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Ollscoil na hÉireann, Corcaigh
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**Relationship between community functional traits,
productivity and soil properties in Irish semi-natural
grassland habitats**

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List of Abbreviations

Abbreviation	Abbreviation description
ANPP	Above-ground net primary productivity
BNPP	Below-ground net primary productivity
CSR	Competitor, stress tolerator, ruderal
CWM-LA	Community weighted mean leaf area
CWM-LCC	Community weighted mean leaf chlorophyll content
CWM-LDMC	Community weighted mean leaf dry matter content
CWM-SLA	Community weighted mean specific leaf area
FDiv	Functional divergence
FDq	Rao's quadratic diversity
FEve	Functional evenness
FRed	Functional redundancy
FRic	Functional richness
GS1	Dry calcareous and neutral grassland
GS2	Dry meadows and grassy verges
GS3	Dry-humid acid grassland
GS4	Wet grassland
LA	Leaf area
LCC	Leaf chlorophyll content
LDMC	Leaf dry matter content
NDVI	Normalized Difference Vegetation Index
RLD(10cm)	Root length density at 10 cm soil depth
RLD(20cm)	Root length density at 20 cm soil depth
SLA	Specific leaf area
SOM	Soil organic matter
UAV	Unmanned aerial vehicle

Declaration

“This is to certify that the work I am submitting is my own and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism and intellectual property.”

Eoin Halpin

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Abstract

Semi-natural grasslands provide many ecosystem services, with biomass production for livestock being of major importance. Both plant species diversity and functional diversity can affect grassland productivity and ecosystem services. However, previous research has revealed positive, negative or unimodal diversity-productivity relationships in grasslands. Previously observed impacts of functional and species diversity on soil carbon have been predominantly positive. This research involved surveys for three Irish semi-natural grassland habitats: dry calcareous and neutral grassland (GS1), dry-humid acid grassland (GS3) and wet grassland (GS4). The three habitats were found to differ significantly in their soil parameters (nitrogen and pH), their vegetation functional strategy according to the competitor, stress tolerator, ruderal (CSR) system and in their functional diversity (functional richness). Based on differences found between the habitats, the hypothesis was tested that diversity-ecosystem process relationships are habitat dependent. Relationships between functional diversity and species diversity were found to differ depending on habitat type. Relationships between productivity (from remote sensing surveying of Normalised Difference Vegetation Index) and diversity were negative, with the strongest relationship found in the GS3 grasslands. Community-weighted means of leaf dry matter content (CWM-LDMC) and community S strategy were also negatively correlated with productivity in GS3 grasslands, but no relationship between CWM-Leaf Area (CWM-LA) or C strategy was found in any of the grasslands. Soil carbon showed no significant correlation with functional diversity and species diversity except in the GS4 habitat. In these GS4 communities soil carbon correlated positively with CWM-LA but negatively with metrics of species and functional diversity. Differences in diversity-productivity relationships in different habitats suggest that management or soil type influence the nature of these relationships. Such differences between sites and habitats likely overshadowed any influence diversity may have had on

productivity or carbon sequestration by their stronger impact on ecosystem functioning. The results indicate that the inherent conditions of grassland ecosystems will strongly influence diversity-productivity relationships, suggesting significant implications for grassland management and monitoring.

Chapter 1 - Introduction

Semi-natural grasslands are one of the most agriculturally important ecosystems world-wide. With the global demand for livestock ever increasing (Hemathilake and Gunathilake, 2022), the intensity of management has increased in grasslands and is leading to a loss of the semi-natural habitat (Bullock et al., 2011). Increases in management intensity have been shown to increase productivity (Lemaire et al., 2012) while having negative effects on functional diversity and species diversity (Guo, 2007; Harpole et al., 2017; Zhang et al., 2023). High species diversity is important for ecosystem health as it is beneficial for pollinator species, decreasing invasibility, and for facilitating species from other trophic levels (Fargione and Tillman, 2005; Bullock et al., 2011; Spehn et al., 2000). Species diversity may also be important for productivity as complementarity effects can lead to overyielding (Loreau et al., 2001). The maintenance of high functional diversity is also imperative for the health of grassland ecosystems (Hallet et al., 2017). As highly dynamic ecosystems, grasslands are very susceptible to influences by environmental perturbations (Hobbs et al., 2007; Liu et al., 2019); therefore there is a strong incentive to maintain a high level of stability for benefits for grassland ecology and productivity. In the 21st century, with more varied and extreme climatic conditions, and changes in management practices, high functional diversity allows grasslands to adapt to climate and other environmental change with minimal impact on productivity and other ecosystem functions (Xu et al., 2018). The potential for grasslands to be a resource for carbon sequestration has also gained considerable attention (Bullock et al., 2010) with the ability of semi-natural grasslands to accumulate carbon and nitrogen placing them as important habitats for climate change mitigation (Carey et al., 2007). High soil nutrient contents also benefit farmers managing semi-natural grasslands, as higher soil fertility can lead to increases in productivity (Fay et al., 2015).

