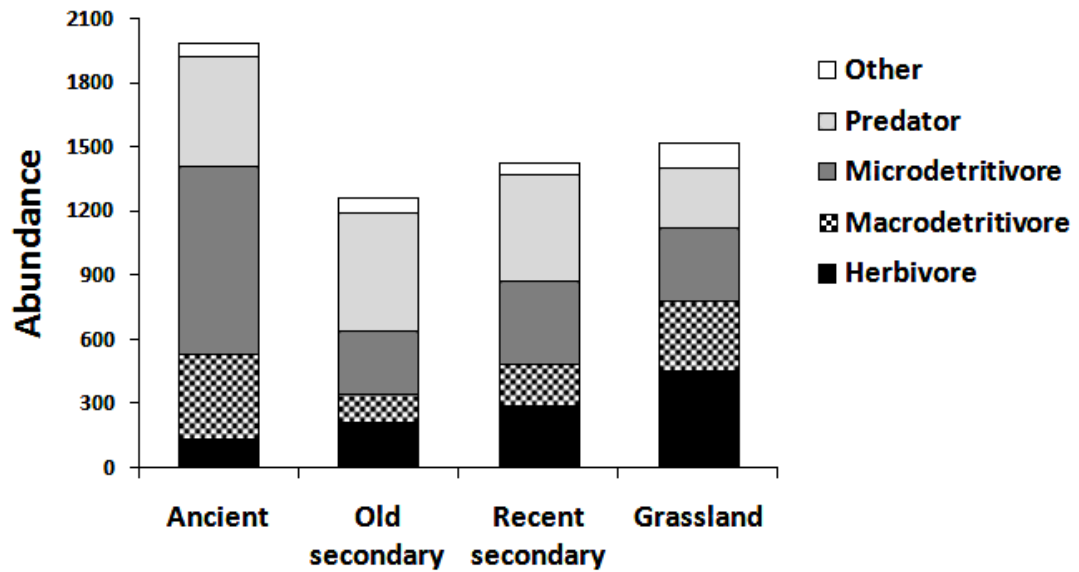


Fig. 6.3 Total number of mobile surface-dwelling individuals according to feeding preference group in each of the four habitat types from the total sampling effort. The three most abundant Collembolan groups (Dicyrtominae, Hypogastrurinae, and Sminthuridinae) were excluded in order to aid interpretation.

6.4.2 Carabid beetles

The most common beetles were from the family Carabidae, representing just over 70 % of the total beetle catch. Carabids tended to occur in highest abundance in old secondary sites. The most abundant carabid species overall, in decreasing order, were *Platynus assimilis* (46 % of carabid catch), *Carabus nemoralis* (15 %), and *Pterostichus melanarius* (13 %). The greatest richness of carabids was found in the old secondary sites, although there was no strong trend for carabid richness to change with woodland age (Table 6.2). There was, however, a significant difference in carabid species evenness; this was greatest in the grassland, followed by the ancient woodland, recent secondary, and old secondary. The grassland had the greatest diversity of carabids overall, and the ancient woodland had greater diversity than either of the secondary woodlands.

The abundances of individual carabid species also showed some interesting trends (Table 6.5). Just a single species, *Platynus assimilis*, accounted for over half the catch in both the old secondary and recent secondary woodlands; however, this species was less abundant in the ancient woodland. Rather, in the ancient

woodland, *Carabus nemoralis*, *Platynus assimilis*, *Pterostichus melanarius*, and *Abax parallelepipedus* were the most numerous species. *Carabus nemoralis* was least abundant in the recent secondary, but increased in frequency with woodland age. The ancient woodland also lacked a number of the species with a preference for open habitats (Luff, 2007), including *Agonum muelleri*, *Bembidion bruxellense*, *Bembidion lampros*, and *Bembidion tetracolum*. *Abax parallelepipedus*, which is associated with woodland habitats (Sroka and Finch, 2006), was absent from the grassland.

The percentage of species in the catch with a preference for woodland habitats was actually greater in the old and recent secondary woodlands than in the ancient woodland (Fig. 6.4, a). Instead, most of the catch in the ancient woodland was composed of generalist species, as was that in the grassland. Most species collected had a preference for either eurytopic (wide range of environmental conditions) or moist habitats (Fig. 6.4, b). While the ancient woodland and grassland had similar amounts of both, the secondary woodland sites were largely composed of species with a preference for moist habitats.

The NMS ordination of the carabid beetles represented 93 % of the variation, with a two-dimensional solution recommended (Fig. 6.5). Axis 1 accounted for 63 % of this variation, whilst axis 2 represented 30 %. Across axis 1, the grassland sites were separated from the three woodland habitats into a relatively distinct group. Across axis 2, the majority of the ancient woodland sites were separated from the secondary woodland sites. The old secondary sites were grouped in the same cluster as the recent secondary sites, along with one of the sites from the ancient woodland. *Pterostichus strenuus* was highly negatively correlated with Axis 1 ($r = -0.91$, d.f. = 18, $P < 0.001$), as was *Loricera pilicornis* ($r = -0.89$, d.f. = 18, $P < 0.001$). This axis is likely to be highly influenced by the presence of these species. Axis 2 showed a strong positive correlation with *Platynus assimilis* ($r = 0.97$, d.f. = 18, $P < 0.01$) and a strong negative correlation with *Carabus nemoralis* ($r = -0.71$, d.f. = 18, $P < 0.01$).

Table 6.5 Abundance (%) of carabid species trapped in the four different habitats of the Gearagh that makes up > 1 % of the catch of at least one habitat during sampling. Results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different superscript letters; any two within a row with a common letter are not significantly different ($P \geq 0.05$). Habitat and micro-habitat preference based on information from Luff (2007).

Species	Ancient woodland	Old secondary woodland	Recent secondary woodland	Grassland	P	Habitat preference	Micro-habitat preference
<i>Abax parallelepipedus</i>	11.93 ^b	5.59 ^b	10.2 ^b	0 ^a	< 0.05	Forest	Moist
<i>Agonum muelleri</i>	0	0.53	0.33	1.08	> 0.05	Open	Eurytopic
<i>Agonum piceum</i>	0	0.53	0	2.15	> 0.05	Generalist	Moist
<i>Bembidion bruxellense</i>	0	0.53	0	2.15	> 0.05	Open	Moist
<i>Bembidion lampros</i>	0	1.33	0.99	1.08	> 0.05	Open	Dry
<i>Bembidion tetracolum</i>	0	1.06	0	1.08	0.063	Open	Eurytopic
<i>Carabus granulatus</i>	5.05	0.8	0.99	9.68	> 0.05	Generalist	Moist
<i>Carabus nemoralis</i>	29.36 ^b	12.23 ^{ab}	8.88 ^a	16.13 ^{ab}	< 0.05	Generalist	Eurytopic
<i>Clivina fossor</i>	0.92	0.8	2.3	3.23	0.346	Open	Moist
<i>Loricera pilicomis</i>	2.29	0.8	1.32	10.75	> 0.05	Generalist	Moist
<i>Nebria brevicollis</i>	0	0.8	1.32	0	> 0.05	Generalist	Eurytopic
<i>Platynus assimilis</i>	24.77 ^a	57.18 ^b	58.55 ^b	11.83 ^a	< 0.01	Forest	Moist
<i>Pterostichus diligens</i>	0.46	0.27	0.33	1.08	> 0.05	Generalist	Moist
<i>Pterostichus melanarius</i>	21.1	12.23	7.89	11.83	0.099	Generalist	Eurytopic
<i>Pterostichus nigrita</i>	0	0.27	0	2.15	> 0.05	Generalist	Moist
<i>Pterostichus strenuus</i>	2.75	3.99	5.92	25.81	> 0.05	Generalist	Eurytopic

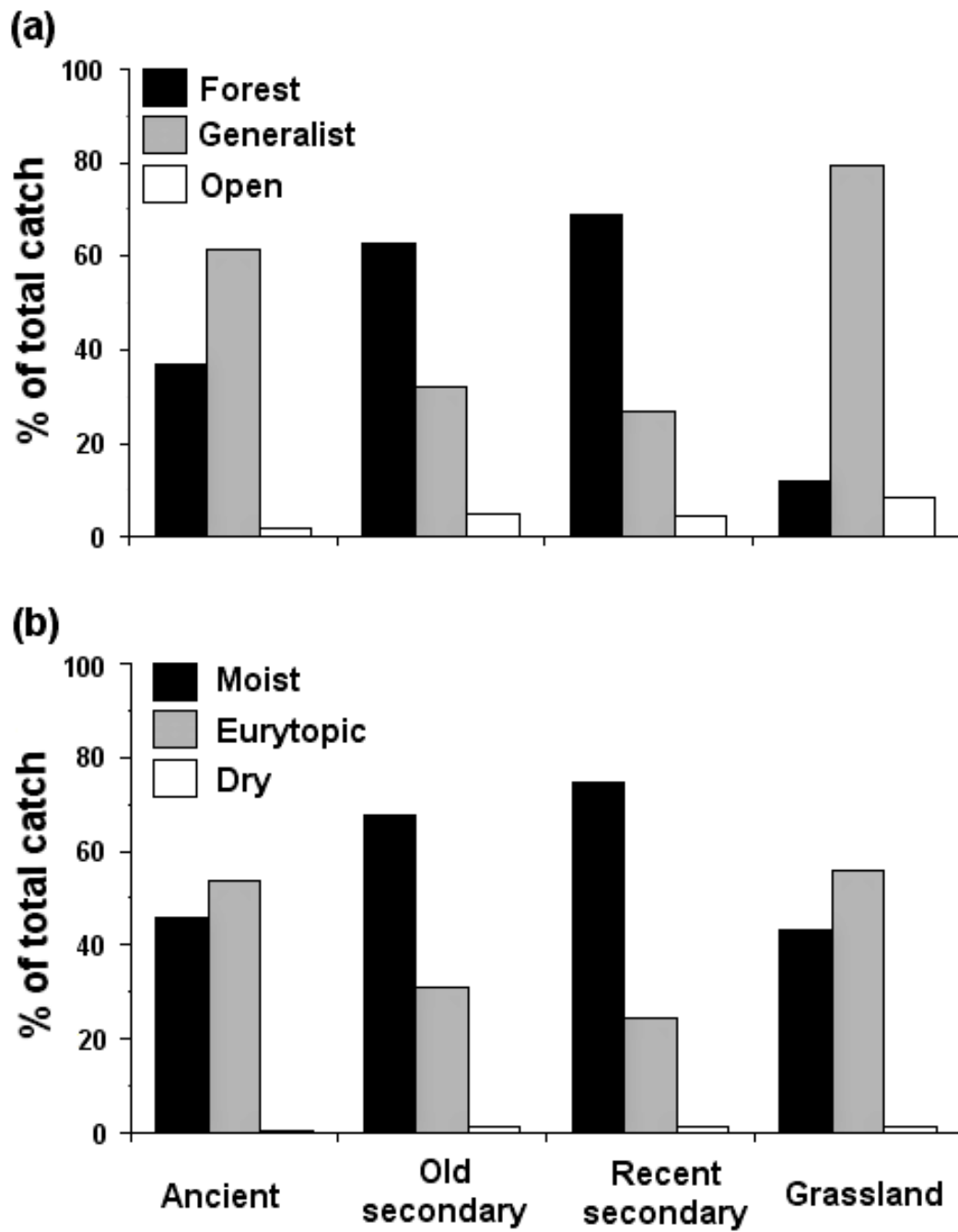


Fig. 6.4 Percentage of individuals in each total habitat catch that belong to each carabid beetle class for (a) habitat preference and (b) microhabitat preference.

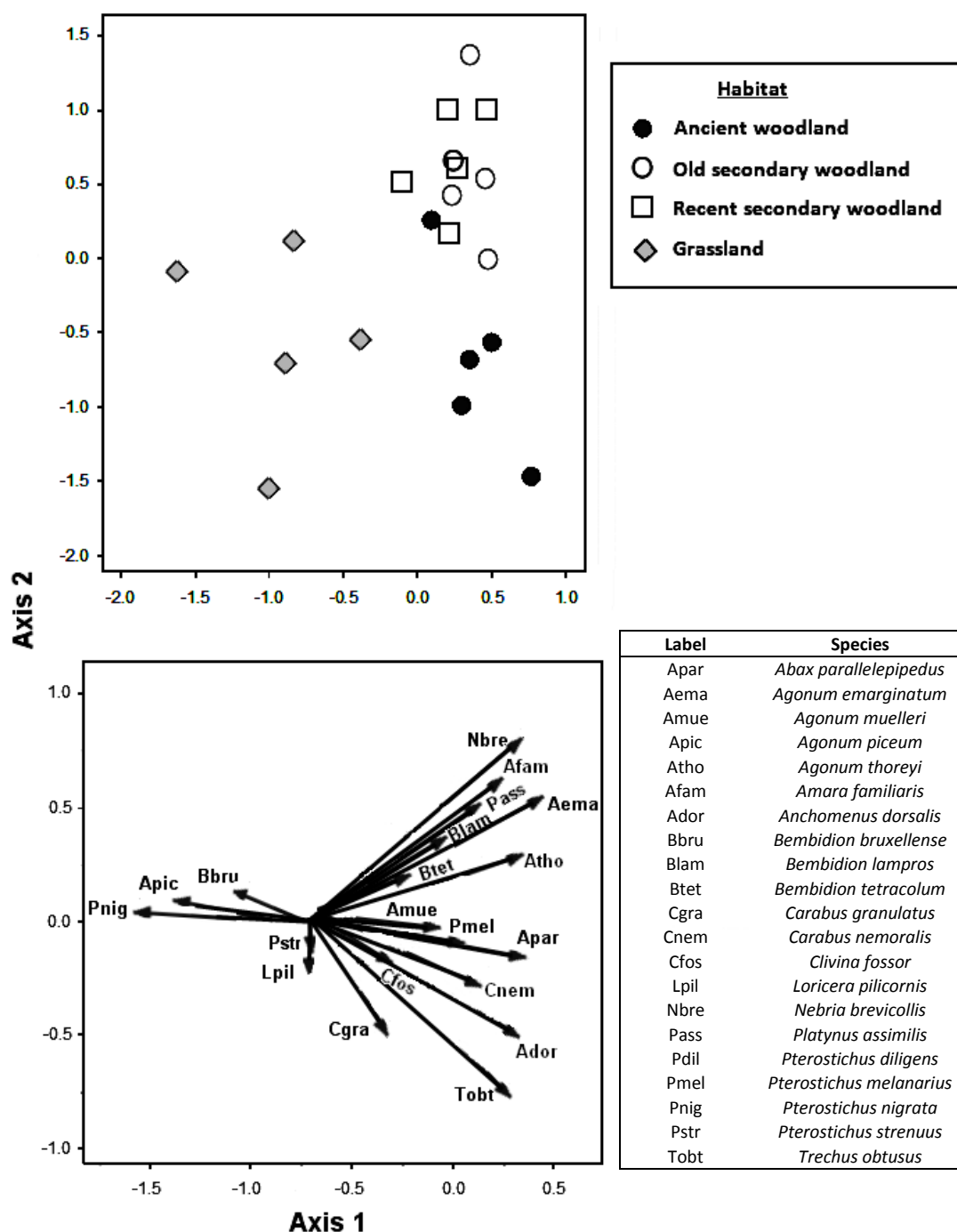


Fig. 6.5 NMS ordination of carabid beetle assemblages captured in pitfall traps. The upper panel shows axis 1 and axis 2 plots for all sites in the four habitat types of the Gearagh. The lower panel shows a joint plot of axis 1 and axis 2 and the carabid species used in the analysis. Cumulative variation in the original dataset explained by the ordination is 93 %: Axis 1 = 63 %; Axis 2 = 30 %; Final stress = 10.21; Final Instability = 0.00001.

6.4.3 Oligochaete communities

Preliminary sampling had proved the liquid-mustard extraction method to be a more efficient technique of sampling earthworms in the Gearagh than the hand-sorting method. Although this is not the normal technique for sampling enchytraeids, and may indeed underestimate their abundance, it still provided a useful means of comparing populations in the different habitats of the Gearagh. Total earthworm populations varied significantly between the four different habitat types of the Gearagh (Fig. 6.6, a). Populations were lowest in the ancient woodland, followed by the grassland, recent secondary, and old secondary. The ancient woodland had low densities of earthworms in comparison with the other woodland sites (mean of 175 individuals m^{-2}), whilst the old secondary had very high densities (mean of 318 individuals m^{-2}). The abundance of juvenile earthworms reflected the trend for the total earthworm community; the ancient woodland had the lowest abundance of juveniles, while the old secondary had the most (Table 6.6). A contrasting trend emerged when the enchytraeid populations were examined (Fig. 6.6, b). Here, the grassland had the lowest abundance of enchytraeids (mean of 148 individuals m^{-2}), followed by the recent secondary woodland (mean of 208 individuals m^{-2}). Enchytraeid population density then increased with woodland age, so that the ancient woodland (mean of 463 individuals m^{-2}) had significantly greater numbers of enchytraeids per square metre than any other habitat.

