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Ecological Solutions and Evidence

RESEARCH ARTICLE

A continuous feast of bramble: *Rubus fruticosus* agg. is a key cross-seasonal dietary resource for a fallow deer population

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Abstract

1. *Context*: Deer (Cervidae) populations are increasing in many global regions, leading to concerns about their impacts on temperate forests. Advancing evidence-based management requires a detailed understanding of the dietary habits of deer and how these are shaped by resource availability.
2. *Methodology*: We studied the diet of fallow deer (*Dama dama*) in North Wales (United Kingdom), using faecal DNA metabarcoding. Samples were collected monthly from three woodlands during 2019–2021. Tree surveys and seasonal ground flora surveys were conducted in these woodlands and seven additional woodlands. Preference analyses were used to assess the consumption of plant taxa relative to their availability.
3. *Results*: The fallow deer consumed high proportions of bramble (*Rubus fruticosus* agg.) across the seasons, especially in the winter months. Diet diversity was significantly lower in winter compared to the other seasons, suggesting that the deer were bulk foraging on a widely available, predictable resource to conserve energy during winter. Grasses did not form a major component of the diet in any season. The preference analysis showed that spatially clustered woody taxa (e.g. *Betula* sp., *Corylus* sp. and *Fraxinus* sp.) occurred less often than expected in the diet, while widespread woody species occurred in the diet more often than expected (e.g. *Rosa* sp., *Prunus* sp. and *Quercus* sp.).
4. *Practical implication*: The expansion of deer populations in the United Kingdom has occurred alongside the recovery and maturation of degraded or planted forests since the middle of the 20th century. Despite reduced light availability in these closed-canopy forests and increased herbivory pressure, bramble has remained a dominant understory plant compared to other less herbivory-tolerant

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plant species. Perhaps as a consequence, bramble has become the winter survival resource for this fallow deer population, remaining a prominent dietary component throughout the year. With increasing disturbance from extreme weather and tree diseases leading to a more open canopy structure, bramble cover is set to increase in European forests, which could support further expansion of deer populations. As we work to expand tree cover and enhance forest resilience and biodiversity, we should seek to understand the dynamic interactions of increasing deer populations with rapidly changing treescapes.

KEYWORDS
Cervidae, deer, diet analysis, faecal DNA metabarcoding, herbivory, resource availability, ungulate

1 | INTRODUCTION

Deer (Cervidae) populations are expanding throughout the temperate zone (Côté et al., 2004; Linnell et al., 2020). Reduced mortality due to a warming climate, introductions of non-native species and human modification of landscapes have facilitated range expansion and population growth of deer species (Ramirez et al., 2018). While deer population growth may be seen as a conservation success story, this growth has led to unprecedented herbivory pressure in these landscapes (Fuller & Gill, 2001; Jarnemo et al., 2022; Reimoser & Putman, 2011; Takarabe & Iijima, 2020). At elevated densities, deer herbivory reduces the structural complexity of woodlands (Eichhorn et al., 2017), diminishing habitat suitability for other woodland fauna (Gill & Fuller, 2007). Intense herbivory pressure can also reduce plant diversity by favouring herbivory-tolerant (Tamura & Yamane, 2017), unpalatable (Ramirez et al., 2019) or more generalist (Boulanger et al., 2018) plant species. Additionally, the herbivory of leading shoots inhibits tree regeneration, sapling growth and timber production (Reimoser, 2003), while intensive grazing reduces arable crop and pasture yield (Corgatelli et al., 2019; Putman et al., 2011). Studying deer foraging behaviour and diet can improve our understanding of the mechanisms by which increasing deer populations are influencing, and being influenced by, human-modified landscapes (Apollonio et al., 2017).

Unlike contiguous old-growth forests, human-modified landscapes are often characterised by forest fragments at varying developmental stages. These fragments provide refuge from predation risk (Bonnot et al., 2013), shelter from adverse weather (Melin et al., 2014), herbaceous grazing material and woody browse. These forest fragments are often intermixed with crop fields and pasture, which contain nutritious grazing material year-round and provide productive edge habitats (Reiner et al., 2023). Whilst the presence of alternative natural foraging resources can divert deer browsing pressure away from tree saplings (Arnold et al., 2018), highly nutritious arable crops build and sustain high deer densities as winter mortality is reduced, and reproductive rates increase (Jarnemo et al., 2022). The resulting herbivory pressure negatively impacts biodiversity conservation, commercial forestry and agricultural productivity (Jarnemo et al., 2022; Putman et al., 2011; Takarabe & Iijima, 2020).

Fallow deer (*Dama dama*) are geographically widespread and increasing in number across their range (Esattore et al., 2022). They have been described as intermediate grazers, primarily consuming low-quality bulk roughage, such as grasses (Borkowski & Obidziński, 2003; Kerridge & Bullock, 1991; Putman et al., 1993). They also consume broadleaved and coniferous tree and shrub browse, climbing lianas such as ivy (*Hedera helix*) and honeysuckle (*Lonicera* spp.), scrambling shrubs such as bramble (*Rubus fruticosus* agg.), and herbs (Bruno & Apollonio, 1991; Jackson, 1977; Nugent, 1990). A recent review of fallow deer feeding ecology and distribution found it to be one of the most widespread and adaptable deer species (Esattore et al., 2022). Because of their dietary flexibility and potential for herding at high densities, fallow deer can substantially impact woodland vegetation (Putman et al., 2011).

DNA metabarcoding offers ecologists an effective method to explore the diet of ungulates, including deer (Erickson et al., 2017; Spitzer et al., 2020). DNA metabarcoding uses high-throughput sequencing with universal primers that bind to conserved DNA regions within a taxonomic group. These regions have enough variation to allow the identification of different taxa within the group (Deiner et al., 2017). For plants, combining the *rbcL* and ITS2 regions ensures a wide range of detection and good taxonomic discrimination, respectively (Brennan et al., 2019; Hollingsworth, 2011). The Barcode UK database (Jones et al., 2021) has improved the reliability of these markers for accurate taxonomic identification of UK plants, making them ideal for studying the diet of herbivores.

Our study aimed to characterise seasonal variation in the diet of a fallow deer population in North Wales (United Kingdom) using DNA metabarcoding of faecal samples. The study landscape was a mosaic of arable land, livestock pasture and woodlands. Typical land management objectives include livestock farming, nature conservation and amenity woodland, with some large-scale commercial forestry, although many woodlands were also unmanaged. Due to high grass availability within this landscape, we hypothesised that the fallow deer would bulk-graze on grassland species for much of the year (Kerridge & Bullock, 1991). We expected that the winter diet would be most diverse compared

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to other seasons, as the deer would feed on a wider variety of plants to meet their nutritional and energetic requirements (Jackson, 1977; Nakahama et al., 2021). To investigate dietary preference and the relative vulnerability of different plant species to herbivory pressure, we collected deer faecal samples alongside surveys of seasonal and spatial variation in resource availability. If certain plant species were positively selected by the deer, they should be overrepresented in the diet relative to their availability.

2 | METHODS

2.1 | Study sites

The Elwy Valley area is a mosaic landscape, with patches of woodland surrounded by a matrix of pastoral and agricultural farmland. Three woodlands were surveyed for fallow deer faeces once per month for 2 years (September 2019 to August 2021), excluding April to June 2020 due to the COVID-19 pandemic (Figure 1). These woodlands are known to be regularly used by fallow deer, with no effective barriers to their movement (Barton, 2023). No other deer species were detected in the study area during the period of data collection, and sheep were absent from the surveyed woodlands (Barton, 2023). Fallow deer home ranges vary between 1 and 10 km^2, depending on sex, season and landscape configuration (Borkowski & Pudełko, 2007; Davini et al., 2004), while their gut retention time is approximately 31 h (Ramanzin et al., 1997). Therefore, deer are likely to enter and leave woodlands multiple times during feeding and digestion, so faecal samples will include plants that deer consume within the woodlands and in the surrounding landscape. As such, the three woodlands sampled for faeces (Figure 1) should be considered as sampling points, not exclusive foraging locations (Jayakody et al., 2011).

To explore how deer diet in a woodland-pasture landscape compared with deer foraging on grassland only, six faecal samples were also collected in December 2020 from the fallow deer enclosure (approx. 200 × 70 metres in size, location: 53.295370 N, −3.749937 W) at the Welsh Mountain Zoo, Colwyn Bay, North Wales.

2.2 | Faecal sample collection

Deer faeces were collected opportunistically from the three woodlands, following established deer pathways. Only distinct faecal

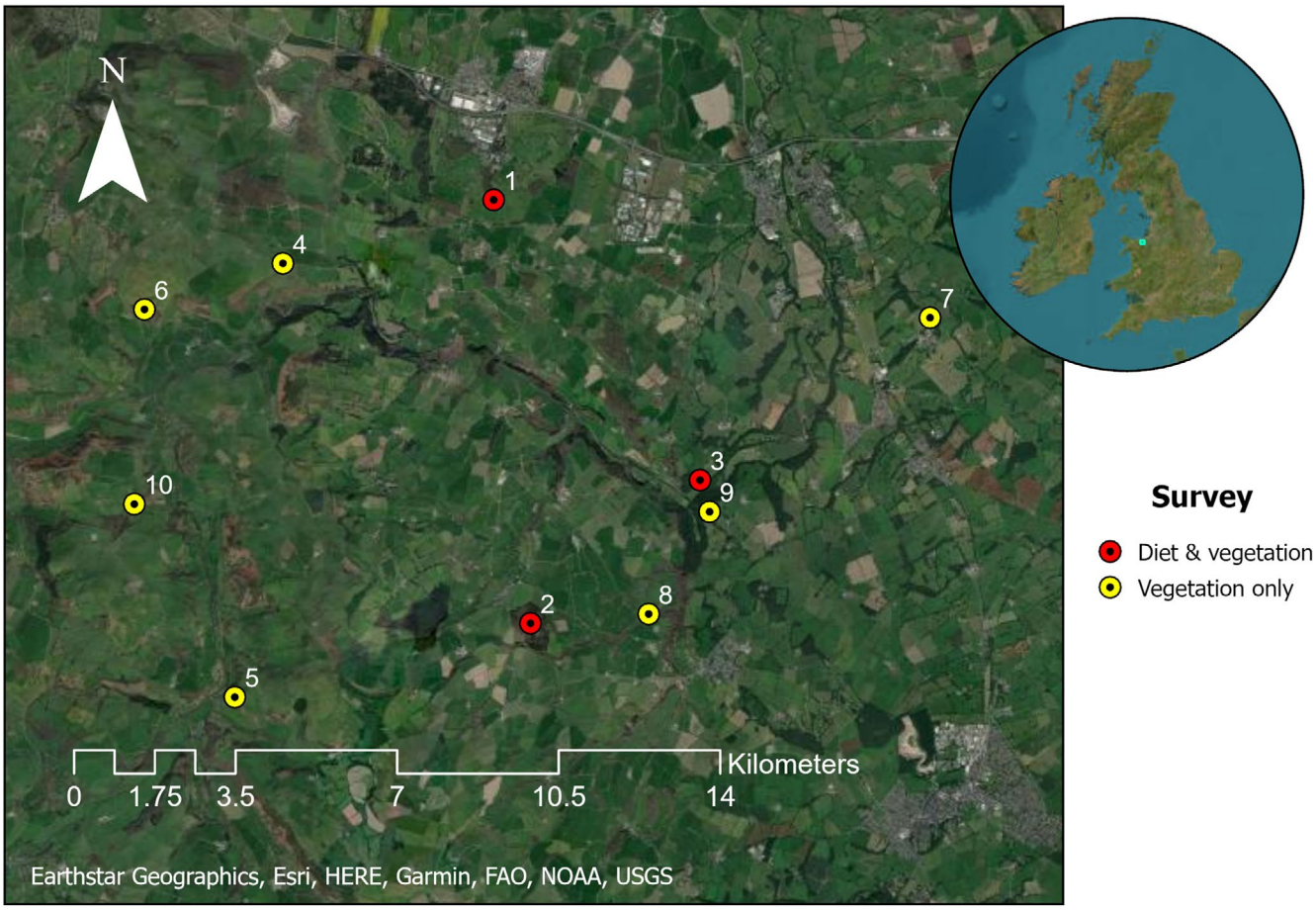

FIGURE 1 The Elwy Valley study area in North Wales within the context of the United Kingdom (marked by the cyan blue box on the inset map), and at the landscape scale. Locations of the 10 surveyed woodlands are shown by points, with survey type indicated by point colour. Points are labelled by site number.

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mounds of six or more pellets were collected. Fresh faeces were prioritised for collection, identified as darker in colour. Faecal samples were placed in labelled 50-ml Falcon tubes using clean nitrile gloves. Up to six faecal samples were collected from each woodland per monthly survey, totalling 353 samples. Seasons were defined: winter = December to February, spring = March to May, summer = June to August and autumn = September to November. The number of samples collected per sampling occasion is shown in Table S1.

The same approach was used to collect a further six samples from the captive deer enclosure at the Welsh Mountain Zoo in December 2020. All samples were double-bagged and stored at −20°C within 8 h of collection.

2.3 | Plant resource availability surveys

In addition to the three woodlands surveyed for faecal samples, seven other woodlands in the landscape were surveyed for their resource availability (Figure 1; Table S2). Woodland ground vegetation cover was surveyed once every 3 months across the 10 woodland sites, from September 2019 to July 2021 (Figure 1; Figure S3). This involved surveying permanent circular sampling plots (15-m radius) containing randomly positioned 0.25-m^2 quadrats. Bramble was surveyed as ground vegetation, as it is a scrambling shrub that can cover a large area. Similarly, lianas—ivy and honeysuckle—were surveyed as ground flora. See Supporting Information, Methodology section for full survey protocol. To sample woody browse availability, the total number of tree and shrub stems >30 cm tall were counted once in each sampling plot across all ten sites (Figure S4).