A similar pattern emerged when some of the individual earthworm species abundances were examined (Table 6.6). For instance, *A. caliginosa*, *A. chlorotica*, and *D. octaedra* are all significantly more abundant in the old secondary than the ancient woodland, with intermediate population densities in the recent secondary woodland. The endogeic species, *A. chlorotica*, was the most abundant species in both the old and recent secondary woodlands. However, *L. rubellus*, which is an epigeic species, was the most common species in the ancient woodland and grassland habitats. The epigeic species, *D. rubidus*, was found in similarly low densities in all of the woodland sites

The population density of earthworms also varied significantly according to their ecological category, as well between habitats (Table 6.7). The abundance of anecic

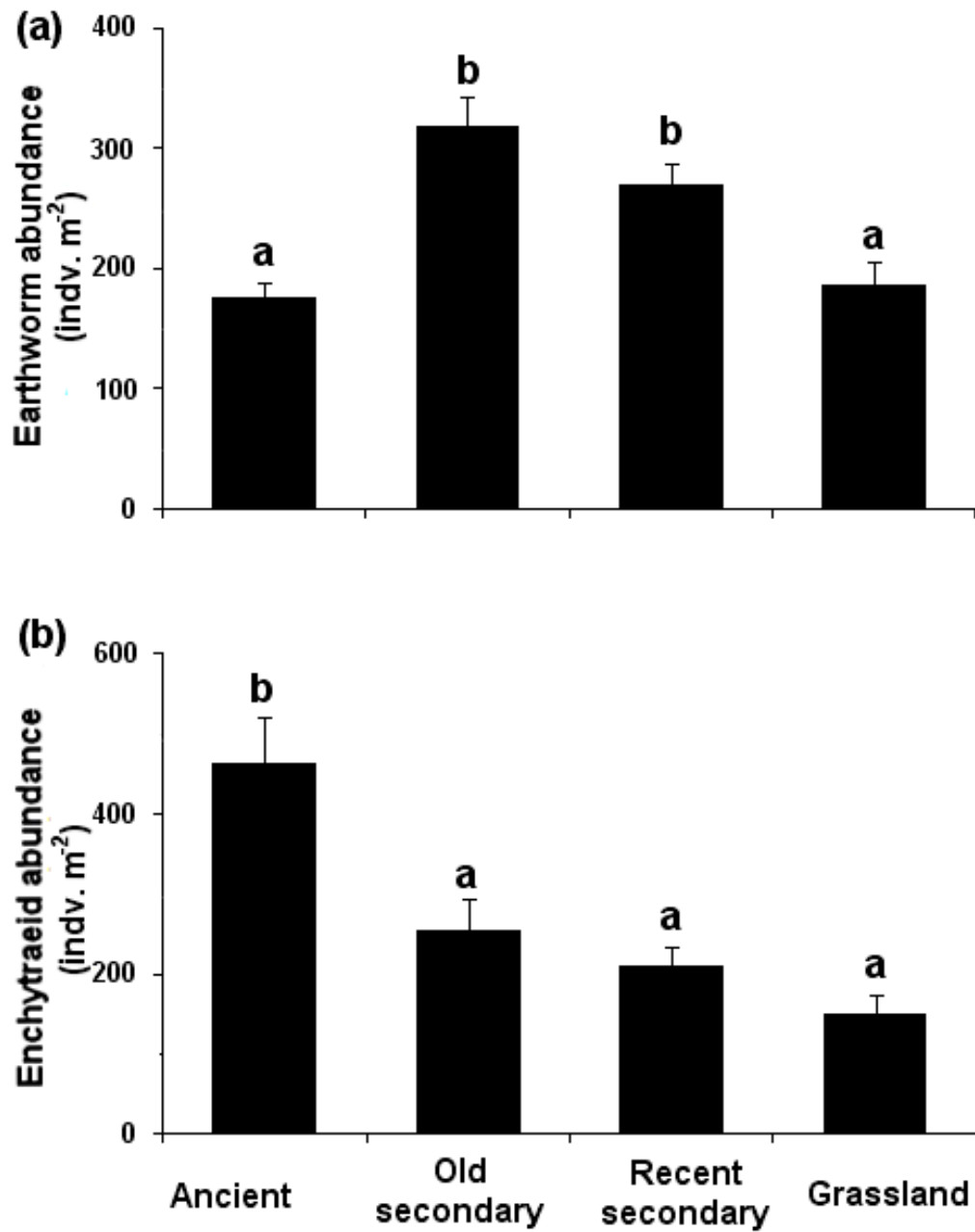


Fig. 6.6 Mean (\pm standard error) abundance (individuals m^{-2}) of (a) earthworms and (b) enchytraeids in the four habitat types of the Gearagh. Letters above each bar signify Tukey's honestly significant differences between the habitat types after testing with ANOVA; any two bars within a bar chart with a common letter are not significantly different ($P \geq 0.05$).

Table 6.6 Mean abundance (individuals/m²) of common earthworm taxa (those occurring in at least 5 % of all samples) in the four habitat types of the Gearagh. Results of Kruskal-Wallis test are given. Significant differences between habitat types are indicated with different superscript letters; any two within a row with a common letter are not significantly different ($P \geq 0.05$).

Earthworm species	Ancient woodland	Old secondary woodland	Recent secondary woodland	Grassland	<i>P</i>
<i>Aporrectodea caliginosa</i>	6.7 ^a	25.7 ^b	7.2 ^a	7.2 ^a	< 0.05
<i>Allolobophora chlorotica</i>	11.2 ^a	28.0 ^b	19.3 ^{ab}	7.7 ^a	< 0.01
<i>Aporrectodea rosea</i>	0.0	1.2	0.7	0.5	> 0.05
<i>Dendrobaena octaedra</i>	1.5 ^a	9.1 ^c	8.7 ^c	4.1 ^b	< 0.05
<i>Dendrodrilus rubidus</i>	4.0	3.5	4.0	0.8	> 0.05
<i>Lumbricus castaneus</i>	3.7	2.0	1.1	0.4	> 0.05
<i>Lumbricus festivus</i>	1.7	0.3	0.3	0.4	0.094
<i>Lumbricus rubellus</i>	23.1	25.2	13.3	12.1	0.096
<i>Lumbricus terrestris</i>	0.3	0.8	0.0	0.4	> 0.05
<i>Octolasion tyrtaeum</i>	0.2	0.8	0.7	1.3	> 0.05
Juvenile	115.1 ^a	203.5 ^c	194.4 ^{bc}	120.1 ^{ab}	< 0.05

species was low in all habitats, whereas the densities of both epigeic and endogeic species were greater, and also varied more between habitats (Fig. 6.7). The average abundance of epigeic species was greatest in the old secondary woodland. The ancient and recent secondary woodlands had a similar abundance of epigeic species, but both were lower than in the old secondary woodland. A clearer trend was evident in the population densities of endogeic species; here, the old secondary woodland had the greatest abundance, followed by the recent secondary, and then the ancient woodland.

6.4.4 Soil bacterial community-level physiological profile

The Biolog EcoPlateTM method is based on sole-carbon-source utilisation patterns, and is frequently used to determine soil bacterial functional diversity (Preston-Mafham *et al.*, 2002). After incubation with the Biolog EcoPlatesTM for 72 hours, significant differences in all the bacterial indices (AWCD, H' , S , and E) were found between the soil bacterial communities of the four habitat types of the Gearagh (Fig. 6.8). The old secondary woodland soil showed higher AWCD (mean of 0.30),

Table 6.7 ANOVA summary of log transformed earthworm abundances comparing the ecological categories (epigenic, endogenic, or anecic) in the four habitat types of the Gearagh (ancient woodland, old secondary woodland, recent secondary woodland, or grassland).

Factor	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Corrected model	11	11.998	50.280	< 0.001
Habitat	3	1.331	5.578	< 0.01
Ecology	2	61.986	259.764	<0.001
Habitat × Ecology	6	0.669	2.804	< 0.05
Error	48	0.239		

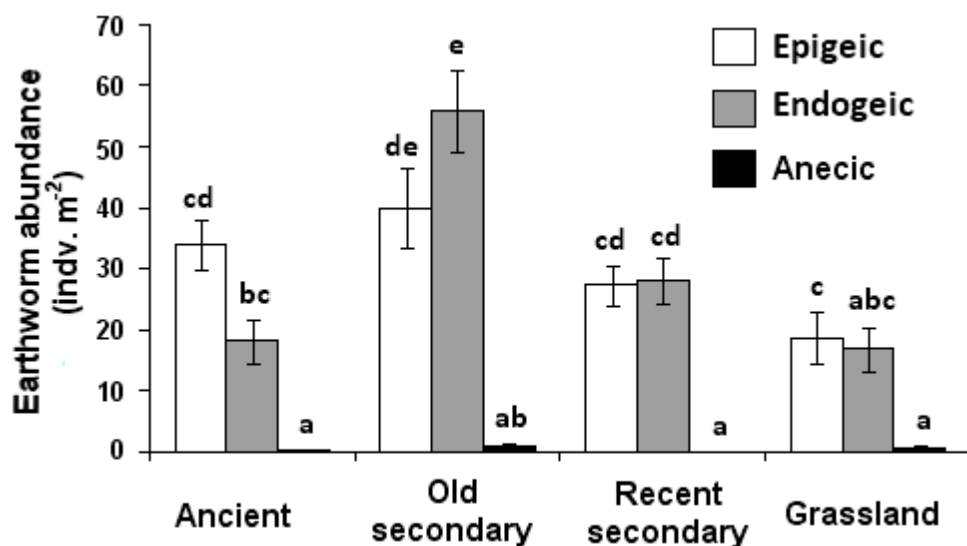


Fig. 6.7 Mean (\pm standard error) abundance (individuals m⁻²) of earthworms divided into ecological categories in the four habitat sites (excluding juveniles). Letters above each bar signify Tukey's honestly significant differences between the habitat types ($P < 0.05$) after testing with ANOVA; any two bars with a common letter are not significantly different.

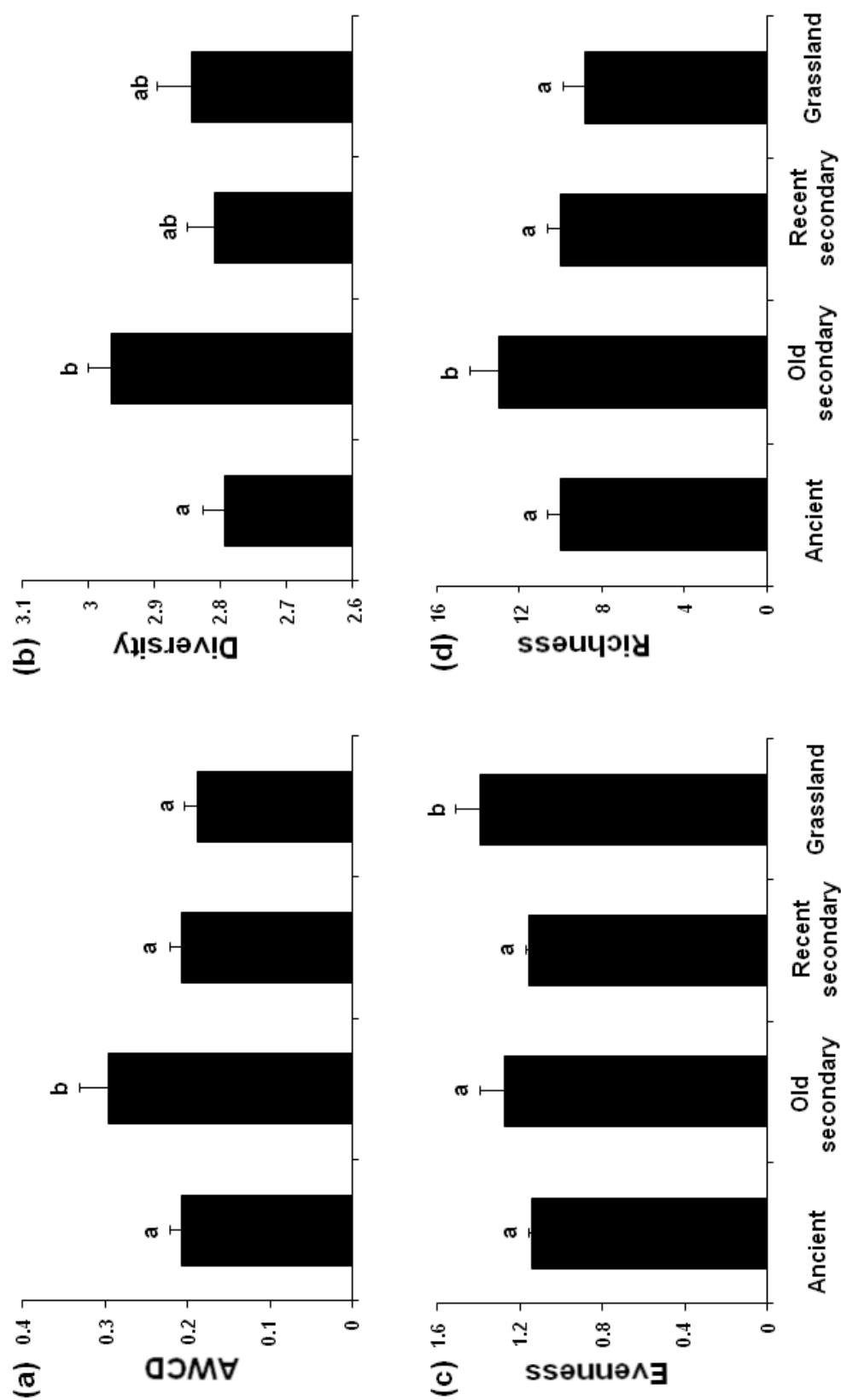


Fig. 6.8 Average well colour development (AWCD) (a), substrate diversity (b), substrate evenness (c), and substrate richness (d) of the microbial community in the four habitat types of the Gearagh after incubation with Biolog EcoPlates™. All show significant differences after Kruskal-Wallis test ($P < 0.05$). Significant differences between habitat types are indicated with different letters; any two bars with a common letter are not significantly different using the Tukey test ($P > 0.05$).

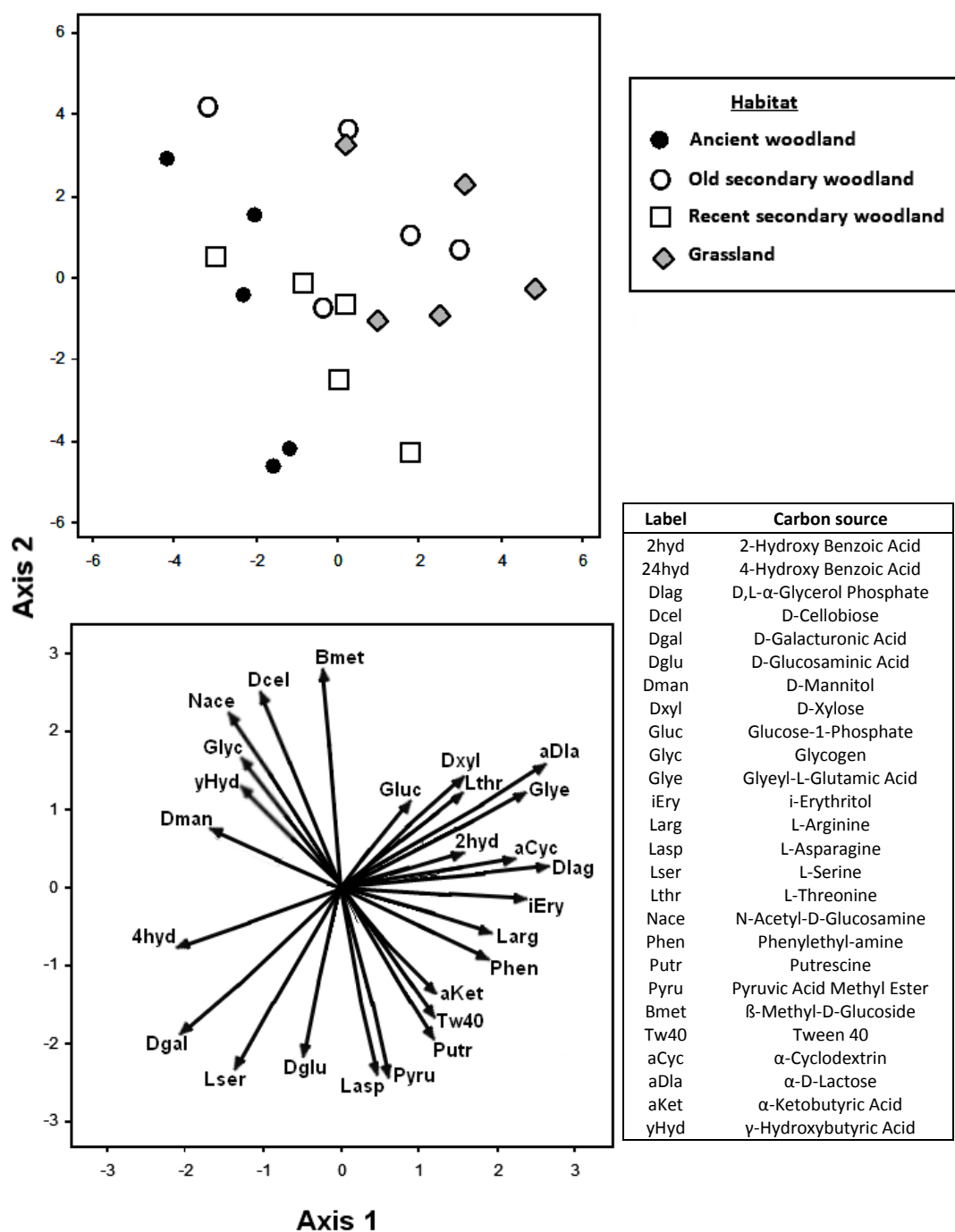


Fig. 6.9 Principal components analysis (PCA) of individual carbon resource utilisation in soils incubated over 72 hours in Biolog EcoPlatesTM. The upper panel shows axis 1 and axis 2 plots for the four habitat types of the Gearagh. The lower panel shows a joint plot between the two axes and the most influential carbon sources from the analysis. The first two axes of the PCA plot account for 37.2 % of the cumulative total variation in carbon source utilisation.

richness (mean of 13), and diversity (mean of 2.97) compared with all other habitats. AWCD and richness were similar for the ancient woodland, recent secondary and grassland soils. However, the ancient woodland had a significantly lower diversity than all other habitats. The evenness values were significantly greater for the grassland soil than for the three woodland habitats (Fig. 6.8).

The Biolog EcoPlates™ results for carbon utilisation were also subjected to principal component analysis (PCA) (Fig. 6.9). The first and second principal components (Axes 1 and 2) explained 21.7 % and 15.5 % of the data variance, respectively. Axis 1 clearly separated the ancient woodland sites from the grassland sites, while axis 2 helped to further separate the old secondary sites from the recent secondary sites. However, a degree of overlap remained between all groups. Carbohydrate substrates such as D,L- α -glycerol phosphate ($r = 0.69$, d.f. = 18, $P < 0.001$) and α -D-Lactos ($r = 0.63$, d.f. = 18, $P < 0.01$), which were positively correlated with axis 1, were used by bacterial communities from the grassland sites. The ancient woodland sites, which had values of less than 0 along axis 1, were related to the use of carbon sources 4-hydroxy benzoic acid ($r = -0.53$, d.f. = 18, $P < 0.05$) and D-mannitol ($r = -0.49$, d.f. = 18, $P < 0.05$). Both α -ketobutyric acid and glycyl-L-glutamic acid recorded optical densities of less than 0.25 (threshold for positive response) for all samples.