2.4 | Dietary metabarcoding

DNA was extracted from faecal samples using the Qiagen DNA Plant Mini kit, following a modified protocol. The target ITS2 and *rbcL* fragments were amplified using a two-step PCR protocol—see Table S5 for primer sequences. PCR libraries were visualised via gel electrophoresis, pooled at approximately equimolar concentrations (Tables S6 and S7) and sequenced on an Illumina MiSeq using a MiSeq Reagent Kit v3 (600-cycle). See Supporting Information, Methodology section for full laboratory protocols.

Data processing was carried out in R version 4.1.0 (R Core Team, 2021) using the Supercomputing Wales (SCW) facility. Cutadapt (Martin, 2011) and the DADA2 pipeline (Callahan et al., 2016) were used for data pre-processing (primer removal, read filtering, error correction, read merging and Amplicon Sequence Variant [ASV] generation [Supporting Information, Methodology section]). The ASVs from each sample were then blasted against a curated ITS2 and *rbcL* plant database from Barcode UK (Jones et al., 2021) using the *blastn* function (Madden & Camacho, 2008) with a percentage identity threshold of 97% and E value of 0.00001. Any matches that did not meet the 97% threshold were discarded. The top 20 genus hits for each ASV were manually inspected to ensure that the best match was assigned by comparing the E value, bit score, percentage identity match, frequency of occurrence of the genus in the top 20 hits, and the likelihood that taxa would have occurred in the study area. Where multiple genus assignments performed equally well or there was no clear best match at genus level, the ASV was resolved to family level. For *rbcL*, 14 ASVs were discounted from the analysis, as there was no clear best match at genus or family level. All grasses were resolved to family, as *rbcL* performs poorly when identifying grasses to genus (Doebley et al., 1990).

After taxonomy assignment, downstream processing was carried out using the *phyloseq* R package (McMurdie & Holmes, 2013). Rarefaction curves were inspected to quantify the coverage of both markers. Samples with less than 100 reads were removed before further analysis. After raw read processing of the ITS2 dataset, no negative extraction or PCR control samples retained enough reads to be considered further. For *rbcL*, three blanks contained one respective ASV in sufficient number that they remained post-filtering. These three ASVs were removed from the final ASV table. The reads from ITS2 and *rbcL* were then joined to give a consensus dataset whereby taxa were assigned to the highest taxonomic level reached by both markers, following methodology from Lowe et al. (2023). For each sample, the number of reads for each consensus taxon was summed for both markers. The proportion of reads per taxon was then used as a measure of relative read abundance per sample (Lowe et al., 2023). For each consensus taxon, we examined the relationship between the percentage of reads per sample for ITS2 and *rbcL* using a Spearman's rank test with Holm correction for multiple testing (Lowe et al., 2023). We treated the metabarcoding data as 'semi-quantitative', acknowledging inherent biases in species detection and DNA extraction, PCR and sequencing (Jones et al., 2022; Lamb et al., 2019; Lowe et al., 2023). Recent work has shown that metabarcoding can be quantitative (Lowe et al., 2022), with Wizenberg et al. (2023) demonstrating relative accuracy in quantitative characterisation through a multi-locus approach using rbcL and ITS2. Therefore, we used proportional read abundance data to assess diet composition and diversity. We also filtered the consensus dataset for taxa which represented 1% or more of reads from a given sample.

2.5 | Data analysis

The Shannon Diversity Index (SDI) was calculated for the taxonomic composition of the faecal samples collected from the wild deer population (Shannon, 1948). A Generalised Linear Mixed Model (GLMM) using the package *lme4* (Bolker et al., 2009) in R was conducted to test how diet diversity (SDI) varied with season using a binary presence/absence matrix of taxa. The model was fitted with the response variable SDI, a fixed effect of season and a random intercept for woodland site, using the restricted maximum likelihood (REML) method.

To visualise the relative contributions of different plant groups to wild deer diet each month, bipartite networks were constructed

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using the proportion of sequences as a measure of relative abundance using the *geom_alluvium* function in the *ggplot2* R package (Wickham, 2016). See Table S8 for classifications of plant taxa into groups (herbaceous, ferns, grasses, bulrushes, rushes, scrambling shrub, sedge, lianas, broadleaf trees, coniferous trees, shrubs).

To test the specificity of the diet of the wild deer relative to resource availability, a preference analysis was carried out using the *econullnetr* package in R (Vaughan et al., 2018). A preference analysis involves comparing the proportion of plant taxa in diet samples with the relative availability of taxa in the environment. If consumption of a species is outside the central 95% of values from the simulations from the null model, this indicates higher or lower percentage content in the diet than expected given its availability (Vaughan et al., 2018). We used presence/absence data, rather than relative read abundance, in our preference analysis, while acknowledging the potential biases associated with presence/absence data from DNA metabarcoding (Cuff et al., 2024). Ground flora was surveyed multiple times to capture seasonal variation, while woody vegetation was surveyed only once. As a result, we only had spatial information for woody vegetation, but spatiotemporal information for the ground flora. Therefore, the preference analysis methodology was applied to subsets of the sequencing data separately for ground flora (herbaceous, ferns, grasses, bulrushes, rushes, scrambling shrub, sedge and liana) and woody plants (broadleaf trees, coniferous trees and shrubs). For the ground flora preference analysis, the diet data were aligned with the plant percentage cover data according to survey month (October 2019, November 2019, etc.).

We used ground flora survey data from all 10 woodland study sites to quantify resource availability. A null model was generated using the *econullnetr* function *generate_null_net* with 500 iterations (Vaughan et al., 2018). This model used two matrices: (1) a consumer matrix, which contained presence/absence data for all plant taxa that were present in the diet (representing ≥1% of reads in a sample) and ground flora surveys and (2) a resource matrix with proportional data of the total ground flora cover, split by survey month, across all 10 woodland sites for each ground flora taxon that was present in both the diet (representing ≥1% of reads in a sample) and vegetation surveys.

For the woody plant preference analysis, each woodland site had only been surveyed once for stem number by taxon, therefore we were unable to temporally link the diet data to woody plant availability. Instead, the proportional availabilities of woody plant taxa were calculated using the total number of stems >30 cm tall counted in all the surveys across all 10 sites. Two matrices were used for this null model: (1) a consumer matrix with presence/absence data for all woody plant taxa present in the diet (representing ≥1% of reads in a sample) and field surveys and (2) a resource matrix containing a single row of proportional data per taxon calculated relative to the total number of recorded stems across all woody taxa that were present in the diet (representing ≥1% of reads in a sample) and field surveys.

A total of 127 wild deer faecal samples contained DNA from taxa found in the ground vegetation survey at ≥1% of reads for any sample. Of the 19 taxa that were present in the ground vegetation survey data (Figure S3), 11 were present in the consensus diet dataset at ≥1% of reads in one or more samples. Therefore, the preference analysis was carried out on these 11 taxa only.

A total of 258 wild deer faecal samples contained DNA from taxa found in the tree and shrub survey at ≥1% of reads for any sample. Of the 37 taxa that were present in the tree and shrub survey data (Figure S4), 22 were present in the consensus diet dataset at ≥1% of reads in one or more faecal samples. The preference analysis was therefore limited to these 22 taxa.

3 | RESULTS

3.1 | Sequencing products (wild deer)

Following the removal of primers and reads that did not contain primer sequences, 6,337,650 forward reads were obtained for ITS2 from 309 faecal samples and 4,868,694 forward reads were obtained for *rbcL* from 319 faecal samples.

A total of 3,273,487 merged reads for ITS2 and 2,384,805 forward reads for *rbcL* survived fastqc quality control. Only forward reads were used for *rbcL* due to poor quality of the reverse reads resulting in heavy losses during the filtering stage. For ITS2, the mean number of sequences per sample was 10,594 ± 537 (SE), with a range of 126 to 41,544. For *rbcL*, the mean number of sequences per sample was 7523 ± 408 (SE), with a range of 107 to 33,444. After taxonomic assignment, a total of 8195 ASVs remained for *rbcL*, resulting in a total of 119 identified genera and 66 identified families. A total of 1386 ASVs remained for ITS2, resulting in a total of 68 identified genera and 35 identified families.

There was a significant positive correlation between the percentage read content of consensus taxa in faecal samples from ITS2 and *rbcL* ($\rho = 0.43$, df = 48,897, $p < 0.001$). The consensus dataset of the ITS2 and *rbcL* sequences from 339 wild deer faecal samples consisted of 151 unique identified taxa at family or genus level. The dataset contained 5,658,370 reads with a mean of 16,691 ± 796 (SE) per sample with a range of 107 to 71,491 reads.

3.2 | Sequencing products (zoo deer)

Of the six faecal samples collected from the fallow deer population at the Welsh Mountain Zoo, all but one survived filtering for at least one marker and three survived filtering for both markers. The ITS2 marker gave a total of 11,491 reads with a mean of 2873 ± 1986 (SE) reads per sample with a range of 663 to 8823 ($n = 4$). The *rbcL* marker gave a total of 12,265 reads, with a mean of 3066 ± 2283 (SE) reads per sample with a range of 372 to 9898 ($n = 4$). The consensus dataset for the zoo samples contained a total of 23,756 reads with a mean of 5368 ± (SE) reads per sample with a range of 372 to 9898 ($n = 5$). The consensus dataset consisted of 11 plant taxa identified to genus level and one to family level (*Poaceae*).

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3.3 | Wild fallow deer seasonal diet diversity

The results from the GLMM showed meteorological season was a significant predictor of the taxonomic diversity of the diet of the wild fallow deer (Table 1). Faecal samples from the winter months had a significantly lower SDI compared to samples from the other seasons (Figure 2). The conditional R^2 for the model was 0.16, and the marginal R^2 was 0.12.

3.4 | Wild fallow deer seasonal diet composition

We identified a dominance of bramble in the diet of the wild fallow deer throughout the year. It contributed 81% of the diet in winter, 71% in spring, 66% in summer and 52% in autumn (Figure 3). Oak (*Quercus* spp.) peaked in autumn (7% of the diet), indicating acorn consumption (Figure 3). Other notable woody components included maple (*Acer* spp., 4% of spring diet) and rose (*Rosa* spp., 8% of the summer diet). Ivy peaked in winter (7% of diet). Grasses (*Poaceae*) remained relatively scarce in the diet compared with woody taxa but were most abundant in the diet in autumn (6%) and winter (4%) (Figures 3 and 4). Coniferous trees did not make up a substantial part of the diet in any season (Figure 4).

3.5 | Wild fallow deer diet preference analyses

Three ground vegetation taxa were consumed at a higher proportion than expected given their availability, most notably bramble (*Rubus* spp.) (Figure 5). Ivy (*Hedera* sp.), nettle (*Urtica* sp.) and grasses (*Poaceae* spp.) were recorded less often than expected in the diet. Bramble and ivy were the most abundant resources in the ground vegetation cover, making up 17% and 23%, respectively See Table S9 for the full results table.

Seven tree and shrub taxa were consumed more often than expected given their availability across the 10 woodland sites. The 'preferred' taxa were roses, cherry (*Prunus* spp.), oak, elm (*Ulmus* spp.), maple and willow

TABLE 1 Output table from the Generalised Linear Mixed Model of Shannon Diversity Index (SDI) generated using the *jtools* R package (Long, 2022), showing the model estimates for each season, standard error, *t* value, degrees of freedom and *p* value. *Significance level of <0.01. The model was fitted with the response variable SDI, a fixed effect of season, and a random intercept for woodland site, using the restricted maximum likelihood method. Winter (December to February) = 92 samples. Spring (March to May) = 61 samples, summer (June to August) = 84 samples and autumn (September to November) = 102 samples. Winter was the reference level (intercept).

Term	Estimate	SE	*t*	df	*p*
Intercept (Winter)	0.59	0.08	7.04	3.79	<0.01*
Spring	0.34	0.08	4.14	333.26	<0.01*
Summer	0.43	0.07	5.78	333.04	<0.01*
Autumn	0.43	0.07	6.04	333.27	<0.01*

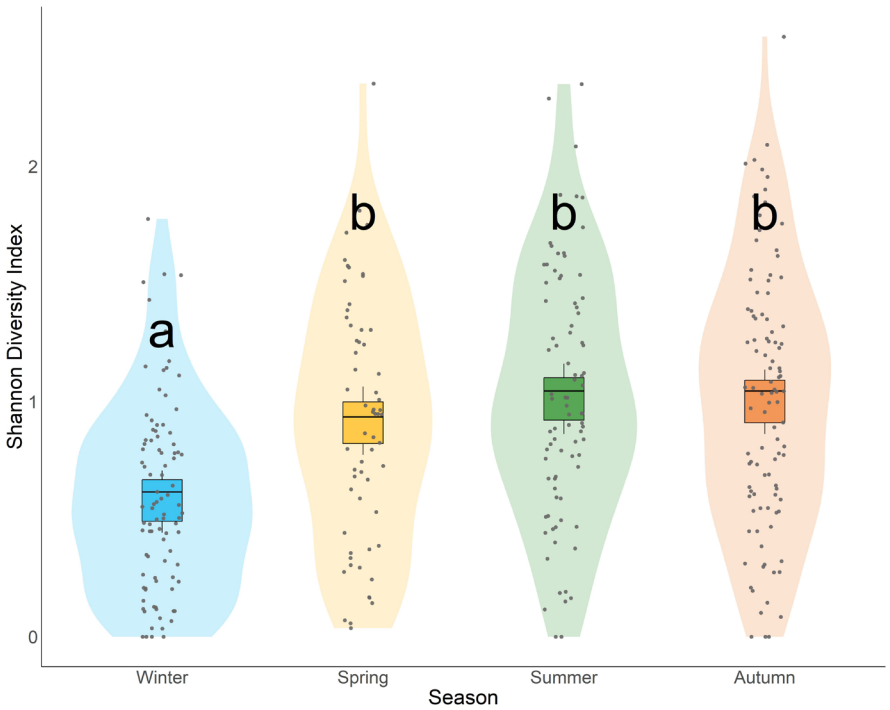

FIGURE 2 The Shannon Diversity Index (SDI) of wild fallow deer faecal samples, plotted against season. The grey dots show the raw SDI scores within seasons, the violins show the distribution of these raw data points and the boxplots show the fitted values from the Generalised Linear Mixed Model. Seasons with the same letter (a or b) are not significantly different from one another in their fitted values, while seasons with different letters are significantly different from one another.