6.4.5 Decomposition dynamics

Hazel was selected as the leaf litter substrate for the experiment, as it is a common component of the litter in the Gearagh. Habitat, mesh size, and position within the soil horizon all proved to be important factors in the determination of decomposition of hazel leaf litter. Significant effects of habitat, mesh size and position, and significant interactions of site and mesh size, and position and mesh size (Table 6.8) were all observed on litter mass loss. Litter decomposed most rapidly in the grassland habitat (56 %, 53 % and 52% in the grassland, ancient and secondary, respectively) and was least decomposed in the fine mesh litterbags (46 %, 56 % and 58 % in the fine, large and medium mesh litterbags, respectively). Decomposition was also significantly slowest on the surface of the woodland floor (48 %) in comparison with treatments that were buried at 5 cm (56 %) and 20 cm

Table 6.8 ANOVA results for the litter decomposition experiment after log transformation of the data. The factorial design consisted of three factors for the evaluation of mass loss: habitat (ancient, secondary or grassland), mesh size (coarse, medium or fine), and position (surface, buried at 5 cm or buried at 20 cm). There were five replicates for each treatment.

Factor	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
Corrected model	26	0.214	6.819	< 0.001
Habitat	2	0.113	3.605	< 0.05
Mesh size	2	0.717	22.824	< 0.001
Position	2	0.332	10.582	< 0.001
Habitat × Mesh size	4	0.638	20.320	< 0.001
Habitat × Position	4	0.050	1.605	> 0.05
Mesh size × Position	4	0.079	2.507	< 0.05
Mesh size × Habitat × Position	8	0.026	0.830	> 0.05
Error	107	0.031		

(56 %) depths. Critically, decomposition in the ancient woodland was higher in the fine mesh bags, whereas the secondary woodland and grassland had greater decomposition in the coarse and medium mesh sizes (Fig. 6.10). Decomposition in coarse mesh litterbags was unaffected by placement position, while decomposition in both medium and fine mesh litterbag decomposition increased when buried beneath the surface.

The amount of leaf litter on the woodland floor varied significantly between the four habitat types (Fig. 6.11). Litter depth ($F = 10.632$; $d.f. = 3$; $P = <0.001$) and quantity ($F = 34.687$; $d.f. = 3$; $P = <0.001$) were both significantly greater in the ancient and old secondary woodland in comparison with the recent secondary and grassland. However, there was no significant difference in total annual litterfall biomass (Fig. 6.12) between the woodland sites ($F = 0.919$; $d.f. = 2$; $P = 0.425$). Although the ancient woodland appeared to have a greater proportion of *Q. robur* litter, this was not significantly different to the other habitats ($F = 0.676$; $d.f. = 2$; $P = 0.527$). Similarly, while *C. avellana* litter seemingly comprised a greater proportion of the recent secondary habitat litterfall, this too did not vary significantly between habitats ($F = 2.570$; $d.f. = 2$; $P = 0.118$).

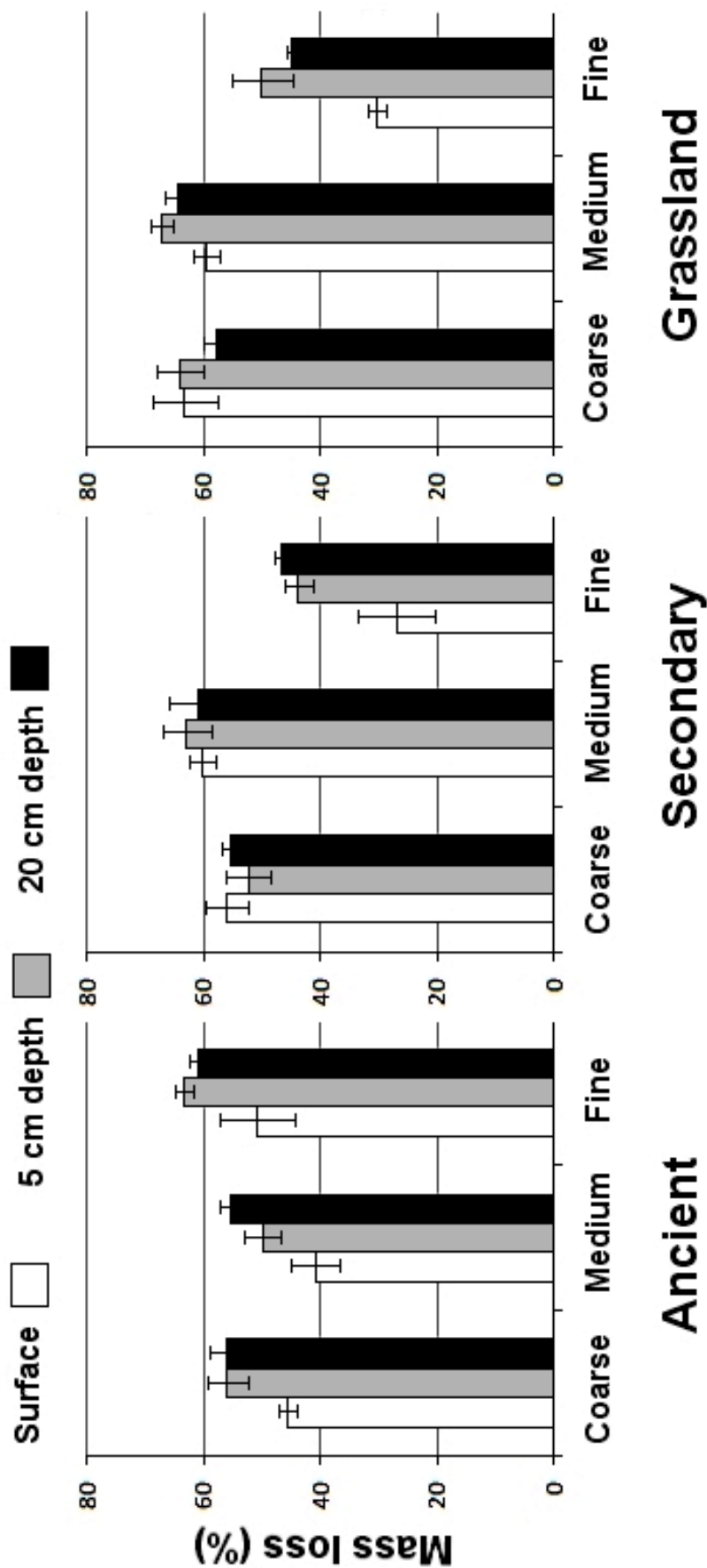


Fig. 6.10 Interaction between habitat (ancient, secondary or grassland), mesh size (coarse (10 mm), medium (2 mm) or fine (0.5 mm)), and position (surface, buried at 5 cm depth, or buried at 20 cm depth). Bars represent mass loss (mean \pm standard error) after 120 days in the field.

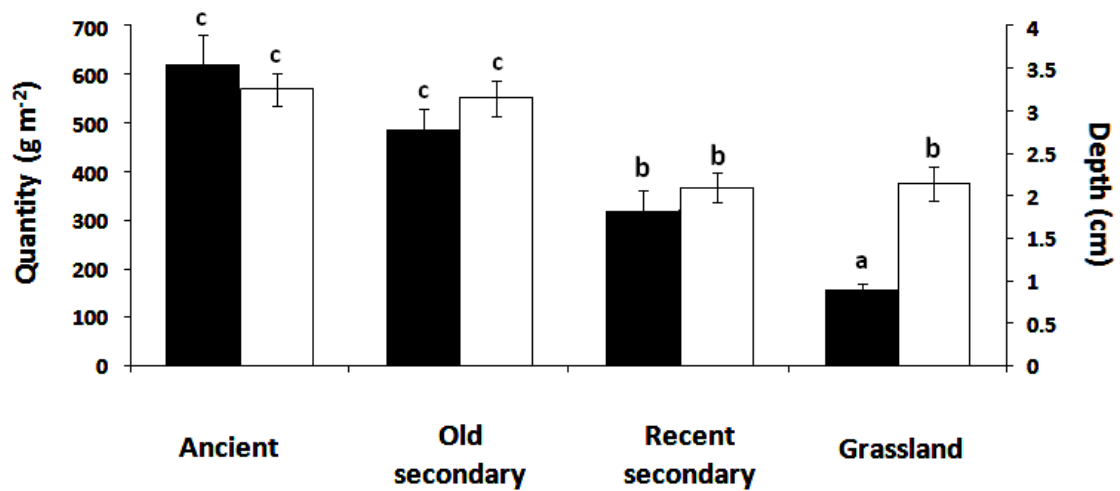


Fig. 6.11 Mean (\pm standard error) quantity (black bars) and depth (white bars) of litter on the woodland floor in each of the four habitat types of the Gearagh. Letters above each bar signify Tukey's honestly significant differences between the habitat types ($P < 0.05$) after testing with ANOVA; any two bars with a common letter are not significantly different.

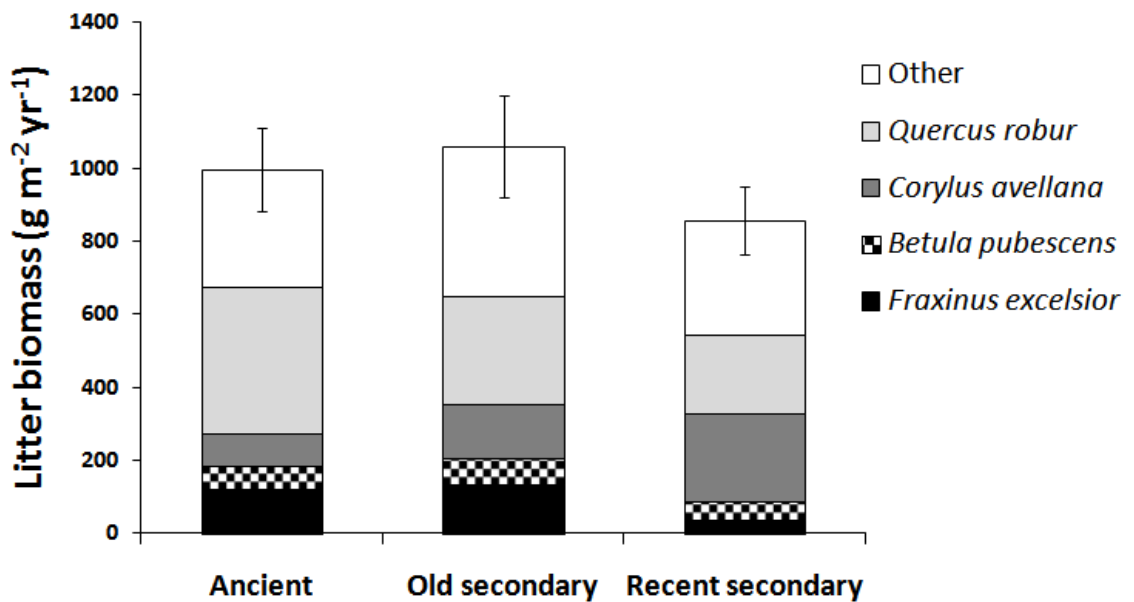


Fig. 6.12 Mean (\pm standard error) annual litterfall biomass in each of the four habitat types of the Gearagh; the main components of the litterfall are also indicated. There is no significant difference in litterfall biomass between the sites after testing with ANOVA.

6.5 Discussion

6.5.1 Community structure and functioning

This study has shown that considerable differences in soil and ground decomposer communities can exist between ancient woodland and adjacent stands of secondary woodland and grassland. Previous studies have noted that direct and indirect effects of past land-use can lead to significant changes in decomposer communities (Assmann, 1999; Huhta, 2002; Fraterrigo *et al.*, 2006). However, these effects can often be quite complex; consequently, not all groups of organisms respond in the same way to past land-use changes. While some species are particularly susceptible to disturbance events, others are able to recover more quickly (Hedlund *et al.*, 2004). These differences may also lead to changes in ecosystem functioning, as indicated by the variation in leaf litter decomposition between the ancient, secondary, and grassland sites. The overall slower rate of decomposition in the ancient woodland is reflected in the deeper litter layer measured there, despite all woodland habitats having similar inputs of litter.

Although fungal biomass was not quantified in this study, there is evidence to suggest that fungi may play a more important role in the ancient woodland than do bacteria. Generally, the microbial biomass in undisturbed soils is largely dominated by fungal species (Scheu, 2002). Indeed, the soil of the ancient woodland in the Gearagh had a remarkably undisturbed profile, as well as a low bulk density, high porosity, and a deep litter layer (Chapter 3). These features create microhabitats which are suited to the growth of fungal hyphae (Ritz and Young, 2004). Bacterial activity and diversity as measured by the Biolog EcoPlatesTM was lowest in the ancient woodland; often in mature ecosystems such as old-growth woodlands there is a switch in dominance from bacterial to fungal biomass (Harris, 2009). However, the lack of distinction of the three woodland habitats on the Biolog EcoPlatesTM suggests that bacteria are not central to the microbial differences between the habitats, thereby indirectly indicating that fungi must be of greater importance.

The core community of the ancient woodland was composed primarily of micro- and macrodetritivores, including species of mites, collembolans, enchytraeids, gastropods, and diplopods. Most of these species obtain their nutrition either

directly from fungi or indirectly through the consumption of detritus enriched with fungi (Petersen and Luxton, 1982). Oribatid mites, for instance, were found in greatest abundance in the ancient woodland. These mites are primarily fungal-feeders and are usually restricted to stable environments because of their low fecundity and sensitivity to disturbance (Maraun and Scheu, 2000). Similar differences in mite communities have previously been recorded between woodlands with different land-use histories (Huhta and Niemi, 2003). The beetle *Anoplotrupes stercorosus* (Coleoptera, Geotrupidae) was only found in the ancient woodland sites. It has a preference for woodland habitats where it feeds primarily on fungi or dung. This again suggests that the ancient woodland is fungal-dominated.

Previous studies have shown secondary woodlands to have lower abundances of fungi than ancient woodlands (Fraterrigo *et al.*, 2006), and that past agricultural activity can significantly reduce fungal abundance (van der Wal *et al.*, 2006; Kulmatiski and Beard, 2008). Furthermore, soil bacteria tend to be more numerous in secondary woodland stands than in ancient woodlands (Fraterrigo *et al.*, 2006). This corresponds to the results of this study, where bacterial activity, richness, and diversity were greatest in the secondary woodland sites. In addition, the community in the secondary woodlands was composed of fewer detritivores than the ancient woodland; in particular, there were fewer diplopods, gastropods, enchytraeids, and mites, suggesting that fungal decomposition was less important than in the ancient woodland. However, the collembolan fauna was relatively similar between the various sites, with the same three groups dominating in each of the four habitats. Collembolan communities have previously been shown to be quite similar in deciduous woodlands with different land-use histories (Huhta and Ojala, 2006). This indicates that recovery from past disturbance events may be rapid for certain groups of collembolans, possible due to their ability to reproduce rapidly once favourable conditions return.

Typical brown earths, such as those found in the ancient woodland, are generally favourable to earthworm colonisation and can often support large populations in comparison with other soil types (Lee, 1985). While the high densities recorded in

both of the secondary woodlands are comparable to those found in other brown earths in Irish deciduous woodlands (Little *et al.*, 2001) and fertile grasslands (Curry *et al.*, 2008), the abundance of earthworms in the ancient woodland was rather low. This indicates that the ancient woodland soil is a less favourable habitat for earthworms than the soils of the secondary woodlands. This difference in earthworm communities can have significant implications for ecosystem functioning, as earthworms are regarded as being the most important component of the soil fauna in terms of promoting processes such as decomposition and mineralisation (Bardgett, 2002). Additionally, most of the earthworms in the ancient woodland are epigeic species; these are usually quite small and only have minor impacts on soil properties in comparison with endogeic species which dominate the secondary woodland (Bohlen *et al.*, 2004). Because of the low abundance of earthworms in the ancient woodland, enchytraeids probably play a more important role in litter degradation (Räty and Huhta, 2003). Indeed, many enchytraeid species have low reproductive rates and so are better suited to the more stable environment of the ancient woodland.

Decomposition processes can be significantly influenced by the composition of the soil and ground faunal communities (Heneghan *et al.*, 1998). Detritivores, for instance, may influence litter decomposition either directly, by removing litter from the surface, or indirectly, by enhancing microbial activity in the litter. The relative abundance of fungi and bacteria in the soil can also play an important role in decomposition dynamics. In the ancient woodland, the exclusion of small fungal-feeding fauna in the fine mesh litterbags would have reduced grazing pressure on fungi. Previous studies have shown that exclusion of microdetritivores and fungivores can increase fungal activity and actually enhance decomposition (Lenoir *et al.*, 2006); this may explain the greater decomposition in the fine-mesh litterbags in the ancient woodland. Conversely, the coarse and medium mesh litterbags would have permitted normal fungivore activity, leading to top-down consumer regulation of fungal biomass and a consequent reduction in decomposition. In the more bacterial-dominated systems of the secondary and grassland sites, decomposition would have occurred at a much faster rate, particularly in the presence of endogeic

earthworms (Bohlen *et al.*, 2004). Exclusion of macrofauna from the fine mesh bags may have therefore resulted in reduced bacterial activity in the litter and ultimately a lower decomposition rate. However, this effect is less pronounced when litter is buried, possibly because the litter is brought into greater contact with microorganisms, regardless of the activity of other soil organisms. This replicates the effects earthworms have when they mix leaf litter in with the mineral soil layer, leading to greater bacterial activity and enhanced decomposition (Saetre, 1998).

Many of the carabid species recorded in the ancient woodland are also found in the other habitats of the Gearagh; most of these species are generalists and so are not restricted to habitats with specific environmental conditions. The lack of many woodland specialists is a feature of Irish woodlands (Mullen *et al.*, 2008; Oxbrough *et al.*, 2010), since many of the large species that are typical of woodlands elsewhere in Europe (e.g. *Carabus hortensis*) are not found in Ireland (Coll *et al.*, 1995). Rather, species assemblages in woodlands predominantly reflect the landscapes in which they occur (Eyre and Luff, 2004; Coll and Bolger, 2007). The secondary woodlands contained a mixture of woodland specialist and generalist species, as well as some with a preference for open habitats. This reflected the close association between the secondary woodland and the adjacent grasslands. There was, however, a notable lack of open specialist species in the ancient woodland, indicating that these stands have remained relatively isolated from processes in the surrounding landscape. While many species of carabid have a high ability to disperse by flight (for example *Loricera pilicornis*, *Amara familiaris*), others have poorly developed wings and wing muscles (for example *Abax parallelepipedus*, *Carabus nemoralis*). Consequently, it is possible that streams in the Gearagh may act as barriers to the dispersal of certain carabid species to different areas of woodland.