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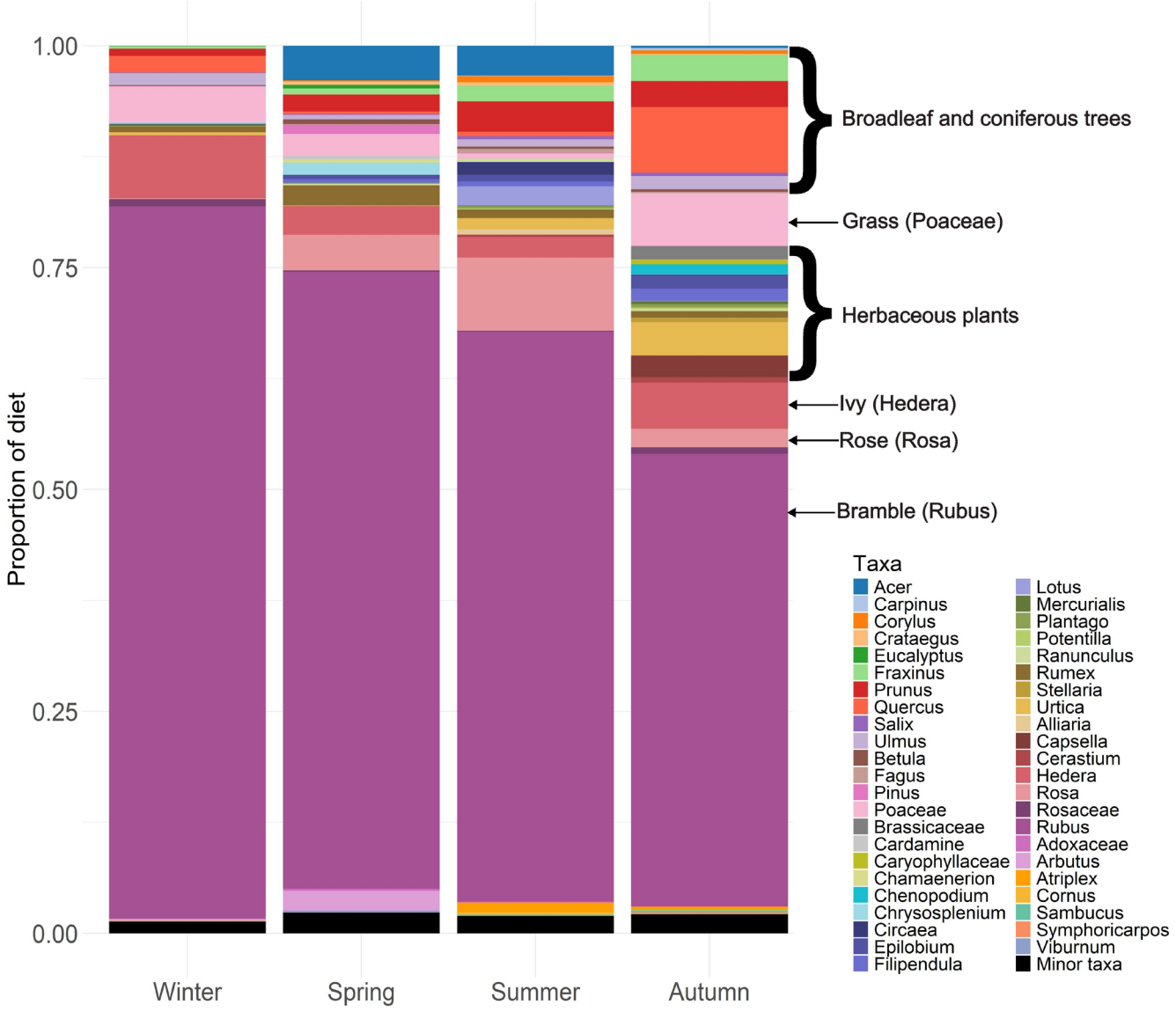

FIGURE 3 Proportion of reads obtained from wild fallow deer faeces using DNA metabarcoding of plant taxa, expressed as proportions of the whole plant community detected in the diet. These data are from the ITS2/*rbcL* consensus dataset, filtered for major taxa (made up ≥10% of reads from any month). The category 'Minor taxa' represents the remaining 106 taxa which represented less than 10% of reads per month. Each column shows samples pooled for each meteorological season. Winter (December to February) = 92 samples, spring (March to May) = 61 samples, summer (June to August) = 84 samples and autumn (September to November) = 102 samples.

(*Salix* spp.). Horse chestnut (*Aesculus* sp.) was labelled as preferred, but no confidence intervals could be generated due to its scarcity in the diet and vegetation survey. Six taxa were recorded less often than expected in faecal samples given their availability, with birch (*Betula* spp.), hazel (*Corylus* sp.) and ash (*Fraxinus* sp.) having the most negative preference scores (Figure 6). See Table S10 for the full results table.

3.6 | Fallow deer faecal samples from Welsh Mountain zoo

The consensus dataset consisted of 12 plant taxa (Figure 7). In contrast to the diet samples from wild deer, the zoo samples were mostly dominated by grasses (*Poaceae*) and small quantities of other plants typically associated with grasslands, such as thistles (*Cirsium* spp.), yarrow (*Achillea* spp.) and vetch (*Vicia* spp.) The woody taxa—bramble and cherry—are likely to have come from hedges adjacent to the enclosure fence.

4 | DISCUSSION

We characterised the diet of a fallow deer population and explored how this varied with landscape-scale resource availability. Overall, bramble was the dominant dietary component throughout the year. The preference analysis for ground vegetation indicated that the deer

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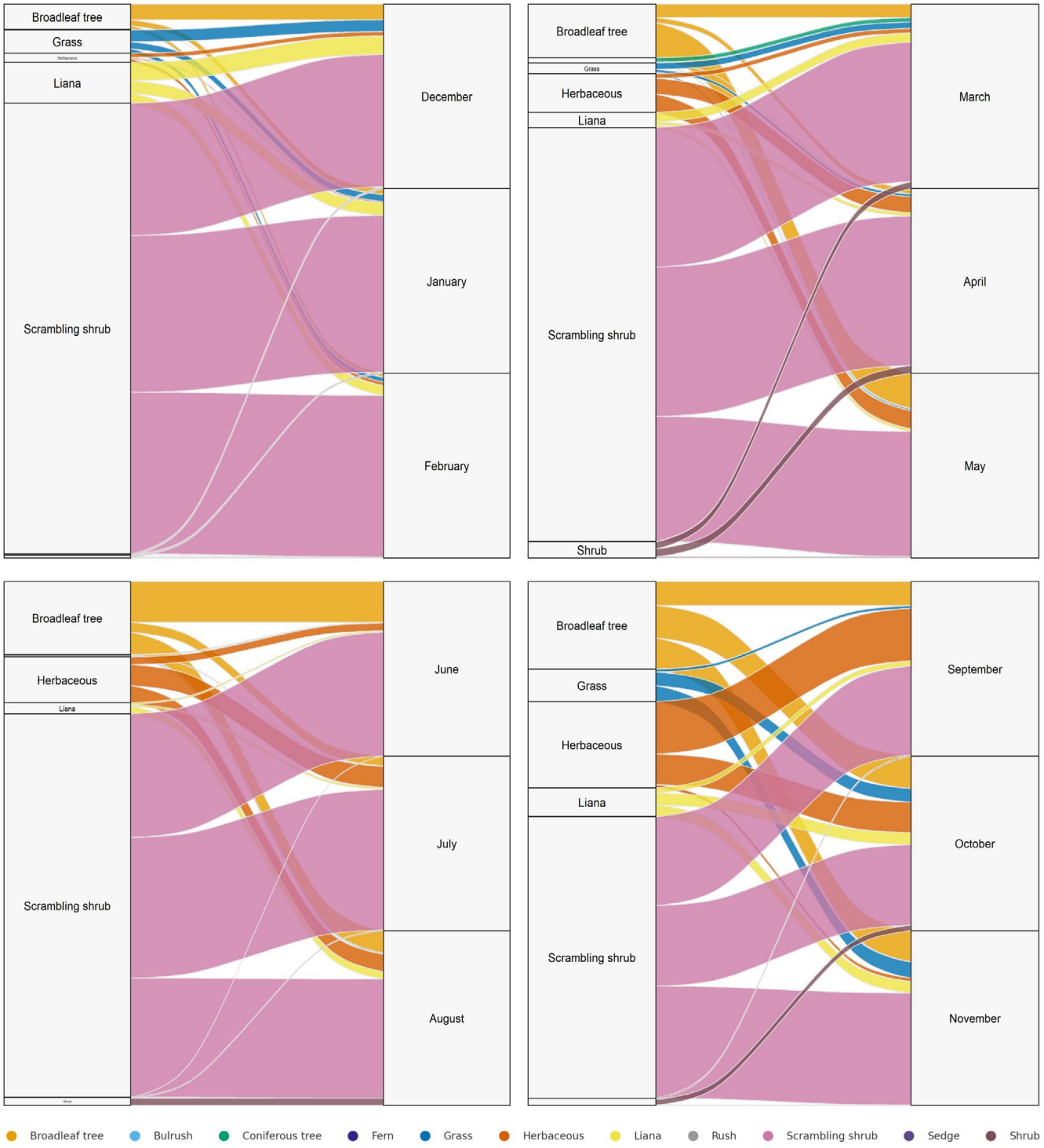

FIGURE 4 Bipartite plots showing the identity and proportion of plant groups (labels in the left panel) present in the wild fallow deer faecal samples for each month (right panel). These data are from the ITS2/*rbcL* consensus dataset, filtered for taxa which made up ≥1% reads of any sample. The plant taxa in each group can be found in Table S8 .

disproportionately consumed bramble relative to its availability in the environment. The remainder of the diet was a mix of broadleaf trees and some shrubs, with grasses forming a surprisingly small component of the diet across seasons, despite the widespread availability of livestock pasture. In contrast, the zoo samples contained proportionally much more grass, as the deer resided in a paddock.

The lack of grass in the diet of the wild fallow deer contradicts our hypothesis and the findings of previous studies, which have characterised the species as an intermediate grazer that mainly utilises woody browse in winter (Borkowski & Obidziński, 2003; Caldwell et al., 1983; Kerridge & Bullock, 1991; Putman et al., 1993). Notably, some of these studies were conducted where grass availability was

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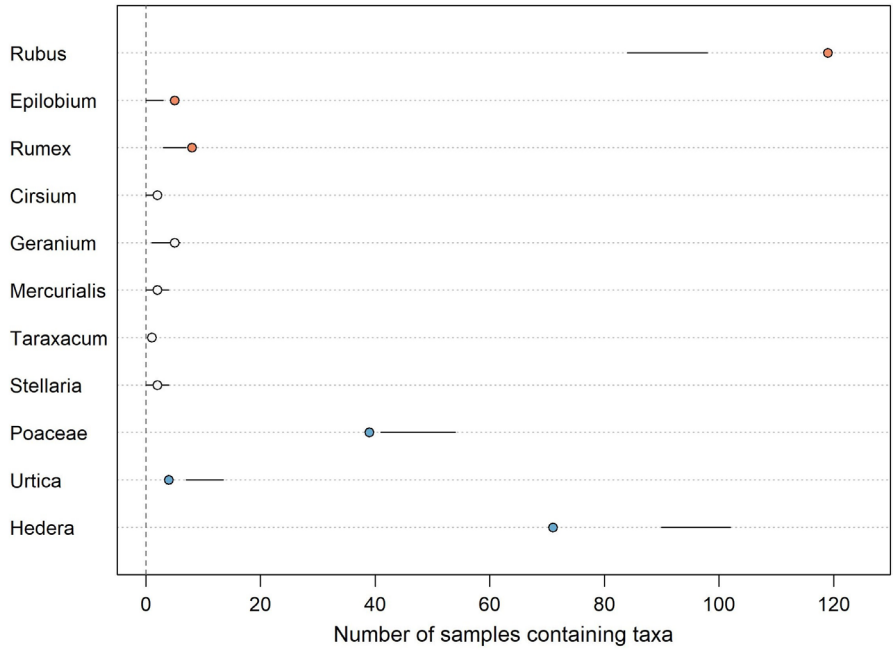

FIGURE 5 Preference plot for the 11 ground vegetation taxa that were present at ≥1% content in one or more of the wild fallow deer faecal samples ($n = 127$) and were also present in the concurrent ground vegetation surveys. Lines indicate the 95% confidence intervals for expected consumption given the null model. The coloured dots indicate the observed number of faecal samples in which each taxon was present. White dots show the taxon was consumed in proportion to its availability; blue shows the taxon was consumed less than expected and orange indicates the genus was consumed more than expected given the null model in the preference analysis.

likely to be relatively high compared with woodland resources, and human activity was more predictable, such as deer parks (Caldwell et al., 1983; Kerridge & Bullock, 1991) and where deer were fed supplementary hay (Borkowski & Obidziński, 2003). The diet of these deer populations is likely to be more similar to our zoo samples—which mainly consisted of grasses and grassland-associated species—than to the wild deer samples.