6.5.2 Factors influencing community structure and functioning in response to land-use change

While more work is needed to understand how certain factors influence the responses of decomposer communities to land-use changes, some are known to have particular effects on several groups of organisms. Some of these differences

may be caused by external factors, such as differences in leaf litter supply and quality, or altered soil and microhabitat conditions, while others may be driven by biotic interactions between different groups of organisms. Strong positive feedback between these factors may shift secondary woodland systems to a persistent alternate state (Suding *et al.*, 2004); recovery to a pre-disturbance state may be extremely slow and difficult.

Resource quality and quantity

The composition of soil fungal communities depends largely on resource quality and properties of leaf litter (Lenoir *et al.*, 2006). The removal of all woody biomass from agricultural fields may negatively affect the survival and long-term development of saprophytic fungi by reducing lignin and cellulose sources. Even changes in the C/N ratio of the litter in secondary woodlands could lead to the formation of distinct fungal communities. The amount and quality of organic matter is also an important determinant for detritus-feeding organisms (Bardgett, 2002). However, previous studies have shown that litter type is only of minor importance in terms of influencing the community structure of microfauna (Maraun and Scheu, 2000; Huhta, 2002). Even if litter differed in quality between the different sites, this is unlikely to fully explain the observed differences in the litter-feeding fauna. However, macrofauna, particularly slugs and snails, are influenced both by the quality and quantity of available litter (Bishop, 1977). The greater availability of litter in the ancient woodland may explain their strong presence there. The depth of the litter layer can also affect the community structure of harvestmen by creating a more loose microstructure (Huhta, 2002).

The quality of leaf litter is acknowledged to influence the abundance of earthworms. Oak litter, for instance, is regarded as being unpalatable to several species of earthworms (Hendriksen, 1990). However, litterfall inputs were similar in both quantity and composition in all of the woodland habitats, and so the slightly greater availability of oak litter in the ancient woodland is unlikely to fully explain the lower abundance of earthworms there. Many earthworm species also have a preference for calcium-rich litter (Ponge *et al.*, 1999); the high calcium concentration in the soils of the old secondary habitat (Chapter 3) may partially

account for the high abundance of earthworms there. However, the recent secondary woodland soils had a relatively dense population of earthworms, but low concentrations of calcium. Calcium therefore is unlikely to fully account for the variation in earthworm communities.

Several studies have highlighted the importance of leaf litter structure in determining the abundance and diversity of carabid beetle assemblages (Koivula *et al.*, 1999; Magura *et al.*, 2000; Poole *et al.*, 2003). Leaf litter can affect microenvironmental conditions such as moisture and temperature, creating more stable conditions which favour carabid reproduction (Magura *et al.*, 2003). Leaf litter also affects niche structure and the availability of prey for carabids (Poole *et al.*, 2003). While there was little difference in carabid species richness or abundance between the woodland sites, the composition of carabid communities in the ancient and secondary woodlands were more or less distinct; the deeper litter layer in the ancient woodland may partially account for this variation. Other studies have emphasised the importance of vegetation composition and structure in affecting carabid assemblages (Ings and Hartley, 1999; Mullen *et al.*, 2008; Oxbrough *et al.*, 2010). The lack of a canopy and differences in herb cover could account for the different carabid community in the grassland sites. However, most of the carabid species in the ancient woodland would easily be able to adapt to the new microhabitats of the secondary woodlands, particularly since most are habitat generalists.

Soil structure and composition

Past land-use can directly influence the microbial community through physical alteration of the rhizosphere (Fraterrigo *et al.*, 2006). Agricultural activity can increase soil compaction, mix soil horizons, and expose previously protected organic matter (Allison *et al.*, 2005). Such activities can cause significant declines in fungi, while increasing the abundance of certain bacteria. Even inputs of manure can alter microbial community composition by promoting certain microorganisms, particularly bacteria, which can exploit forms of carbon that are more readily transformed. Inputs of phosphorus through manure additions can also adversely affect mycorrhizal fungi (Amijee *et al.*, 1993). Grazing by cattle can enhance root

exudation and turnover, leading to further increases in microbial biomass (Bardgett *et al.*, 2001). Past applications of lime can also result in an increase total microbial biomass, particularly of bacteria (Räty and Huhta, 2003). It is likely, therefore, that past agricultural activities greatly modified the soil microbial communities of the secondary woodland and grassland sites.

Densities of soil microfauna generally increase with greater amounts of soil organic matter and moisture, but decrease in relation to increased acidity and soil bulk density (Blair *et al.*, 1994). Such changes in soil conditions may affect certain collembolan species, particularly those with small local populations which may be more sensitive to disturbance events (Cassagne *et al.*, 2006). In this study, populations of the less abundant groups of collembola, including Entomobryidae, Neanuridae, and Onychiuridae, were greater in the undisturbed ancient woodland than in other habitats. Collembola are also sensitive to acidity, and acid-tolerant and acid-intolerant species are generally separated at a threshold pH value of 5 (Ponge, 2000). In this study, however, most soils were below pH 5 and so this factor could not explain the differences in collembola. The distribution of endogeic earthworms also depends largely on soil properties such as texture, structure, pH, organic matter content, and depth. For instance, soil texture affects earthworms indirectly through its effect on soil moisture. The low bulk density and the greater pore space in the ancient woodland soil results in a drier soil, which may restrict the abundance of certain earthworm species (Frelich *et al.*, 2006). Astigmatid mites often increase in abundance in pastures after the application of rich manures. The greater availability of food in the form of dung from grazing cattle may partly account for the higher densities of these mites in the grassland sites.

Carabid beetles can be affected by soil factors as their larvae are predominantly soil-dwelling (Lovei and Sunderland, 1996). The larval stage is among the most sensitive during beetle development; their ability to survive and develop in a particular soil type can determine adult fertility and habitat occupation. For instance, many larvae are sensitive to pH, while increased soil compaction can impede egg laying for those species that need to dig holes to deposit their eggs (Magura *et al.*, 2003). Increased soil moisture as a result of past woodland

clearance could also be an important factor, as most species recorded either favour or tolerate moist sites. The importance of soil moisture for carabid communities in woodlands has previously been discussed (Antvogel and Bonn, 2001; Sroka and Finch, 2006).

The high densities of earthworms in the secondary woodlands can alter soil properties. In the long term, they can reduce the availability and increase the leaching of nitrogen and phosphorus (Bohlen *et al.*, 2004; Frelich *et al.*, 2006). They also greatly alter soil structure by mixing the surface litter in with the mineral soil horizons, thereby increasing microbial access to substrates in the soil (Saetre, 1998). They can even gradually increase the bulk density of undisturbed woodland soils by cementing soil particles together (Frelich *et al.*, 2006). Greater earthworm activity may even gradually counteract soil acidity (Haimi and Huhta, 1990). Enchytraeids can also affect soil structure through their burrowing activities and by the production of faecal pellets (Van Vliet *et al.*, 1995). Soils with high enchytraeid populations, such as the ancient woodland, tend to have a good structure with a small aggregate size (Setälä *et al.*, 1991). This can improve the water-holding capacity of the soil and make conditions more favourable for fungal growth (Rantalainen *et al.*, 2004). A decrease in enchytraeid populations as a result of increased soil disturbance and litter removal due to agricultural activities may result in an altered soil structure and consequently a change in the microbial community.

Dispersal ability

In newly established grasslands or woodlands, one of the most important factors influencing community structure and function is the ability of species to successfully disperse into that habitat (Hedlund *et al.*, 2004). Most flying insects, including many beetles, can disperse relatively easily, while other ground-dwelling beetles and spiders disperse effectively by land. For instance, many carabid species frequently disperse into new woodlands from the surrounding landscape. Consequently, species richness is often greatest in young secondary woodlands due to the influx of species with a preference for open habitats (Koivula *et al.*, 2002; Magura *et al.*, 2003; Yu *et al.*, 2008). The results of this study show that these species may still be present even 150 years after the re-establishment of woodland. Many

mesostigmatid and astigmatid mites can attach to other organisms for transportation to new locations (Szymkowiak *et al.*, 2008). In contrast, it is likely that the dispersal ability of most soil organisms is rather poor; many microfauna may take up to 30 years to colonise a distance of only 30 m (Ojala and Huhta, 2001).

Fungi, fungal-feeding organisms and their predators generally have a low ability to disperse in time and passively disperse in space (Hedlund *et al.*, 2004). These organisms take longer to recover from disturbances than those in the bacterial pathway; the latter therefore will tend to dominate new habitats. Furthermore, a reduction in the abundance of enchytraeids may decrease the ability of fungi to recover after a disturbance event. Fungal dispersal by vegetative growth alone tends to be inefficient compared with dispersal by enchytraeids (Rantalainen *et al.*, 2004). Enchytraeids, however, appear to have little effect on the dispersal of bacteria.

It is likely that passive transport by man is a crucial element in the dispersal of many organisms, particularly earthworms (Lee, 1985). Earthworms are known to be slow dispersers. Therefore, the dispersal of earthworms throughout Europe since the end of the last glacial period was most likely facilitated by the expansion of Neolithic agriculture throughout the continent (Richter, 2010). The need for human activity to establish viable earthworm populations can still be seen in several locations in Europe today, including Scotland (Butt and Lowe, 2004), Iceland (Bengtson *et al.*, 1975), the Faroe Islands (Enckell and Rundgren, 1988), Finland (Räty and Huhta, 2004), and Russia (Tiunov *et al.*, 2006), as well as in North America (Bohlen *et al.*, 2004; Frelich *et al.*, 2006). The high abundance of earthworms in many present-day deciduous woodlands may therefore be related to previous land-use history and human activity (Räty and Huhta, 2004). These formerly cultivated soils are able to maintain their populations for over 800 years after human activity has ceased (Enckell and Rundgren, 1988). Ancient woodlands then, because of their isolation from the cultural landscape, may be expected to have a poorer earthworm community than otherwise similar habitats (Räty, 2004).

Interspecific interactions

Competition and other biotic interactions between species plays an important role in determining the composition and function of woodland communities (Hedlund *et al.*, 2004). Earthworms can have positive effects on other soil fauna, but these effects are usually relatively small and transient (Migge-Kleian *et al.*, 2006). In the long-term, they have been found to suppress populations of other soil animals, particularly enchytraeids (Schaefer and Schauer mann, 1990; Rätty and Huhta, 2003; Bohlen *et al.*, 2004) and oribatid mites (Maraun and Scheu, 2000). Such effects were also observed in this study. Many microfauna, including certain groups of collembola such as Neanuridae and Onychiuridae, both of which were most abundant in the ancient woodland, are particularly sensitive to disturbances related to increased earthworm activity (Maraun *et al.*, 2003). These disturbances can disrupt the microhabitats and reduce the resources of many microfauna (Maraun and Scheu, 2000; Migge-Kleian *et al.*, 2006). The larger endogeic species, which were more common in the secondary woodland, can be particularly disruptive (Frelich *et al.*, 2006). For instance, they contribute to the more rapid disappearance of the litter layer (Bohlen *et al.*, 2004). In the ancient woodland, the greater depth and quantity of litter is most likely due to the lower abundance of earthworms there.

Generally, those species that are able to adapt quickly to disturbance and change are more likely to persist in earthworm-dominated soils than those species that are sensitive to disturbance or which compete with earthworms (Migge-Kleian *et al.*, 2006). The presence of high densities of earthworms can therefore shift the soil system from one which is slow-cycling and fungal-dominated to a faster-cycling, more bacterial-dominated system (Bohlen *et al.*, 2004). The effects of earthworms are not limited to other soil fauna; they can even lead to substantial alterations in seed germination and the woodland herb community (Bohlen *et al.*, 2004; Frelich *et al.*, 2006).

6.6 Conclusions

The composition of woodland communities is largely determined by the history of the site. The impacts of past land-use on soil and ground decomposer communities can influence ecosystem function, yet not necessarily in straightforward ways. Essentially, the ancient woodlands may be a fungal-dominated system, containing many species of detritivores and large numbers of enchytraeids but few earthworms. The historical clearance of woodland and conversion to agriculture was a major disturbance event, from which the original woodland community was slow to recover. Ultimately, it resulted in the establishment of a distinct community in the secondary woodland, which was characterised by high abundances of earthworms, fewer microdetritivores, and faster decomposition rates.

6.7 References

- Allison, V.J.M., Jastrow, R.M., Matamala, J.D., Zak, R. & Donald, R. (2005) Changes in soil microbial community structure in a tallgrass prairie chronosequence. *Soil Science Society of America Journal*, **69**, 1412-1421.
- Amijee, F., Stribley, D.P. & Lane, P.W. (1993) The susceptibility of roots to infection by an arbuscular mycorrhizal fungus in relation to age and phosphorus supply. *New Phytologist*, **125**, 581-586.
- Antvogel, H. & Bonn, A. (2001) Environmental parameters and microspatial distribution of insects: a case study of carabids in an alluvial forest. *Ecography*, **24**, 470-482.
- Assmann, T. (1999) The ground beetle fauna of ancient and recent woodlands in the lowlands of north-west Germany (Coleoptera, Carabidae). *Biodiversity and Conservation*, **8**, 1499-1517.
- Bardgett, R.D. (2002) Causes and consequences of biological diversity in soil. *Zoology*, **105**, 367-375.
- Bardgett, R.D., Jones, A.C., Jones, D.L., Kemmitt, S.J., Cook, R. & Hobbs, P.J. (2001) Soil microbial community patterns related to the history and intensity of grazing in sub-montane ecosystems. *Soil Biology and Biochemistry*, **33**, 1653-1664.

- Bengtson, S.A., Nilsson, A., Nordström, S. & Rundgren, S. (1975) Habitat selection of lumbricids in Iceland. *Oikos*, **26**, 253-263.
- Bishop, M.J. (1977) The mollusca of acid woodland in west Cork and Kerry. *Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science*, **77**, 227-244.
- Blair, J., Parmelee, R. & Wyman, R. (1994) A comparison of the forest floor invertebrate communities of four forest types in the northeastern US. *Pedobiologia*, **38**, 146-160.
- Blower, J.G. (1985) *British Millipedes (Diplopoda) with Keys to Species. Synopses of the British Fauna (New Series). No 35*. The Linnaean Society of London, Backhuys Publishers, Avon, UK, pp. 249.
- Bohlen, P.J., Scheu, S., Hale, C.M., McLean, M.A., Migge, S., Groffman, P.M. & Parkinson, D. (2004) Non-native invasive earthworms as agents of change in northern temperate forests. *Frontiers in Ecology and the Environment*, **2**, 427-435.
- Bouché, M.B. (1977) Strategies lombriciennes. *Ecological Bulletins*, **25**, 122-132.
- Butt, K.R. & Lowe, C.N. (2004) Anthropic influences on earthworm distribution, Isle of Rum National Nature Reserve, Scotland. *European Journal of Soil Biology*, **40**, 63-72.
- Cameron, R.A.D. (2003) *Keys for the Identification of Land Snails in the British Isles*. Field Studies Council, Preston Montford, UK, pp. 82.
- Cameron, R.A.D., Jackson, N. & Eversham, B. (1983) *A Field Key to the Slugs of the British Isles*. Field Studies Council, Preston Montford, UK, pp. 36.
- Cassagne, N., Bal-Serinb, M.-C., Charles Gersa & Gauquelina, T. (2004) Changes in humus properties and collembolan communities following the replanting of beech forests with spruce. *Pedobiologia*, **48**, 267-276.
- Cassagne, N., Gauquelin, T., Bal-Serin, M.-C. & Gers, C. (2006) Endemic Collembola, privileged bioindicators of forest management. *Pedobiologia*, **50**, 127-134.
- Chumak, V., Duelli, P., Rizun, V., Obrist, M. & Wirz, P. (2005) Arthropod biodiversity in virgin and managed forests in Central Europe. *Forest, Snow and Landscape Research*, **79**, 102-109.

- Coleman, D.C., Crossley, J.D.A. & Hendrix, P.F. (2004) *Fundamentals of Soil Ecology*, Second edition edn. Elsevier Academic Press, Burlington, USA, pp. 386.
- Coll, M. & Bolger, T. (2007) Biodiversity and species composition of Carabidae in Irish coniferous forests: additional insight from the use of paired sites in comparisons with the fauna of open habitats. *Biology & Environment: Proceedings of the Royal Irish Academy*, **107**, 1-11.
- Coll, M.T., Heneghan, L. & Bolger, T. (1995) Carabidae fauna in two Irish conifer stands: a comparison with those of some other European forests. *Biology and Environment: Proceedings of the Royal Irish Academy*, **95B**, 171-177.
- Compton, J.E. & Boone, R.D. (2002) Soil nitrogen transformations and the role of light fraction organic matter in forest soils. *Soil Biology and Biochemistry*, **34**, 933-943.
- Curry, J.P., Doherty, P., Purvis, G. & Schmidt, O. (2008) Relationships between earthworm populations and management intensity in cattle-grazed pastures in Ireland. *Applied Soil Ecology*, **39**, 58-64.
- David, J., Ponge, J. & Delecour, F. (1993) The saprophagous macrofauna of different types of humus in beech forests of the Ardenne (Belgium). *Pedobiologia*, **37**, 49-56.
- Day, K., Marshall, S. & Heaney, C. (1993) Associations between forest type and invertebrates: ground beetle community patterns in a natural oakwood and juxtaposed conifer plantations. *Forestry*, **66**, 37-50.
- Dufrene, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345-366.
- Enckell, P.H. & Rundgren, S. (1988) Anthrophochorous earthworms (Lumbricidae) as indicators of abandoned settlements in the Faroe Islands. *Journal of Archaeological Science*, **15**, 439-451.
- Eyre, M.D. & Luff, M.L. (2004) Ground beetle species (Coleoptera, Carabidae) associations with land cover variables in northern England and southern Scotland. *Ecography*, **27**, 417-426.