In contrast, the wild Elwy Valley fallow deer population exists in a mosaic of woodlands and farmland where deer can move freely, but human activity is less predictable across the landscape (Barton, 2023). Forests may offer safe refuge from disturbance by humans and livestock (Gaudiano et al., 2021; Uzal et al., 2013), leading to lower feeding rates in open areas and reduced grass content in the diet. The findings of our study support those of a larger-scale study of the Elwy Valley fallow deer, which found a positive effect of tree cover and negligible effects of hunting on deer woodland use at the landscape scale (Barton, 2023). The consistent consumption by deer of woodland plants is likely to hamper any efforts to restore understory vegetation cover and broadleaf tree regeneration despite current deer management efforts. Conversely, the lack of grasses and arable crops in the diet may indicate minimal impacts on agricultural and pastoral activity, but further investigation is needed to confirm this. Similarly, the lack of coniferous trees in the diet indicates that the deer are not likely to have significant impacts on coniferous forestry in the area.

Dietary diversity was lowest in the winter months, contradicting our initial prediction. Bramble remained a key resource; indeed, the ground flora preference analysis showed a strong overall preference for bramble across all seasons. The legacy effect of browsing across the Elwy Valley has led to an open understory structure in many woodlands, with bramble being one of the only palatable, evergreen plant species to persist at relatively high abundance. In addition to being widespread, bramble is highly palatable to deer (Harmer et al., 2010; Obidziński et al., 2013). New leaves contain high concentrations of nitrogen, potassium and phosphorus, while older leaves have notable concentrations of calcium and magnesium (Taylor, 1982). Perhaps this combination of high availability and nutritional quality is what has made bramble such an important winter resource.

From the perspective of optimal foraging theory (Emlen, 1968; MacArthur & Pianka, 1966), the fallow deer may bulk browse on bramble during winter to optimise energy efficiency whilst resources are limited, as the energy cost of foraging could outweigh the benefits of diversifying their diet. During the plant-growing season, available resources increase in diversity and abundance, and temperatures are milder. These generalist herbivores can then afford to forage over larger spatial scales. As a result, the diversity of their diet increases. Whilst ungulates often increase their home range size to compensate for low resource availability (Morellet et al., 2013; Wagler et al., 2024), they may reduce their home range size where resources are sufficient and stable in availability (Borowik et al., 2021; Viana et al., 2018). Indeed, a landscape-scale study in the Elwy Valley found that detection rates on camera traps were noticeably lower post-rut (January to March) compared to the rut (September to November) and birthing period (May to July), perhaps indicating reduced rates of movement (Barton, 2023). The deer may decrease their travel distance during foraging bouts in winter to conserve energy and recover post-rut (Simoneaux et al., 2016), consuming bramble as the most convenient, widely available and relatively nutritious resource. In the plant-growing season, the deer took advantage of the increased diversity and abundance of other plants, whilst continuing to utilise bramble as a bulk-forage resource.

The tree and shrub preference analysis indicated that taxa with a patchy distribution across the landscape and high-localised stem densities were under-represented in the diet relative to their

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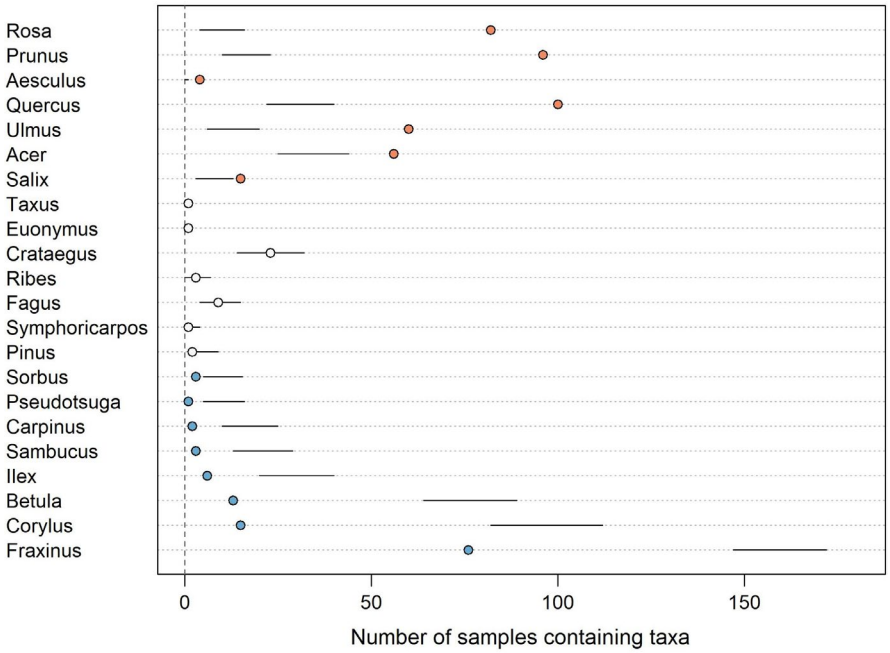

FIGURE 6 Preference plot for the 22 woody plant taxa that were present at ≥1% content in one or more of the wild fallow deer faecal samples ($n = 258$) and were also present in the tree and shrub surveys. Lines indicate 95% confidence intervals for expected consumption given the null model. The coloured dots indicate the observed number of faecal samples in which each taxon was present. White dots show the taxon was consumed in proportion to its availability; blue shows the taxon was consumed less than expected and orange indicates the taxon was consumed more than expected given the null model in the preference analysis.

overall availability. This included ash, birch, hornbeam (*Carpinus* sp.) and hazel. In contrast, taxa that were more widespread but less clustered were a preferred resource in the diet, such as oak, rose, cherry, maple and elm. This pattern is indicative of a generalist herbivore. Indeed, it is likely that the deer did not seek out the 'preferred' species but were simply more likely to encounter them compared to the more highly clustered species (Duparc et al., 2020; Wang et al., 2010). It is also important to note that the results from our field survey may overestimate foliage availability from trees with a higher crown base, leading to woody plants with a lower crown base being deemed a preferred resource. We measured availability as the number of stems present for each woody species and did not account for the presence of foliage at deer browsing height. Blackthorn (*Prunus spinosa*) and dogrose (*Rosa canina*) are typically low shrubs, while elm and sycamore can produce suckers from the main stem (Bleay, 1987). These growth forms are more likely to present available foliage at browsing height, compared to more light-demanding species such as birch and ash, which typically have a higher crown base.

Deer populations in Britain have been experiencing rapid landscape changes over recent decades. The general trend across British woodlands since 1971 has been an increase in tree canopy density and shade (Smart et al., 2024). Although bramble is typically associated with canopy gaps, it can also tolerate shade (Balandier et al., 2013). As a result, bramble has retained its considerable dominance of around 10% ground cover in British forests during this period (Smart et al., 2024). However, in the last 10 years, there has been a rapid reduction in canopy density due to disturbances such as extreme weather events (Halstead et al., 2024), and widespread mortality from ash dieback (Mitchell et al., 2014; Smart et al., 2024). Ash dieback is already resulting in a notable increase in bramble cover in some affected woodlands (J. Healey pers. obs.; K. Kirby pers. comm., September 2024). Smart et al. (2024) showed that bramble has noticeably increased in 'low deer risk' areas, which could support the expansion of deer populations. In addition, bramble has remained stable in medium and high deer-risk areas, indicating that it can persist despite heavy browsing pressure, as seems to be the case in our study system. While there is concern for the impacts that increasing deer populations are having on woodlands, deer may be an important source of disturbance to maintain heterogeneous understory habitats in canopy gaps. Increasing bramble cover in northern temperate forests may provide a physical barrier to sapling browsing and increase tree regeneration (Jensen et al., 2012). while deer browsing may simultaneously serve to regulate bramble growth and prevent it from outcompeting saplings and other understory vegetation (Laurent et al., 2017; Walters et al., 2020). There is, therefore, a complex nexus of forest disturbance, abundance of bramble and levels of deer browsing, together influencing the potential for tree regeneration and conservation of ground vegetation biodiversity. These interactions must be given careful attention in predicting the full impacts of management interventions such as tree felling, bramble cutting or control of deer populations.

5 | CONCLUSIONS

We characterised the dietary composition of an expanding fallow deer population using DNA metabarcoding and identified how the diet varied with resource availability. Contrary to expectations, grasses were not a dominant component of the diet and diet diversity was lowest in winter compared to the other seasons. Bramble was an important dietary component throughout the year, especially in the winter months. Bramble cover is set to increase with more frequent disturbances to forests across northern Europe. As we strive to increase tree cover and improve woodland resilience in the face of rapid environmental change, we must also understand the concurrent role that growing deer populations will play in shaping forest dynamics. There is great potential in the use of metabarcoding to strengthen our understanding of this

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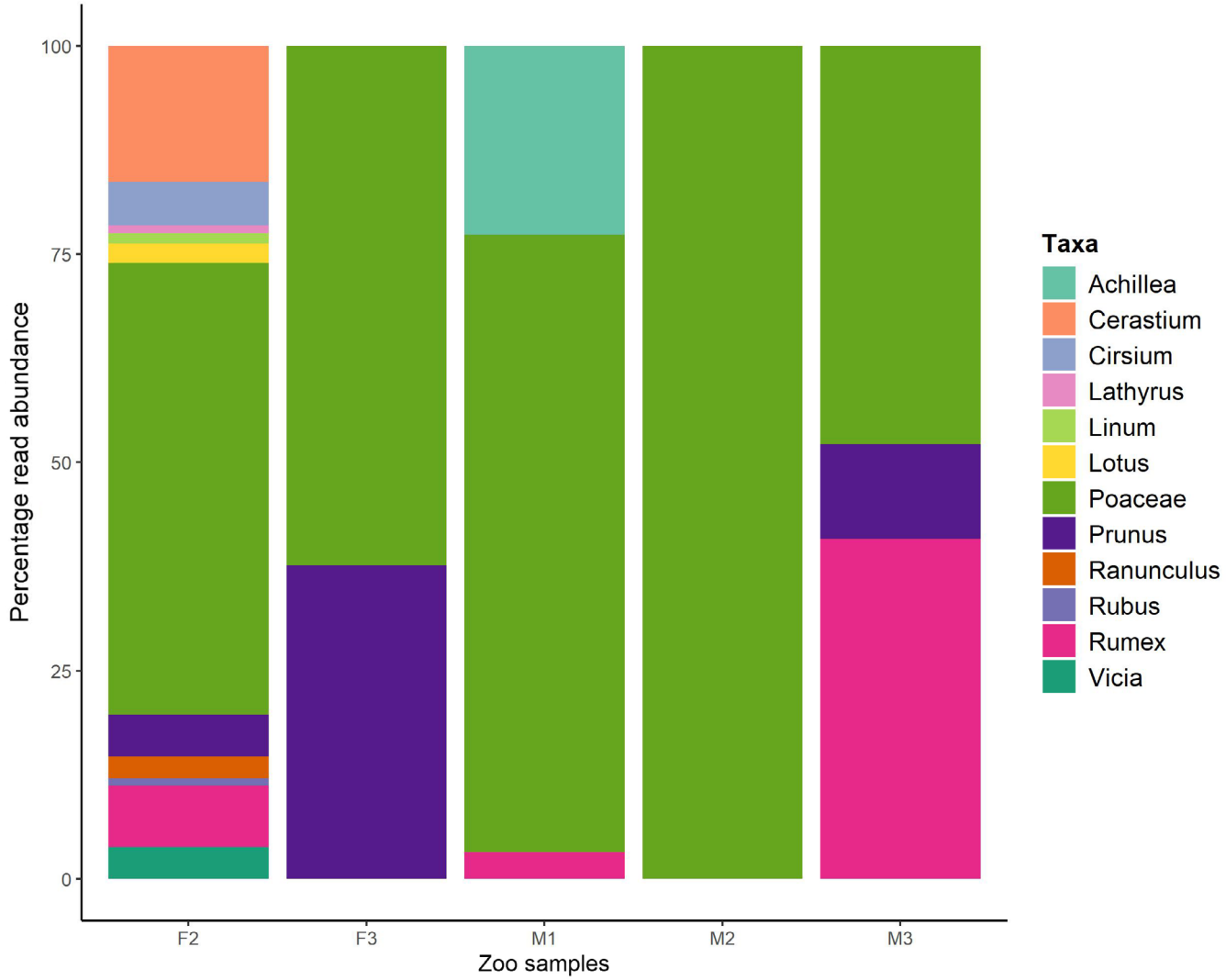

FIGURE 7 Percentage read abundance of plant taxa present in the zoo fallow deer faecal samples that survived filtering. This represents a consensus dataset containing combined data from ITS2 and *rbcL* markers. Sample F3 represents ITS2 data only, and M3 represents *rbcL* data only, as they did not survive filtering through both pipelines.

context-specific variation in the diets of generalist herbivores such as the fallow deer. The complex interactions between deer, woodland ground vegetation and landscape change will resist simplistic solutions to the challenge posed by growing deer populations.

AUTHOR CONTRIBUTIONS

Amy Gresham led conceptualisation, data collection, curation and writing the manuscript. John R. Healey, Markus P. Eichhorn, Simon Creer and Graeme Shannon supervised conceptualisation, study design and draft development. Kirthana Pillay, Amy Ellison and Abigail Lowe contributed to method development. Line Cordes produced the graphical abstract. All authors contributed critically to drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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DATA AVAILABILITY STATEMENT

The raw sequencing data are available via the NCBI Sequence Read Archive: http://www.ncbi.nlm.nih.gov/bioproject/PRJNA1014003 (Bangor University, 2023)

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1.

Supplementary methodological details, including full laboratory protocols, and supplementary tables and figures.

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