- Fraterrigo, J.M., Balser, T.C. & Turner, M.G. (2006) Microbial community variation and its relationship with nitrogen mineralisation in historically altered forests. *Ecology*, **87**, 570-579.
- Frelich, L., Hale, C., Scheu, S., Holdsworth, A., Heneghan, L., Bohlen, P. & Reich, P. (2006) Earthworm invasion into previously earthworm-free temperate and boreal forests. *Biological Invasions*, **8**, 1235-1245.
- Garland, J.L. & Mills, A.L. (1991) Classification and characterization of heterotrophic microbial communities on the basis of patterns of community-level sole-carbon-source utilization. *Applied and Environmental Microbiology*, **57**, 2351-2359.
- Giller, P.S. (1996) The diversity of soil communities, the 'poor man's tropical rainforest'. *Biodiversity and Conservation*, **5**, 135-168.
- Goßner, M., Engel, K. & Jessel, B. (2008) Plant and arthropod communities in young oak stands: are they determined by site history? *Biodiversity and Conservation*, **17**, 3165-3180.
- Grove, S.J. (2002) Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics*, **33**, 1-23.
- Haimi, J. & Huhta, V. (1990) Effects of earthworms on decomposition processes in raw humus forest soil - a microcosm study. *Biology and Fertility of Soils*, **10**, 178-183.
- Harris, J. (2009) Soil microbial communities and restoration ecology: facilitators or followers? *Science*, **325**, 573-574.
- Harris, J.A. & Hill, T.C.J. (1995) Soil biotic communities and new woodland. In: *The Ecology of Woodland Creation* (ed. R. Ferris-Kaan), pp 91-112. Wiley, Chichester, UK.
- Hattenschwiler, S., Tiunov, A.V. & Scheu, S. (2005) Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology and Systematics*, **36**, 191-218.
- Hedlund, K., Griffiths, B., Christensen, S., Scheu, S., Setälä, H., Tschantke, T. & Verhoef, H. (2004) Trophic interactions in changing landscapes: responses of soil food webs. *Basic and Applied Ecology*, **5**, 495-503.

- Hendriksen, N.B. (1990) Leaf litter selection by detritivore and geophagous earthworms. *Biology and Fertility of Soils*, **10**, 17-21.
- Heneghan, L., Coleman, D.C., Zou, X., Crossley, D.A. & Haines, B.L. (1998) Soil microarthropod community structure and litter decomposition dynamics: a study of tropical and temperate sites. *Applied Soil Ecology*, **9**, 33-38.
- Hillyard, P.D. (2005) *British Harvestmen, Synopses of the British Fauna (New Series). No.4. (Third Edition)*. EJ Brill, Leiden, UK, pp. 352.
- Hopkin, S.P. (2007) *A Key to the Collembola (Springtails) of Britain and Ireland*. Field Studies Council, Shrewsbury, UK, pp. 245.
- Huhta, V. (2002) Soil macroarthropod communities in planted birch stands in comparison with natural forests in central Finland. *Applied Soil Ecology*, **20**, 199-209.
- Huhta, V. & Niemi, R. (2003) Communities of soil mites (Acarina) in planted birch stands compared with natural forests in central Finland. *Canadian Journal of Forest Research*, **33**, 171-180.
- Huhta, V. & Ojala, R. (2006) Collembolan communities in deciduous forests of different origin in Finland. *Applied Soil Ecology*, **31**, 83-90.
- Ings, T.C. & Hartley, S.E. (1999) The effect of habitat structure on carabid communities during the regeneration of a native Scottish forest. *Forest Ecology and Management*, **119**, 123-136.
- Insam, H. (1997) A new set of substrates proposed for community characterization in environmental samples. In: *Microbial Communities: Functional Versus Structural Approaches*. (eds H. Insam & A. Rangger), pp. 260–261. Springer, Berlin, Germany.
- Kang, S. & Mills, A.L. (2004) Soil bacterial community structure changes following disturbance of the overlying plant community. *Soil Science*, **169**, 55.
- Koivula, M., Kukkonen, J. & Niemelä, J. (2002) Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. *Biodiversity and Conservation*, **11**, 1269-1288.
- Koivula, M., Punttila, P., Haila, Y. & Niemelä, J. (1999) Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. *Ecography*, **22**, 424-435.

- Krantz, G.W. (1978) *A Manual of Acarology*. Oregon State University Book Stores, Oregon, USA, pp. 509.
- Kruskal, J.B. (1964) Nonmetric multidimensional scaling: a numerical method. *Psychometrika*, **29**, 115-129.
- Kulmatiski, A. & Beard, K.H. (2008) Decoupling plant-growth from land-use legacies in soil microbial communities. *Soil Biology and Biochemistry*, **40**, 1059-1068.
- Lawrence, A.P. & Bowers, M.A. (2002) A test of the 'hot' mustard extraction method of sampling earthworms. *Soil Biology and Biochemistry*, **34**, 549-552.
- Lee, K.E. (1985) *Earthworms: Their Ecology and Relationships with Soils and Land Use*. Academic Press, Sydney, Australia, pp. 411.
- Lenoir, L., Persson, T., Bengtsson, J., Wallander, H. & Wirén, A. (2006) Bottom-up or top-down control in forest soil microcosms? Effects of soil fauna on fungal biomass and C/N mineralisation. *Biology and Fertility of Soils*, **43**, 281-294.
- Little, D.J., Boyle, G.M., Ryan, D. & Farrell, E.P. (2001) *Intensive Monitoring of an Oak Woodland in Western Ireland: Development of an Irish Ecological Monitoring Network (IEMN)*. COFORD, Dublin, Ireland, pp. 99.
- Lovei, G.L. & Sunderland, K.D. (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, **41**, 231-256.
- Luff, M.L. (2007) *RES Handbook Volume 4 Part 2: The Carabidae (Ground Beetles) of Britain and Ireland*. Field Studies Council, Shropshire, UK, pp. 247.
- Magura, T., Tóthmérész, B. & Bordán, Z. (2000) Effects of nature management practice on carabid assemblages (Coleoptera: Carabidae) in a non-native plantation. *Biological Conservation*, **93**, 95-102.
- Magura, T., Tóthmérész, B. & Elek, Z. (2003) Diversity and composition of carabids during a forestry cycle. *Biodiversity and Conservation*, **12**, 73-85.
- Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell Publishing, Malden, USA, pp. 256.
- Maraun, M., Salamon, J.-A., Schneider, K., Schaefer, M. & Scheu, S. (2003) Oribatid mite and collembolan diversity, density and community structure in a moderate beech forest (*Fagus sylvatica*): effects of mechanical perturbations. *Soil Biology and Biochemistry*, **35**, 1387-1394.

- Maraun, M. & Scheu, S. (2000) The structure of oribatid mite communities (Acari, Oribatida): patterns, mechanisms and implications for future research. *Ecography*, **23**, 374-383.
- McCune, B. & Mefford, M.J. (2006) *PC-ORD: Multivariate Analysis of Ecological Data, Version 5*. MjM Software Design, Gleneden Beach, USA.
- McLaughlin, Ó.B., Jonsson, T. & Emmerson, M.C. (2010) Temporal variability in predator-prey relationships of a forest floor food web. *Advances in Ecological Research*, **42**, 171-264.
- McLean, M.A., Migge-Kleian, S. & Parkinson, D. (2006) Earthworm invasions of ecosystems devoid of earthworms: effects on soil microbes. *Biological Invasions*, **8**, 1257-1273.
- Migge-Kleian, S., McLean, M., Maerz, J. & Heneghan, L. (2006) The influence of invasive earthworms on indigenous fauna in ecosystems previously uninhabited by earthworms. *Biological Invasions*, **8**, 1275-1285.
- Moore, J., Berlow, E., Coleman, D., Ruiters, P., Dong, Q., Hastings, A., Johnson, N., McCann, K., Melville, K. & Morin, P. (2004) Detritus, trophic dynamics and biodiversity. *Ecology Letters*, **7**, 584-600.
- Mullen, K., O'Halloran, J., Breen, J., Giller, P., Pithon, J. & Kelly, T. (2008) Distribution and composition of carabid beetle (Coleoptera, Carabidae) communities across the plantation forest cycle: implications for management. *Forest Ecology and Management*, **256**, 624-632.
- Ojala, R. & Huhta, V. (2001) Dispersal of microarthropods in forest soil. *Pedobiologia*, **45**, 443-450.
- Oosterbroek, P. (2007) *The European families of the Diptera – Identification, Diagnosis, Biology*. KNNV Publishing, Utrecht, Netherlands, pp. 205.
- Oxbrough, A., Irwin, S., Kelly, T.C. & O'Halloran, J. (2010) Ground-dwelling invertebrates in reforested conifer plantations. *Forest Ecology and Management*, **259**, 2111-2121.
- Paquin, P. & Coderre, D. (1997) Changes in soil macroarthropod communities in relation to forest maturation through three successional stages in the Canadian boreal forest. *Oecologia*, **112**, 104-111.

- Pawlett, M., Hopkins, D., Moffett, B. & Harris, J. (2009) The effect of earthworms and liming on soil microbial communities. *Biology and Fertility of Soils*, **45**, 361-369.
- Petersen, H. & Luxton, M. (1982) A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos*, **39**, 288-388.
- Ponge, J.F. (2000) Acidophilic Collembola: living fossils? *Contributions from the Biological Laboratory*, **29**, 65-74.
- Ponge, J.F., Patzel, N., Delhay, L., Devigne, E., Levieux, C., Beros, P. & Wittebroodt, R. (1999) Interactions between earthworms, litter and trees in an old-growth beech forest. *Biology and Fertility of Soils*, **29**, 360-370.
- Poole, A., Gormally, M. & Sheehy Skeffington, M. (2003) The flora and carabid beetle fauna of a mature and regenerating semi-natural oak woodland in south-east Ireland. *Forest Ecology and Management*, **177**, 207-220.
- Preston-Mafham, J., Boddy, L. & Randerson, P.F. (2002) Analysis of microbial community functional diversity using soil-carbon-source utilisation profiles - a critique. *FEMS Microbiology Ecology*, **42**, 1-14.
- Rantalainen, M.-L., Fritze, H., Haimi, J., Kiikkilä, O., Pennanen, T. & Setälä, H. (2004) Do enchytraeid worms and habitat corridors facilitate the colonisation of habitat patches by soil microbes? *Biology and Fertility of Soils*, **39**, 200-208.
- Räty, M. (2004) Growth of *Lumbricus terrestris* and *Aporrectodea caliginosa* in an acid forest soil, and their effects on enchytraeid populations and soil properties. *Pedobiologia*, **48**, 321-328.
- Räty, M. & Huhta, V. (2003) Earthworms and pH affect communities of nematodes and enchytraeids in forest soil. *Biology and Fertility of Soils*, **38**, 52-58.
- Räty, M. & Huhta, V. (2004) Earthworm communities in birch stands with different origin in central Finland. *Pedobiologia*, **48**, 283-291.
- Richter, K. (2010) *Genetic Structure in European Populations of the Earthworm Lumbricus terrestris*. PhD thesis, Kassel University, Germany.
- Ritz, K. & Young, I.M. (2004) Interactions between soil structure and fungi. *Mycologist*, **18**, 52-59.
- Saetre, P. (1998) Decomposition, microbial community structure, and earthworm effects along a birch-spruce soil gradient. *Ecology*, **79**, 834-846.

- Schaefer, M. & Schauer mann, J. (1990) The soil fauna of beech forests: comparison between a mull and a moder soil. *Pedobiologia*, **34**, 299-314.
- Scheu, S. (2002) The soil food web: structure and perspectives. *European Journal of Soil Biology*, **38**, 11-20.
- Scheu, S., Albers, D., Alphei, J., Bury n, R., Klages, U., Migge, S., Platner, C. & Salamon, J. (2003) The soil fauna community in pure and mixed stands of beech and spruce of different age: trophic structure and structuring forces. *Oikos*, **101**, 225-238.
- Seastedt, T.R. (1984) The role of microarthropods in decomposition and mineralization processes. *Annual Review of Entomology*, **29**, 25-46.
- Seastedt, T.R. & Crossley, J., D. A (1984) The influence of arthropods on ecosystems. *BioScience*, **34**, 157-161.
- Setälä, H. & McLean, M.A. (2004) Decomposition rate of organic substrates in relation to the species diversity of soil saprophytic fungi. *Oecologia*, **139**, 98-107.
- Setälä, H., Tyynismaa, M., Martikainen, E. & Huhta, V. (1991) Mineralization of C, N and P in relation to decomposer community structure in coniferous forest soil. *Pedobiologia*, **35**, 285-296.
- Sims, R.W. & Gerard, B. (1999) *Earthworms: Notes for the Identification and Study of British Species*. Field Studies Council, Shrewsbury, UK, pp. 171.
- Spence, J., Langor, D., Niemelae, J., Carcamo, H. & Currie, C. (1996) Northern forestry and carabids: the case for concern about old-growth species. *Annales Zoologici Fennici*, **33**, 173-184.
- Sroka, K. & Finch, O.-D. (2006) Ground beetle diversity in ancient woodland remnants in north-western Germany (Coleoptera, Carabidae). *Journal of Insect Conservation*, **10**, 335-350.
- Suding, K.N., Gross, K.L. & Houseman, G.R. (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, **19**, 46-53.
- Szymkowiak, P., Gorski, G. & Bajerlein, D. (2008) Passive dispersal in arachnids. *Biological Letters*, **44**, 75-101.
- Terrell-Nield, C. (1990) Is it possible to age woodlands on the basis of their carabid beetle diversity? *The Entomologist*, **109**, 136-145.

- Tilling, S. (1987) *A Key to the Major Groups of British Terrestrial Invertebrates*. Field Studies Council, Shrewsbury, UK, pp. 71.
- Tiunov, A.V., Hale, C.M., Holdsworth, A.R. & Vsevolodova-Perel, T.S. (2006) Invasion patterns of Lumbricidae into the previously earthworm-free areas of northeastern Europe and the western Great Lakes region of North America. In: *Biological Invasions Belowground: Earthworms as Invasive Species* (ed. P.F. Hendrit), pp. 23-34. Springer, Netherlands.
- Tiunov, A.V. & Scheu, S. (2005) Arbuscular mycorrhiza and collembola interact in affecting community composition of saprotrophic microfungi. *Oecologia*, **142**, 636-642.
- Tueben, A. & Smidt, G. (1992) Soil arthropod numbers and biomass in two pine forests on different soils, related to functional groups. *Pedobiologia*, **36**, 79-89.
- Unwin, D. (1988) *A Key to the Families of British Beetles*. Field Studies Council, Preston Montford, UK, pp. 49.
- Van der Wal, A., van Veen, J.A., Smant, W., Boschker, H.T.S., Bloem, J., Kardol, P., van der Putten, W.H. & de Boer, W. (2006) Fungal biomass development in a chronosequence of land abandonment. *Soil Biology and Biochemistry*, **38**, 51-60.
- Van Vliet, P.C.J., Beare, M. & Coleman, D. (1995) Population dynamics and functional roles of Enchytraeidae (Oligochaeta) in hardwood forest and agricultural ecosystems. *Plant and Soil*, **170**, 199-207.
- Yu, X.-D., Luo, T.-H. & Zhou, H.-Z. (2008) Distribution of carabid beetles among 40-year-old regenerating plantations and 100-year-old naturally regenerated forests in Southwestern China. *Forest Ecology and Management*, **255**, 2617-2625.
- Zak, J.C., Willig, M.R., Moorhead, D.L. & Wildman, H.G. (1994) Functional diversity of microbial communities: A quantitative approach. *Soil Biology and Biochemistry*, **26**, 1101-1108.

CHAPTER 7

GENERAL DISCUSSION

7.1 Importance of study

Native woodlands currently cover less than 2% of the land area of Ireland (Perrin *et al.*, 2008). Very few of these (only 123 stands) are ancient woodlands (Perrin & Daly, 2010). Ancient woodlands are therefore extremely rare features of the Irish landscape and warrant special conservation and management. However, until relatively recently, the ecological importance of these woodlands was not fully appreciated. The study presented here highlights the value of ancient woodlands by showing that they differ in a number of significant ways from younger woodlands. These results also emphasise the important role that land-use history can play in shaping the present day ecology of woodlands.

Most similar studies investigating the effects of past land-use on woodland ecology originate from either central Europe or North America. Unlike these studies, the Gearagh is located close to sea-level in north-western Europe where it is characterised by an extreme oceanic climate with high annual rainfall. Nonetheless, it is notable that the effects of past agriculture observed in this study were often similar to those found in other temperate deciduous woodlands in Britain, continental Europe, and even North America. Although secondary woodlands may comprise the majority of wooded areas in most countries, this study shows that they do not always support the same range of plant species and invertebrate groups as ancient woodlands. Even after over a century of woodland cover, stands of secondary woodland can still remain distinct from adjacent areas of ancient woodland. Indeed, it is possible that the effects of past land-use may shift some secondary woodlands to a persistent alternate stable state (Suding *et al.*, 2004), so that they may return to a pre-disturbance state only after extremely long periods of time, if at all. These findings are important in terms of the continued conservation of Irish native woodlands, as well as for the future management and restoration of native deciduous woodlands.

A comprehensive assessment of both ancient woodland and the impacts of past land-use on the recovery of native woodland was facilitated by the multi-disciplinary approach of this study. Information on diverse subjects was brought together, including geography, history, hydrology, pedology, edaphology,

phytosociology, and community ecology. The comparison of these multiple components across four adjacent habitats of distinct land-use histories provided a wider understanding of past, current, and future processes in native woodlands and established a valuable baseline against which to measure the effects of human disturbance on long-term woodland dynamics (Goldberg *et al.*, 2007). The location of adjacent stands within 1 km of each other eliminated the effect of climatic and topographic factors from the study and showed that land-use legacies can have considerable impacts even on a local scale. The ecosystem approach of the study may help to inform management strategies for entire woodland habitats by enabling the identification of the most appropriate targets for future monitoring and restoration projects (Bakker *et al.*, 2000). Few studies in Ireland have ever taken this expansive approach, although Brackloon Wood in County Mayo has been the focus of a broad range of ecological monitoring programmes since the early 1990s (Little *et al.*, 2001). Unlike the Gearagh, however, this wood has a history of extensive exploitation and disturbance since at least the early Bronze Age (Cunningham, 2005), which have resulted in considerable alterations of environmental conditions and biodiversity.

Nonetheless, it should be acknowledged that the sampling approach used in this study does have a number of limitations. The broad scope of the project meant that many aspects of the soil, vegetation, seeds, and decomposer communities could not be investigated in great detail. For instance, the analysis of other soil characteristics such as nitrogen, dithionite-citrate-bicarbonate extractable iron, and cation exchange capacity would have provided further useful information on soil processes, but these had to be omitted due to time and budget constraints. The quadrat style approach used for sampling the ground flora likely discovered fewer indicator species than a survey based on the whole stand would have. However, the difficulties in gaining access to the sites and the island nature of the woodland made whole site surveys problematical. In the seed-sowing experiment, the inclusion of a grassland species would have provided more information on the ability of non-woodland species to recruit successfully in woodland habitats, but the value of this was not anticipated when planning the project. The use of pitfall traps

meant that in effect only surface activity was sampled rather than the actual occurrence of individuals. Additionally, it would have been of great benefit to sample both the pitfall traps and the oligochaete communities a number of times throughout the year as this would have identified additional species that are only active during certain months, and may have helped to further distinguish the sites. Additional sampling of the soil microbial community would also have been extremely informative, as the Biolog EcoPlates™ do not characterise fungal communities. Equally, it was not possible to investigate all aspects of woodland ecology in the Gearagh, and other potential studies include surveys of lichens, bryophytes, mammals, flying insects, fungi, etc. Yet despite these limitations, this research nonetheless provides novel and valuable insights into the ecological differences between ancient and secondary woodlands.

7.2 Indicators of ancient woodland

Although the findings of this study are specific to the Gearagh woodland, it reveals patterns and processes that are relevant to other wooded habitats not only in Ireland but also throughout north-western Europe. One particularly important outcome is the numerous ways in which ancient woodland can be distinguished from more recent woodland. While some of these indicators appear to be diagnostic of ancient woodland habitat (particularly biotic and abiotic components of the soil), others are merely associated with ancient woodland (e.g. tree profile, species of ground flora) and require confirmation from other sources of evidence (Table 7.1).

Lists of vascular plant species that are thought to be associated with ancient woodland are frequently used in woodland surveys (Hermy & Verheyen, 2007). However, many woodland specialists are naturally absent from certain regions due to differences in climate and geology, while others commonly occur in secondary woodlands (Rose, 1999), particularly if they are located near to ancient woodlands. For instance, in the Gearagh, there were few obvious differences in vegetation composition between the ancient and secondary habitats; it was only through a

Table 7.1 Summary of main findings indicating differences between the ancient woodland and the other habitats of the Gearagh. Some markers are only suggestive of woodland history (vegetation, carabid beetles), while others are stronger indicators of ancient woodland (soil type, oligochaetes, seed bank density).

Feature	Ancient woodland	Old secondary woodland	Recent secondary woodland	Grassland
Vegetation				
5 most frequent tree species (% relative density)	<i>Corylus avellana</i> (41 %) <i>Quercus robur</i> (20 %) <i>Ilex aquifolium</i> (14 %) <i>Betula pubescens</i> (13 %) <i>Crataegus monogyna</i> (6 %)	<i>Corylus avellana</i> (60 %) <i>Quercus robur</i> (12 %) <i>Betula pubescens</i> (10 %) <i>Crataegus monogyna</i> (6 %) <i>Fraxinus excelsior</i> (5 %)	<i>Corylus avellana</i> (52 %) <i>Crataegus monogyna</i> (22 %) <i>Betula pubescens</i> (12 %) <i>Quercus robur</i> (5 %) <i>Fraxinus excelsior</i> (4 %)	- - - - -
5 most frequent ground flora species (% cover abundance)	<i>Hedera helix</i> (16 %) <i>Allium ursinum</i> (13 %) <i>Lonicera periclymenum</i> (9 %) <i>Filipendula ulmaria</i> (7 %) <i>Rubus fruticosus</i> (6 %)	<i>Hedera helix</i> (19 %) <i>Anemone nemorosa</i> (16 %) <i>Allium ursinum</i> (10 %) <i>Ranunculus ficaria</i> (7 %) <i>Filipendula ulmaria</i> (5 %)	<i>Hedera helix</i> (26 %) <i>Filipendula ulmaria</i> (7 %) <i>Anemone nemorosa</i> (6 %) <i>Veronica montana</i> (4 %) <i>Fraxinus excelsior</i> (4 %)	<i>Agrastis stolonifera</i> (44 %) <i>Urtica dioica</i> (11 %) <i>Deschampsia caespitosa</i> (10 %) <i>Filipendula ulmaria</i> (8 %) <i>Poa trivialis</i> (6 %)
Soil				
Soil type	Acid brown earth	Brown podzolic	Brown podzolic	Brown podzolic
Evidence of leaching and/or podzolisation	No	Yes	Yes	Yes
Litter quantity (g m^{-2})	618	485	319	156
Bulk density (g cm^{-3})	0.47	0.51	0.70	0.85
Surface pH (CaCl_2)	5.01	4.73	4.50	4.75
Surface organic matter content (% LOI)	28	24	25	24
Soil moisture content (%)	4	4	5	7
Seed dynamics				
Seed bank density (seeds m^{-2})	4,625	17,369	21,794	32,460
<i>Juncus effusus</i> seed density (seeds m^{-2})	2,077	13,428	18,195	19,658
<i>Anemone nemorosa</i> germination (%)	7	5	3	-
<i>Hyacinthoides non-scripta</i> germination (%)	12	13	11	-
<i>Primula vulgaris</i> germination (%)	16	2	1	-
Invertebrates				
5 most abundant carabid beetle species	<i>Carabus nemoralis</i> (29 %) <i>Platynus assimilis</i> (25 %) <i>Pterostichus melanarius</i> (21 %) <i>Abax parallelepipedus</i> (12 %) <i>Carabus granulatus</i> (5 %)	<i>Platynus assimilis</i> (57 %) <i>Carabus nemoralis</i> (12 %) <i>Pterostichus melanarius</i> (12 %) <i>Abax parallelepipedus</i> (6 %) <i>Pterostichus strenuus</i> (4 %)	<i>Platynus assimilis</i> (59 %) <i>Abax parallelepipedus</i> (10 %) <i>Carabus nemoralis</i> (9 %) <i>Pterostichus melanarius</i> (8 %) <i>Pterostichus strenuus</i> (6 %)	<i>Pterostichus strenuus</i> (26 %) <i>Carabus nemoralis</i> (16 %) <i>Platynus assimilis</i> (12 %) <i>Pterostichus melanarius</i> (12 %) <i>Loricera pilicornis</i> (11 %)
Density of earthworms (indv. m^{-2})	175	318	270	185
Density of enchytraeids (indv. m^{-2})	463	255	208	148
Number of Opiliones per trap site	27	20	13	1
Number of Oribatid mites per trap site	106	31	31	27

detailed floristic survey that the ancient woodland could clearly be distinguished from the secondary stands. The occurrence of ancient woodland indicator species is therefore not a wholly reliable indicator of ancientness (Glaves *et al.*, 2009). Consequently, woodland age and origin is usually verified through a combination of historical maps and documents (Rotherham *et al.*, 2008; Perrin & Daly, 2010). However, documentary records are often unreliable and scarce (Hall, 1997), and require careful interpretation in order to confirm woodland continuity (Glaves *et al.*, 2009).

Other more robust field-based evidence may be used to support map and archive evidence. In fertile lowland woods with little history of disturbance such as the Gearagh, the soil structure and composition can prove to be a useful local diagnostic tool of ancient woodland. Although soils can be highly variable, evidence of lack of disturbance in the soil profile may be a valuable indicator of ancient status. The lack of diagnostic features in the soil horizons is evidence of either very young soils or, as in the case of the Gearagh, soils that have not been greatly influenced by factors such as climate (particularly precipitation) and human disturbances (Brady & Weil, 2002). For the ancient woodland soil, the presence of a continuous cover of trees over a great many years will have reduced the effects of leaching and of consequent podzolisation, while the tree roots will have ensured the efficient recycling of nutrients from litter (Little *et al.*, 1997). In addition, the presence of high organic matter content throughout the soil profile, particularly in lower layers, in conjunction with a deep surface litter layer may be typical of ancient woodland (Wilson *et al.*, 1997). However, despite the potential usefulness of soil as a diagnostic feature and the crucial role that it plays in woodland structure and functioning (Peterken, 1993), it is rarely used in the assessment of ancient woodland sites (Kirby & Goldberg, 2002; Rotherham *et al.*, 2008; Glaves *et al.*, 2009).

Differences in the soil and ground decomposer communities also appear to reflect differences in woodland history. The low abundance of earthworms and the greater abundance of detritivores such as enchytraeids, oribatid mites and the beetle *Anoplotrupes stercorosus* in the ancient woodland suggest that this area does not

have a history of major disturbances; high earthworm populations can remain in formerly cultivated soils for hundreds of years after agricultural abandonment (Enckell & Rundgren, 1988), while many of the detritivores found in the ancient woodland are thought to be particularly sensitive to disturbance (Maraun & Scheu, 2000; Rätty & Huhta, 2004a). Conversely, the association of larger earthworms with the secondary woodland soils of the Gearagh appears to parallel the patterns of non-native invasive earthworms in temperate forests of North America (Bohlen *et al.*, 2004). These findings suggest that earthworms are naturally rare in undisturbed north-western European deciduous woodlands. It is possible that their relatively high abundance in secondary woodlands is a legacy of former agricultural activity (Enckell & Rundgren, 1988; Rätty & Huhta, 2004b), and that human activity facilitated the establishment of viable earthworm populations throughout Europe (Richter, 2010). The prevalence of lumbricids, however, has important implications for ecosystem functioning of woodlands as earthworms can significantly alter soil properties and microbial communities, suppress other soil animals (particularly enchytraeids), and even affect seed germination through seed burial (Frelich *et al.*, 2006). The invasion of native North American woodlands by non-native earthworms has been shown to be accompanied by deleterious changes to the ecosystem, including reductions in the thickness of organic layers, increased soil bulk density, reduced availability of nitrogen and phosphorus in areas where most fine roots are concentrated, declines in the abundance of certain woodland plants, increased occurrence of invasive plant species, decreased fungal community diversity, and long-term declines in the abundance of indigenous soil faunal groups (Bohlen *et al.*, 2004; Migge-Kleian *et al.*, 2006). It is possible that such earthworm-mediated changes have also occurred in the past in European woodlands. The widespread occurrence of earthworms in woodlands in north-west Europe, however, may mask their real impact on woodland ecosystems.

One clear diagnostic marker of woodland age that was revealed in this research was the composition of the soil seed bank. The absence of many plant species in the seed bank, particularly open-habitat species such as *Juncus effusus*, may be an effective indicator of ancient woodland. Equally, the presence in soils of high

densities of the seeds of open-habitat species may help to confirm the occurrence of formerly disturbed conditions in a woodland. These findings correspond with previous studies of ancient woodland seed banks (Leckie *et al.*, 2000; Bossuyt *et al.*, 2002; Plue *et al.*, 2008), and indicate that the use of the seed bank as a diagnostic tool for determining woodland history may have widespread application.

Previous studies have highlighted the importance of ancient woodlands as habitats for populations of rare and threatened vascular plant species (Peterken & Game, 1984; Matlack, 1994; Hermy *et al.*, 1999). While the plant communities of ancient woodlands in much of Europe and North America are generally richer than those of more recent woods, this pattern is less apparent in Ireland due to the impoverished nature of the Irish flora (Webb, 1983). Ancient woodlands are also of importance to local communities for their recreational and aesthetic values, and can form important historical linkages to past management and uses (Glaves *et al.*, 2009). However, the results of this research indicate that the ancient woodland system as a whole is extremely important, and may provide a range of ecosystem services and process that only develop after hundreds and possibly thousands of years of continuous woodland cover. They also provide valuable information on natural disturbance regimes, soil development, biogeochemical cycling, and species distributions that only develop in the absence of major human disturbances (Foster *et al.*, 1996). The ancient woodland of the Gearagh has likely remained largely unchanged over hundreds of years and thus represents an extremely stable habitat. However, it will take many years before woods of more recent origin attain such ecosystem stability; the composition and structure of these secondary communities will thus continue to change over the coming centuries.

7.3 Survival of ancient woodland

The importance of the Gearagh is usually ascribed to the unusual geomorphology of the River Lee and the anastomosing channel pattern that characterises the system. No comparable systems have been described in Britain (Peterken, 1993; Brown *et al.*, 1997), although multi-channel rivers are thought to have once been relatively common in north-west Europe (Brown, 2002). Additionally, this study has shown

that, until relatively recently, anastomosing channels containing vegetative islands were a notable feature of certain rivers in south-west Ireland. Yet, the Gearagh is frequently described as one of the last remaining semi-natural alluvial forests in Europe (Cross & Kelly, 2003; Kelly, 2005), with the underlying assumption that the vegetation is dominated by unusual flood-tolerant species, particularly alder, *Alnus glutinosa* (Toner & Keddy, 1997), which is actually rare within the study areas of the Gearagh. This classification of the vegetation arose from descriptions made by Braun-Blanquet and Tüxen (1952) during their brief visit to the Gearagh. However, their main objective was to determine the distributions of plant associations over Ireland as a whole; they were less concerned with gathering detailed accounts of particular sites such as the Gearagh (O'Reilly, 1955), and only visited a small section of the woodland (White, 1985). While parts of the woodland, including much of the secondary area, certainly correspond to Fossit's (2000) wet pedunculate oak-ash woodland (WN4) category of Irish habitats, the ancient woodland clearly belongs to Fossit's (2000) oak-ash-hazel woodland (WN2) category; this is typical of base-rich soils that are generally dry or well-drained. Therefore, while the Gearagh does have an unusual geomorphological setting, the predominant vegetation is similar to that of many other Irish native woods. Rather, the most remarkable feature of the Gearagh is its age and relative lack of historical disturbance.

The ancient woodland areas of the Gearagh have likely been continuously wooded for far longer than 400 years, making it unusual not only in terms of Irish woodlands, but also in a European context. In addition, multiple lines of evidence throughout the thesis (including soils, decomposer communities, and seed bank characteristics) point towards the remarkably low levels of disturbance and exploitation in this area of the Gearagh. Several key factors have ensured the relative isolation and inaccessibility of the Gearagh throughout its history, most notably the proximity of a large wetland area (Annahalabog) and the anastomosing channel pattern of the river Lee. Great effort and expense would have been required to channelize a small wooded system such as the Gearagh (Brown, 2002), as evidenced by the description of improvements that were made to a similar but smaller system on the river Bride in the early 1700s (Smith, 1774). However, much

of the landscape in the vicinity of the Gearagh remained underdeveloped until recent decades (O'Flanagan & Buttimer, 1993); it therefore seems unlikely that local landowners would have been able to commit to such a costly project.

As evidenced by the Gearagh, a combination of geographical, historical and ecological factors is often necessary to ensure the continued survival of a wood. In North America, large wooded areas could have remained intact simply because Europeans never reached those areas during the period of agricultural expansion in the 17th and 18th centuries. However, in Europe, woodlands could only survive if there were specific reasons for man not to historically exploit them. Most wooded areas in Europe were cleared at some point for agriculture, or were destroyed during periods of political upheaval. Many of those that remained were situated on land that was never suitable for agriculture; instead, they were heavily exploited due to activities such as coppicing, wood-harvesting, litter extraction, sod-cutting, and grazing (Kirby & Watkins, 1998). Others, such as Białowieża Forest, which was declared a hunting reserve in the 1500s (Kuemmerle *et al.*, 2007), survived because they were protected over the course of many centuries by successive landowners. Other wooded areas were rarely exploited because of their location in isolated and inaccessible areas, particularly upland regions such as the Eastern Carpathians range (Falinski & Faliński, 1978) and in the mountains of the Balkan peninsula (Čurović *et al.*, 2011).

It should be acknowledged that ancient woodlands are highly varied in both structure and composition (Rackham, 1980), not only because of regional differences in climate and geology, but also because of differences in historical management. In England, areas of ancient woodland with non-native trees planted on them (Plantations on Ancient Woodland Sites) are distinguished from areas of ancient semi-natural woodland (Goldberg *et al.*, 2007). Such differences may have important consequences for biotic diversity and ecosystem processes (e.g. nutrient cycling, decomposition). In addition, the threshold date used to define these continuously wooded areas varies between countries: England 1600 (Rackham, 1980), Sweden 1660-1770 (Cousins *et al.*, 2003), Belgium 1770 (Kirby & Watkins, 1998), Germany 1780 (Wulf, 2004), Netherlands 1800 (Kirby & Watkins, 1998),

Denmark c.1800 (Honnay *et al.*, 2004). To this extent, some ancient woodlands may be more ‘ancient’ than others. Comparisons of ancient woodlands from different areas should therefore be made with caution.

7.4 Woodland management and restoration

Ancient woodland is regarded as the most important category of woodland for nature conservation (Thomas *et al.*, 1997). Fortunately, the Gearagh is currently protected by a number of national and international designations, although these were implemented before its status as ancient woodland could be confirmed. It is conserved as a Special Area of Conservation under the EU Directive 92/43/EEC and as a Statutory Nature Reserve, while it also qualifies as a Council of Europe Biogenetic Reserve and a Ramsar Convention site. The wet pedunculate oak-ash vegetation (WN4 category) which dominates the secondary sites loosely corresponds to the Annex 1 habitat of alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (Alno-padion, Alnion incanae, Salicion albae) (91E0). These habitats often contain a wide diversity of species, but only small areas remain in Europe; consequently, they are considered to be a priority habitat. The oak-ash-hazel vegetation (WN2 category) in the ancient woodland, although not listed under Annex 1 of the EU Habitats Directive, is limited in extent in Ireland and should also be considered of conservation importance (Fossitt, 2000).

Unlike the Gearagh, however, most ancient woodlands in Britain and Ireland are highly fragmented and small (Spencer & Kirby, 1992; Perrin & Daly, 2010), and are isolated within a largely cultural landscape; as a result, many lie outside specially protected sites (Thomas *et al.*, 1997). Yet it is possible to enable effective protection of wooded areas that lie outside nature reserves through a variety of measures, e.g. through statutory land-use policies and voluntary conservation (Kirby, 2003). Such protection is vital to ensure the continued survival of ancient woodlands, which are highly sensitive to disturbances and remain vulnerable to numerous threats, including fragmentation, pollution, overgrazing, and pathogens (Rackham, 2008). However, evidence from the seed bank study suggests that ancient woodlands may be less susceptible to invasion by exotic and non-woodland

species than are secondary woodlands. Even so, it should be acknowledged that the strongly modified nature of many ancient woods in Ireland still puts them at greater risk to invasive species (such as *Rhododendron ponticum*, and *Impatiens glandulifera*) than those woods with little history of disturbance.

The continued loss and fragmentation of woodland habitats throughout the world has led to the acknowledgement by conservation biologists of the increasing importance of biodiversity recovery and management in secondary woodlands (Bowen *et al.*, 2007). However, the results of this study show that the complete restoration of native flora and fauna assemblages to a pre-disturbance state may be problematic (Fig. 7.1). Although most of the native tree species (*Q. robur*, *F. excelsior*, *C. avellana*, *B. pubescens*) easily colonised the secondary woodland, the structure remained somewhat different from that of the ancient woodland. Similarly, while most species of ground flora that were associated with the ancient woodland also occurred in the secondary woodland, some of these species (e.g. *Anemone nemorosa*, *Ranunculus ficaria*, *Veronica montana*) were able to become far more abundant than others (e.g. *Blechnum spicant*, *Euphorbia hyberna*). Many soil and ground-dwelling invertebrates which are sensitive to disturbance found it difficult to re-establish in new habitats (e.g. Oribatid mites, enchytraeids), while those that are able to adapt quickly to environmental perturbations were more likely to persist in secondary sites (e.g. certain groups of rapidly-reproducing collembolans). The ability of species to successfully establish in secondary woodlands depends partly on local site conditions which, as in this study, may have been modified to a certain extent by past land-use. Therefore, the regeneration of secondary woodlands and the subsequent conservation value may vary widely, even for the same woodland type, as it is strongly dependant on the type, duration, and intensity of past land-use (Foster *et al.*, 2003).

In addition, new plant and animal species that invade cleared areas may then be able to persist in secondary woodland sites (e.g., Huhta & Rätty, 2005). For instance, the results of the seed bank study show how species associated with grassland areas have the potential to survive in secondary woodland habitats. This may result in altered species composition and, in more extreme cases, may even represent

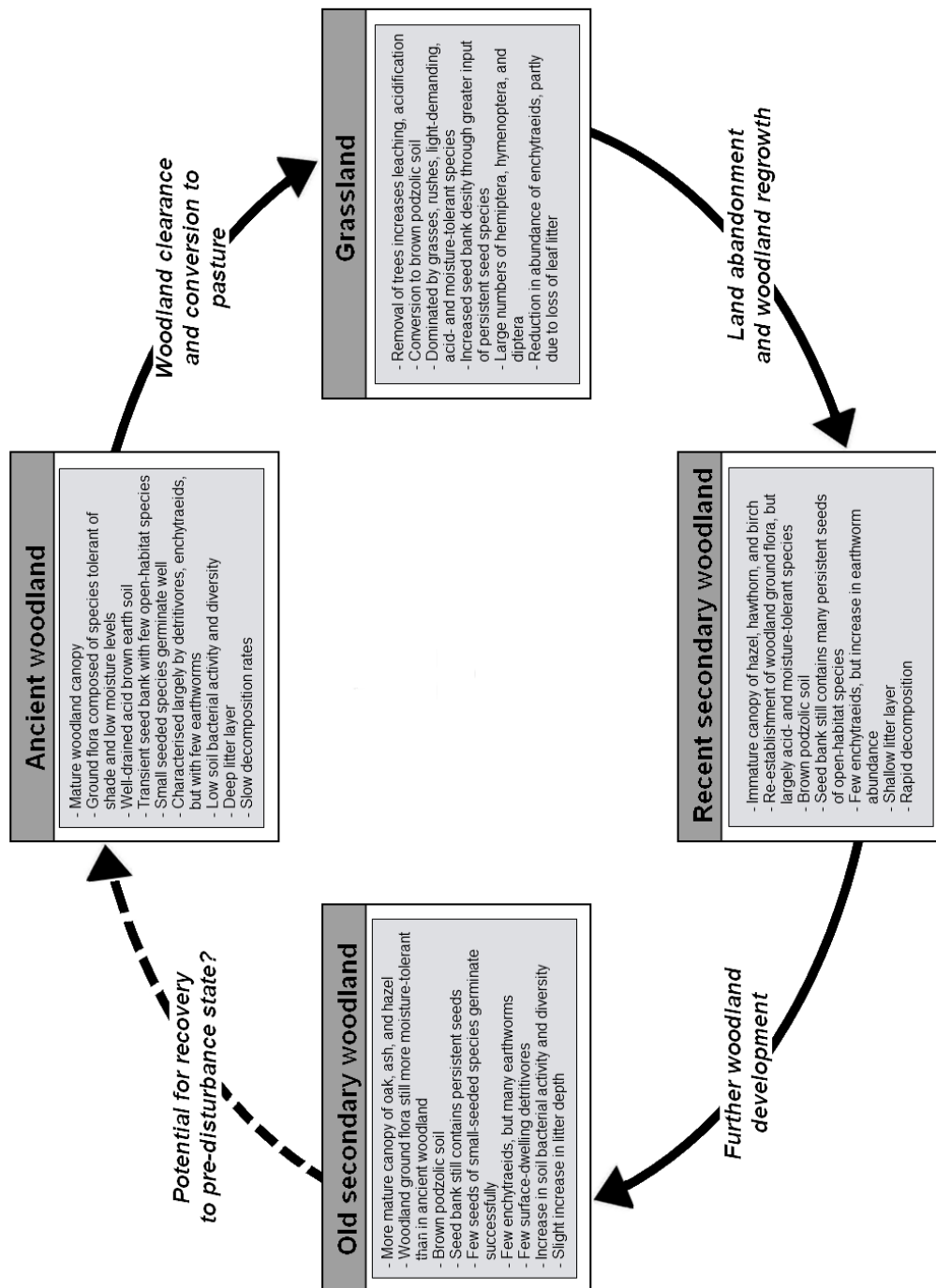


Fig. 7.1 Diagram illustrating the main changes and processes that occurred in the Gearagh during conversion of ancient woodland to grassland and the subsequent regrowth and development of woodland from recent secondary to old secondary.

novel ecosystems with indeterminate ecological values (Hobbs *et al.*, 2006). Ecosystem restoration may then necessitate the eradication of the invasive plant or animal from the woodland (Kardol & Wardle, 2010), although this can be extremely difficult and often impractical in reality. For instance, there are few effective ways to remove invasive belowground organisms (e.g. earthworms, ants, some plant-pathogenic fungi), although interventions that indirectly reduce their density may have some potential. For example, the removal of invasive plant species has been shown to reduce the abundance of non-native earthworms (Madritch & Lindroth, 2009).

The most common targets for woodland management include the enlargement of existing ancient woodland sites and the restoration of sites that have been highly modified in the past (e.g. through conifer felling). This is best facilitated through the establishment of new woodland adjacent to ancient woodland patches (Honnay *et al.*, 2002), although it may be prudent to concentrate management efforts in landscapes that have many ancient woodland patches with potential source populations of plant and animal species (Vellend, 2003). However, most management policies aim to simply restore woodland tree and plant communities (Thompson *et al.*, 2003; The Woodland Trust, 2005). While new woodland can be rapidly created by planting saplings and through direct seeding (Willoughby *et al.*, 2004), recovery of the ground flora may be slow, particularly if the site is isolated from other woodlands (Matlack, 1994; Brunet & Von Oheimb, 1998; Dzwonko, 2001). One possible strategy would be to introduce seeds of exceptionally slow-colonising species (e.g. *Hyacinthoides non-scripta*) into secondary woodlands, although this is not without risks (McLachlan *et al.*, 2007), particularly if other biotic and abiotic factors are not taken into consideration.

While new woods may give the appearance of functional woodland communities, the results of this research show that the structure of their biotic communities and ecosystem functions may differ considerably from those of undisturbed ancient woodlands. Indeed, restoration that does not consider the broader ecological system could potentially lead to negative impacts or undesirable outcomes (Bullock *et al.*, 2011). For instance, recovery of the soil and ground decomposer community

will be crucial not only for woodland decomposition process, but will also influence nutrient cycling, soil structure, and soil organic matter turnover (Seastedt, 1984). As part of this, knowledge of the land-use history will be essential to facilitate the full recovery of woodland biodiversity and processes (Foster, 2000; Jackson & Hobbs, 2009), particularly since the effects of land-use legacies may continue to affect woodland community dynamics for several hundreds and even thousands of years after agricultural abandonment (Dupouey *et al.*, 2002; Foster *et al.*, 2003). Since these effects frequently differ among stands within the same woodland (Verheyen *et al.*, 1999), it may be necessary to tailor management options to stands with different land-use histories rather than implementing a single scheme for the entire woodland. Indeed, broad prescriptions are often ineffective and do not provide managers with the detail of information necessary to develop a successful restoration project (Eviner & Hawkes, 2008). Many restoration efforts fail due to site-specific issues that were not taken into account (Wassenaar *et al.*, 2007), particularly those relating to local variability in soil properties. Effective restoration is challenging and needs to consider multiple species, multiple functions, and their interactions. It is therefore necessary to develop stronger collaborations between researchers and restoration practitioners in order to gain a more complete understanding of these site-specific issues (Eviner & Hawkes, 2008).

In some cases, past land-use may have modified biotic and abiotic factors to such an extent that the system may become fixed in a permanently degraded state (Suding *et al.*, 2004), imposing, for instance, limitations on the colonisation capacity of certain plant species (Baeten *et al.*, 2009). In these situations, knowledge of soil composition and ecology can greatly improve restoration success (Callaham *et al.*, 2008), largely due to the strong links that exist between above-ground and below-ground structure and communities (Kardol & Wardle, 2010). Yet, soils are often overlooked in woodland restoration (Callaham *et al.*, 2008), perhaps because they are simply seen as a medium for plant growth (Thompson *et al.*, 2003). However, the present thesis provides evidence that soil legacies of past agriculture can impede the establishment of woodland plant species and can also alter decomposition dynamics through changes in the soil and ground decomposer

communities. Since natural recovery of degraded soils may take up to 1,000 years to complete (Willis *et al.*, 1997), active amelioration of soil properties should therefore be considered. However, when this is not regarded as feasible (e.g. too costly, too large area, etc.), it may be necessary to mitigate the impact of these soil legacies. In secondary woods, this can be carried out simply by maintaining low light levels at the woodland floor (e.g. through the promotion of a dense shrub layer and the discontinuation of coppicing) to prevent undesirable species germinating from the seed bank and out-competing other woodland species (De Keersmaecker *et al.*, 2004).

Despite the potential negative developments in secondary woodlands, the results from the Gearagh suggest that restoration of native woodland to a state similar to that of ancient woodland is largely possible, particularly if the main focus is simply on the restoration of tree and plant communities. Conservation efforts in such woodlands should simply concentrate on protecting the site from disturbances (such as over-grazing, clearances and fragmentation, pollution from external sources), making the woodland area as large as possible, and limiting the spread of non-native plant species. Then, if given enough time, the wood will naturally progress to a more mature state. Complications only arise if the aim is to fully recreate the ecosystem functions and processes of ancient woodland, as this may involve modification of both aboveground and belowground communities (Kardol & Wardle, 2010). For instance, efforts to improve the growth of slow-growing woodland plants at the expense of fast-growing open-habitat species may involve the addition of high quality carbon substrates which stimulate nitrogen immobilisation by the decomposer community, thereby temporarily reducing soil fertility (Kardol *et al.*, 2008). Such developments are unlikely to occur quickly, particularly if soil amelioration is required (e.g. soil spreading, mycorrhizal inoculations), and it may be hundreds of years before a secondary woodland begins to resemble the conditions of an ancient woodland. Yet regardless of conservation objectives, secondary woodlands will, for the most part, ultimately have a beneficial effect of increasing habitat area for many woodland species, even if it is just to increase the connectivity between surviving ancient woodland sites.

7.5 Suggestions for further research

Most European habitats exist in a cultural landscape, and have done so for at least several hundred years. Ecosystems therefore should not be viewed without an acknowledgement of the impact of past human activity. It is advisable that research translates the current knowledge about the effects of land-use history into practical management guidelines. Future research should involve applied site-specific studies with the aim of linking ecological theory with local conditions in a more comprehensible manner for managers and decision makers. This includes determining suitable soil conditions for favourable ground flora community development, assessing the effects of soil fauna on soil structure, litter decomposition, and vegetation development, and evaluating different cutting regimes of the tree and shrub layer. Such guidelines may aid in the management and restoration of woodland sites, particularly in light of future woodland expansion throughout Europe. Site management should, however, also account for ecosystem attributes and services other than biodiversity, e.g. site productivity and nutrient cycling.

The results of this study show that knowledge of the history of a site can provide valuable information for understanding the current structure, composition, and function of a woodland. However, information on the historical uses of individual woodlands is generally lacking. More detailed pollen analyses are therefore needed to confirm the prehistory and history of ancient woodlands in Ireland. This would provide greater information on the extent of past disturbances and on any changes that arose in species composition of the woodland due to historical activities such as planting, selective felling or coppicing. More detailed investigations on the history of individual woodlands may even lead to the identification of additional ancient woods. Since many woodlands are composed of a mosaic of stands with contrasting histories, it is possible that small areas of relatively undisturbed ancient woodland may survive within larger wooded areas. These pockets of ancient woodland may act as important source populations for the restoration of other woodlands. Greater research should be carried out on the ecology of surviving ancient woods so as to substantiate some of the findings from the Gearagh and to

evaluate some of the indicators of ancient woodland. However, because of their scarcity and likely small size, they may be particularly vulnerable to a number of threats and therefore urgently require protection.

Soils may be an extremely useful way of confirming the presence of ancient woodland. In particular, the identification of a relatively undisturbed soil profile may be an effective method of distinguishing woodlands that have been subject to minimal human interference. However, there is very little information available on the nature of ancient woodland soils. A description of soil properties is also crucial for assessing the legacies of past land-use that may still be affecting present-day woodland plant and animal communities. However, ecologists are often discouraged from examining soil properties in detail due to difficulties in the measurement and interpretation of soil characteristics. Few ecological studies examine the whole soil profile; frequently, only easily-quantified properties such as pH are measured and usually only from the top 10 cm of soil. Future studies should therefore aim to encourage greater collaboration between soil scientists and ecologists, and endeavour to make the discipline of soil science more accessible to a wider audience.

The majority of investigations examining the effects of past land-use have focused solely on the vegetation communities. However, the results here indicate that soil and decomposer communities may also be significantly affected by past land-use, particularly since many of the plant species associated with ancient woodland are poor dispersers and often take a long time to recover from disturbances. Yet, woodland soil systems are complex and remain poorly understood, particularly with regards to soil ecology. Greater attention should therefore be paid to the ecology of woodland decomposers, particularly earthworms and enchytraeids, as they play a crucial role in processes such as decomposition and mineralisation. A multi-disciplinary approach will be particularly useful for future work on woodlands and should involve people from diverse backgrounds, e.g. mycologists, soil scientists, ecologists, etc.

The findings of this study indicate that the partial recovery of a woodland understorey is largely possible, particularly if the new woodland is located nearby a source population. However, the often persistent effects of past land-use means that secondary woodlands may remain distinct from ancient woodlands for a very long time; the decomposer communities of the soil and litter layer may be particularly slow to recover. Because of this, woodlands that have been subject to minimal disturbance in the past, such as the Gearagh, are extremely rare in both the Irish and European landscape. It is therefore crucial that such woodlands be protected from any future disturbances.

7.6 References

- Baeten, L., Hermy, M. & Verheyen, K. (2009) Environmental limitation contributes to the differential colonization capacity of two forest herbs. *Journal of Vegetation Science*, **20**, 209-223.
- Bakker, J.P., Grootjans, A.P., Hermy, M. & Poschlod, P. (2000) How to define targets for ecological restoration? — Introduction. *Applied Vegetation Science*, **3**, 3-6.
- Bohlen, P.J., Scheu, S., Hale, C.M., McLean, M.A., Migge, S., Groffman, P.M. & Parkinson, D. (2004) Non-native invasive earthworms as agents of change in northern temperate forests. *Frontiers in Ecology and the Environment*, **2**, 427-435.
- Bossuyt, B., Heyn, M. & Hermy, M. (2002) Seed bank and vegetation composition of forest stands of varying age in central Belgium: consequences for regeneration of ancient forest vegetation. *Plant Ecology*, **162**, 33-48.
- Bowen, M.E., McAlpine, C.A., House, A.P.N. & Smith, G.C. (2007) Regrowth forests on abandoned agricultural land: A review of their habitat values for recovering forest fauna. *Biological Conservation*, **140**, 273-296.
- Brady, N.C. & Weil, R.R. (2002) *The Nature and Properties of Soils*. Prentice Hall, New Jersey, USA, pp. 960.
- Braun-Blanquet, J. & Tuxen, R. (1952) Irische Pflanzengesellschaften. In: *Die Pflanzenwelt Irlands* (ed. W. Ludi), pp. 224-421. Hans Huber, Bern, Switzerland.

- Brown, A.G. (2002) Learning from the past: palaeohydrology and palaeoecology. *Freshwater Biology*, **47**, 817-829.
- Brown, A.G., Harper, D. & Peterken, G.F. (1997) European floodplain forests: structure, functioning and management. *Global Ecology and Biogeography*, **6**, 169-178.
- Brunet, J. & Von Oheimb, G. (1998) Migration of vascular plants to secondary woodlands in southern Sweden. *Journal of Ecology*, **86**, 429-438.
- Bullock, J.M., Aronson, J., Newton, A.C., Pywell, R.F. & Rey-Benayas, J.M. (2011) Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends in Ecology & Evolution*, **26**, 541-549.
- Callaham, M.A., Rhoades, C.C. & Heneghan, L. (2008) A striking profile: soil ecological knowledge in restoration management and science. *Restoration Ecology*, **16**, 604-607.
- Cousins, S.A.O., Lavorel, S. & Davies, I. (2003) Modelling the effects of landscape pattern and grazing regimes on the persistence of plant species with high conservation value in grasslands in south-eastern Sweden. *Landscape Ecology*, **18**, 315-332.
- Cross, J.R. & Kelly, D.L. (2003) Wetland woods. In: *Wetlands of Ireland: Distribution, Ecology, Uses and Economic Value* (ed. M.L. Otte), pp. 160-173. University College Dublin Press, Dublin, Ireland.
- Cunningham, D. (2005) *Brackloon: The story of an Irish oak wood*. COFORD, Dublin, Ireland, pp. 164.
- Čurović, M., Stešević, D., Medarević, M., Cvjetičanin, R., Pantić, D. & Spalević, V. (2011) Ecological and structural characteristics of monodominant montane beech forests in the National Park Biogradska Gora, Montenegro. *Archives of Biological Sciences*, **63**, 429-440.
- De Keersmaecker, L., Martens, L., Verheyen, K., Hermy, M., De Schrijver, A. & Lust, N. (2004) Impact of soil fertility and insolation on diversity of herbaceous woodland species colonizing afforestations in Muizen forest (Belgium). *Forest Ecology and Management*, **188**, 291-304.
- Dupouey, J.L., Dambrine, E., Laffite, J.D. & Moares, C. (2002) Irreversible impact of past land use on forest soils and biodiversity. *Ecology*, **83**, 2978-2984.

- Dzwonko, Z. (2001) Effect of proximity to ancient deciduous woodland on restoration of the field layer vegetation in a pine plantation. *Ecography*, **24**, 198-204.
- Enckell, P.H. & Rundgren, S. (1988) Anthropochorous earthworms (Lumbricidae) as indicators of abandoned settlements in the Faroe Islands. *Journal of Archaeological Science*, **15**, 439-451.
- Eviner, V.T. & Hawkes, C.V. (2008) Embracing variability in the application of plant-soil interactions to the restoration of communities and ecosystems. *Restoration Ecology*, **16**, 713-729.
- Falinski, J.B. & Faliński, J.B. (1978) Uprooted trees, their distribution and influence in the primeval forest biotope. *Vegetatio*, **38**, 175-183.
- Fossitt, J. (2000) *A Guide to Habitats in Ireland*. The Heritage Council, Kilkenny, Ireland, pp. 115.
- Foster, D.R. (2000) From bobolinks to bears: interjecting geographical history into ecological studies, environmental interpretation, and conservation planning. *Journal of Biogeography*, **27**, 27-30.
- Foster, D.R., Orwig, D.A. & McLachlan, J.S. (1996) Ecological and conservation insights from reconstructive studies of temperate old-growth forests. *Trends in Ecology & Evolution*, **11**, 419-424.
- Foster, D.R., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D. & Knapp, A. (2003) The importance of land-use legacies to ecology and conservation. *BioScience*, **53**, 77-88.
- Frelich, L., Hale, C., Scheu, S., Holdsworth, A., Heneghan, L., Bohlen, P. & Reich, P. (2006) Earthworm invasion into previously earthworm-free temperate and boreal forests. *Biological Invasions*, **8**, 1235-1245.
- Glaves, P.M., Handley, C., Rotherham, I.D., Birbeck, J. & Wright, B. (2009) *The Identification of Ancient Woodland: Demonstrating Antiquity and Continuity - Issues and Approaches*. Woodland Trust, Sheffield, UK, pp. 32.
- Goldberg, E., Kirby, K., Hall, J. & Latham, J. (2007) The ancient woodland concept as a practical conservation tool in Great Britain. *Journal for Nature Conservation*, **15**, 109-119.

- Hall, V.A. (1997) The development of the landscape of Ireland over the last two thousand years; fresh evidence from historical and pollen analytical studies. *Chronion*, **1**, 1–22.
- Hermý, M., Honnay, O., Firbank, L., Grashof-Bokdam, C. & Lawesson, J.E. (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation*, **91**, 9–22.
- Hermý, M. & Verheyen, K. (2007) Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. *Ecological Research*, **22**, 361–371.
- Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vilà, M., Zamora, R. & Zobel, M. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1–7.
- Honnay, O., Bossuyt, B., Verheyen, K., Butaye, J., Jacquemyn, H. & Hermý, M. (2002) Ecological perspectives for the restoration of plant communities in European temperate forests. *Biodiversity and Conservation*, **11**, 213–242.
- Honnay, O., Verheyen, K., Bossuyt, B. & Hermý, M. (2004) *Forest Biodiversity: Lessons From History For Conservation*. CABI Publishing, Wallingford, UK, pp. 320.
- Huhta, V. & Rätý, M. (2005) Soil Animal Communities of Planted Birch Stands in Central Finland. *Silva Fennica*, **39**, 5–19.
- Jackson, S.T. & Hobbs, R.J. (2009) Ecological restoration in the light of ecological history. *Science*, **325**, 567–569.
- Kardol, P., Van der Wal, A., Bezemer, T.M., de Boer, W., Duyts, H., Holtkamp, R. & Van der Putten, W.H. (2008) Restoration of species-rich grasslands on ex-arable land: Seed addition outweighs soil fertility reduction. *Biological Conservation*, **141**, 2208–2217.
- Kardol, P. & Wardle, D.A. (2010) How understanding aboveground-belowground linkages can assist restoration ecology. *Trends in Ecology & Evolution*, **25**, 670–679.

- Kelly, D.L. (2005) Woodland on the western fringe: Irish oakwood diversity and the challenges of conservation. *Botanical Journal of Scotland*, **57**, 21-40.
- Kirby, K.J. (2003) Woodland conservation in privately-owned cultural landscapes: the English experience. *Environmental Science & Policy*, **6**, 253-259.
- Kirby, K.J. & Goldberg, E. (2002) *Ancient Woodland: Guidance Material for Local Authorities*. English Nature, Peterborough, UK, pp. 22.
- Kirby, K.J. & Watkins, C. (1998) *The Ecological History of European Forests*. CAB International, Wallingford, UK, pp. 384.
- Kuemmerle, T., Hostert, P., Radeloff, V.C., Perzanowski, K. & Kruhlov, I. (2007) Post-socialist forest disturbance in the Carpathian border region of Poland, Slovakia, and Ukraine. *Ecological Applications*, **17**, 1279-1295.
- Leckie, S., Vellend, M., Bell, G., Waterway, M.J. & Lechowicz, M.J. (2000) The seed bank in an old-growth, temperate deciduous forest. *Canadian Journal of Botany*, **78**, 181-192.
- Little, D., Farrell, E. & Collins, J. (1997) Land-use legacies and soil development in semi-natural ecosystems in the marginal uplands of Ireland. *Catena*, **30**, 83-98.
- Little, D.J., Boyle, G.M., Ryan, D. & Farrell, E.P. (2001) *Intensive Monitoring of an Oak Woodland in Western Ireland: Development of an Irish Ecological Monitoring Network (IEMN)*. COFORD, Dublin, Ireland, pp. 99.
- Madritch, M. & Lindroth, R. (2009) Removal of invasive shrubs reduces exotic earthworm populations. *Biological Invasions*, **11**, 663-671.
- Maraun, M. & Scheu, S. (2000) The structure of oribatid mite communities (Acari, Oribatida): patterns, mechanisms and implications for future research. *Ecography*, **23**, 374-383.
- Matlack, G.R. (1994) Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology*, **75**, 1491-1502.
- McLachlan, J.S., Hellmann, J.J. & Schwartz, M.W. (2007) A framework for debate of assisted migration in an era of climate change. *Conservation Biology*, **21**, 297-302.

- Migge-Kleian, S., McLean, M., Maerz, J. & Heneghan, L. (2006) The influence of invasive earthworms on indigenous fauna in ecosystems previously uninhabited by earthworms. *Biological Invasions*, **8**, 1275-1285.
- O'Flanagan, P. & Buttimer, C.G. (1993) *Cork: History and Society: Interdisciplinary Essays on the History of an Irish County*. Geography Publications, Dublin, Ireland, pp. 1000.
- O'Reilly, H. (1955) Survey of the Gearagh, an area of wet woodland on the River Lee, near Macroom, Co. Cork. *The Irish Naturalists' Journal*, **11**, 279-286.
- Perrin, P., Martin, M., Barron, S., O'Neill, F., McNutt, K. & Delaney, A. (2008) *National Survey of Native Woodlands 2003-2008: Volume I: Main Report*. Unpublished report to the National Parks & Wildlife Service, Dublin, Ireland, pp. 187.
- Perrin, P.M. & Daly, O.H. (2010) *A Provisional Inventory of Ancient and Long-Established Woodland in Ireland*, Irish Wildlife Manuals, No. 46. National Parks and Wildlife Service, Department of the Environment, Heritage and Local Government, Dublin, Ireland, pp. 71.
- Peterken, G.F. (1993) *Woodland Conservation and Management*. Chapman & Hall, London, UK, pp. 374.
- Peterken, G.F. & Game, M. (1984) Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *The Journal of Ecology*, **72**, 155-182.
- Plue, J., Hermy, M., Verheyen, K., Thuillier, P., Saguez, R. & Decocq, G. (2008) Persistent changes in forest vegetation and seed bank 1,600 years after human occupation. *Landscape Ecology*, **23**, 673-688.
- Rackham, O. (1980) *Ancient Woodland: Its History, Vegetation and Uses in England*. Edward Arnold, London, UK, pp. 624.
- Rackham, O. (2008) Ancient woodlands: modern threats. *New Phytologist*, **180**, 571-586.
- Räty, M. & Huhta, V. (2004a) Communities of Enchytraeidae (Oligochaeta) in planted birch stands as compared with natural forests in central Finland. *Biology and Fertility of Soils*, **40**, 413-420.

- Räty, M. & Huhta, V. (2004b) Earthworm communities in birch stands with different origin in central Finland. *Pedobiologia*, **48**, 283-291.
- Richter, K. (2010) *Genetic Structure in European Populations of the Earthworm Lumbricus terrestris*. PhD thesis, Kassel University, Germany.
- Rose, F. (1999) Indicators of ancient woodland: the use of vascular plants in evaluating ancient woods for nature conservation. *British Wildlife*, **10**, 241-251.
- Rotherham, I.D., Jones, M., Smith, L. & Handley, C. (2008) *The Woodland Heritage Manual: A Guide to Investigating Wooded Landscapes*. Wildtrack Publishing, Sheffield, UK, pp. 225.
- Seastedt, T.R. (1984) The role of microarthropods in decomposition and mineralization processes. *Annual Review of Entomology*, **29**, 25-46.
- Smith, C. (1774) *The Ancient and Present State of the County and City of Cork: Containing a Natural, Civil, Ecclesiastical, Historical, and Topographical Description Thereof*. W. Wilson, Dublin, Ireland, pp. 443.
- Spencer, J.W. & Kirby, K.J. (1992) An inventory of ancient woodland for England and Wales. *Biological Conservation*, **62**, 77-93.
- Suding, K.N., Gross, K.L. & Houseman, G.R. (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, **19**, 46-53.
- The Woodland Trust (2005) *The Conservation and Restoration of Plantations on Ancient Woodland Sites: A Guide for Woodland Owners and Managers*. The Woodland Trust, Grantham, UK, pp. 11.
- Thomas, R.C., Kirby, K.J. & Reid, C.M. (1997) The conservation of a fragmented ecosystem within a cultural landscape - the case of ancient woodland in England. *Biological Conservation*, **82**, 243-252.
- Thompson, R., Humphrey, J., Harmer, R. & Ferris, R. (2003) *Restoration of Native Woodland on Ancient Woodland Sites*. Forestry Commission, Edinburgh, UK, pp. 58.
- Toner, M. & Keddy, P. (1997) River hydrology and riparian wetlands: a predictive model for ecological assembly. *Ecological Applications*, **7**, 236-246.
- Vellend, M. (2003) Habitat loss inhibits recovery of plant diversity as forests regrow. *Ecology*, **84**, 1158-1164.

- Verheyen, K., Bossuyt, B., Hermy, M. & Tack, G. (1999) The land use history (1278-1990) of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. *Journal of Biogeography*, **26**, 1115-1128.
- Wassenaar, T.D., Ferreira, S.M. & Van Aarde, R.J. (2007) Flagging aberrant sites and assemblages in restoration projects. *Restoration Ecology*, **15**, 68-76.
- Webb, D. (1983) The flora of Ireland in its European context. *Journal of Life Sciences of the Royal Dublin Society*, **4**, 143-160.
- White, J. (1985) The Gearagh Woodland, Co. Cork. *The Irish Naturalists' Journal*, **21**, 391-396.
- Willis, K.J., Braun, M., Sümegi, P. & Tóth, A. (1997) Does soil change cause vegetation change or vice versa? A temporal perspective from Hungary. *Ecology*, **78**, 740-750.
- Willoughby, I., Jinks, R., Gosling, P. & Kerr, G. (2004) *Creating New Broadleaved Woodland by Direct Seeding*. Forestry Commission, Edinburgh, UK, pp. 40.
- Wilson, B.R., Moffat, A.J. & Nortcliff, S. (1997) The nature of three ancient woodland soils in southern England. *Journal of Biogeography*, **24**, 633-646.
- Wulf, M. (2004) Relative importance of habitat quality and forest continuity for floristic composition of ancient, old and recent woodland. In: *Forest Biodiversity: Lessons from History for Conservation* (eds O. Honnay, K. Verheyen, B. Bossuyt & M. Hermy), pp. 67-80. CABI Publishing, Wallingford, UK.

ACKNOWLEDGEMENTS

This project would not have been completed without the help and support from a large number of colleagues and friends. My greatest debt is to Dr. Simon Harrison and Prof. Peter Jones who supervised the research. Their interest, insight, and boundless enthusiasm were absolutely vital to the project. I thank them both sincerely for their support and patience; without them, none of this would have been possible. I am also grateful to the Irish Research Council for Science, Engineering and Technology for providing funding for this research under the EMBARK scholarship.

I would like to express my sincere appreciation to all in the School of BEES (formerly Department of ZEPS), especially all of the technicians who provided a helping hand throughout the project, and to our administrative staff for having made life as a postgraduate much easier. Special thanks to Mick Mackey for driving me out to the Gearagh in the early stages of fieldwork and for his amazing photographs of the soil profiles. I would also like to thank Don Kelleher, Frank Morrissey, and David White for their help in the laboratory, and Mairead Kiely for help with the soil seed bank and seed germination experiment.

I want to express my gratitude to the staff at the Boole Library in UCC for their assistance in locating historical maps of the Gearagh and for their help in using microfilm readers. Thanks also to the technicians at the Department of Geography for the particle soil analysis, and to Ted Hickey for help with supplying soil sampling equipment. Karen Galvin in the School of Food and Nutritional Sciences helped enormously with the measurement of soil nutrient concentrations. I also wish to thank Dave and Siobhan Barry at Ballintubber Farm in Carrigtwohill for allowing me to use the polytunnels on their land. Thanks also to the ESB for granting access to the Gearagh.

Thanks to all of the staff and fellow students in BEES for providing support and friendship throughout, particularly during those long hours in the lab. I am grateful also to Kevin Kelleher for his work on the Fairy Gardens woodland in Dunmanway and for confirming that the Gearagh is not an oddity. I also want to acknowledge Prof. Matthijs Schouten with whom I had the privilege of working with during the Burren fieldtrips for instilling in me a deep appreciation of the Irish landscape, both in the past and in the present-day.

Finally, I thank my family for helping with practical issues, and for their absolute support and encouragement on this epic journey. A special mention also to Bruce for being there to take me home after long and mostly wet days in the field. Thank you Colin for providing the necessary distractions, for your endless tolerance, and for all your loving support throughout the last few years.

APPENDIX

APPENDIX A: Ground flora species area curve

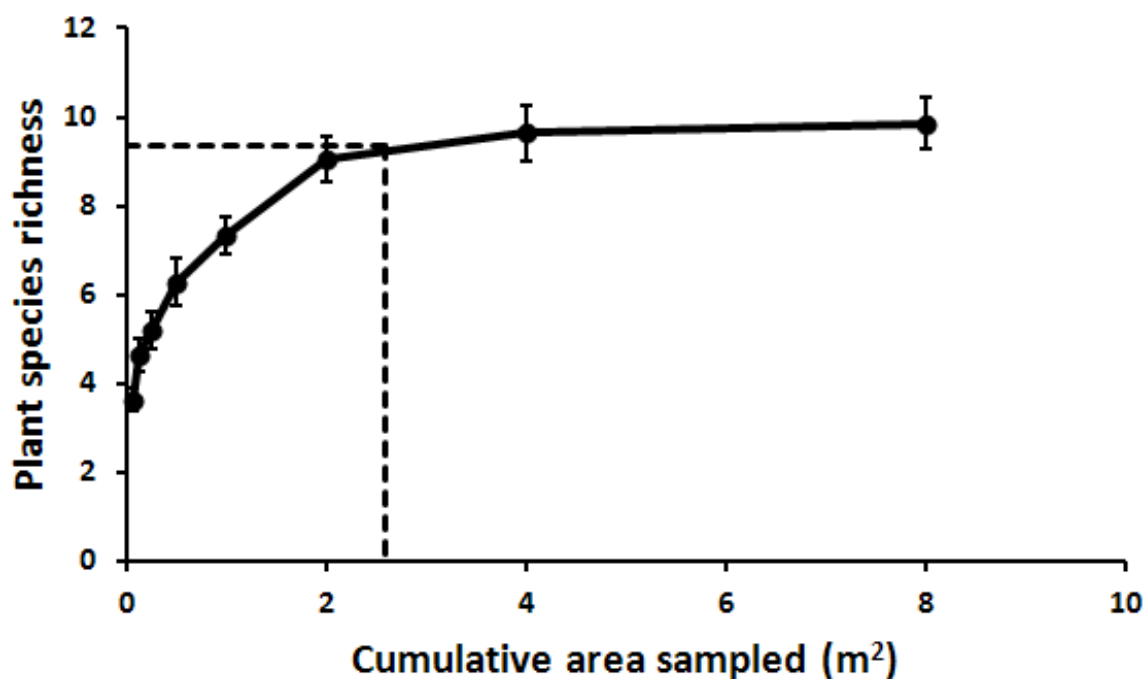


Fig. A.1 Species area curve of ground flora collected using nested quadrats, which was used to determine the minimal sampling area required to sample the plant communities in the Gearagh (Chapter 4). The point on the curve that represents the area which contains 95 % of the total number of species is indicated with a dashed line. Each point represents the mean of 14 samples (\pm standard error).