Semi-natural grassland habitats in Ireland are threatened by climate change and agricultural intensification (Schils et al., 2020). These grasslands contain high amounts of biodiversity and unique species assemblages but these are negatively affected by the aforementioned threats; Increased drought frequency and fertiliser application have especially detrimental effects on grassland biodiversity (Zhang et al., 2023; Basto et al., 2018). The ability for grassland ecosystems to store carbon is also impeded by climate change and agricultural intensification (Carey et al., 2007). It is clear therefore that the proper maintenance of grassland ecosystem functioning is pertinent if Ireland wishes to achieve any climate mitigation goals.

The functioning of vegetation can ultimately influence how the ecosystem functions as a whole, and so assessing any changes that may occur in plant functional traits is essential for understanding the stability of an ecosystem and its functional services (Polley et al., 2020). There are multiple ways in which certain functional traits allow plants to thrive and, in some cases, alter ecosystems. Many metrics have been suggested as indicators of an individual plant's role in an ecosystem (Diaz & Cabido, 2001). On the individual and species level the ecological survival strategy can be allocated following Grime's Competitor, Stress tolerator, Ruderal (CSR) strategies (Grime, 1979). On the scale of the vegetation community, a weighted average value for individual traits can be used to indicate the community's ecological strategy (Diaz & Cabido, 2001). The most novel approach in assessing the functioning of a vegetative community is by using functional diversity indices. By including weighted values of species abundance and assessing multiple functional traits in tandem, these functional diversity indices provide a more in-depth perspective on vegetation community ecology (van't Veen et al., 2020).

Species diversity alone provides a poor explanation of the impact of environmental change on grassland productivity (Xu et al., 2018). Instead, the diversity of functional traits (functional diversity) was shown to have a higher explanatory power than species diversity on both productivity (Petchey et al., 2004) and soil carbon content ((Zou et al., 2016; Roscher et al., 2012). Many studies have analyzed the relationship between functional diversity, species diversity and grassland productivity (e.g. Roscher et al., 2012; Polley et al., 2013; Harpole et al., 2016; Zhang et al. 2017). The literature suggests that increased biodiversity in grasslands has positive effects on productivity and yield stability (Tilman et al., 1996; Tilman et al., 2001; Binder et al., 2018; Korrell et al., 2024). Evidence suggests that this relationship is likely due to an increase in diversity of functional traits that can often co-occur with increases in biodiversity (Petchey et al., 2004). Since ecosystem services such as yield and stability are reliant on the functioning of ecosystem processes, and since these processes are driven in part by the functioning of plant communities, it follows that values that indicate the functioning of vegetation (functional diversity metrics) may have a greater predictive power than values that indicate phylogenetic complexity (biodiversity metrics) (De Bello et al., 2006; Brun et al., 2019). Past studies have found unimodal diversity-productivity relationships that are dependent on management intensity, indicating an optimum management strategy that benefits both productivity and diversity (Wang et al., 2022). However, high intensity management can shift this to a more negative relationship (Brun et al., 2019). With the availability of subsidies for more biodiverse grasslands, there is incentive for both farmers and ecologists to maximize both diversity and productivity.

Community weighted mean (CWM) values of resource acquisitive traits and CSR strategies may also predict productivity and soil carbon as, according to the mass ratio hypothesis (Grime, 1998), the traits of the most dominant species will influence the ecosystem functioning (Wirth et al., 2024). This can occur irrespective of species diversity and in some

cases, due to competitive exclusion, may negatively affect both species and functional diversity (Zhang et al., 2025). Most semi-natural grasslands are nutrient deficient and studies of CSR strategies reflect this with most grasslands being ruderal or stress tolerant/ruderal dominated (Li et al., 2024). Increases in soil nutrients, however, have been shown to increase resource acquisitive CWM leaf traits and a competitive strategy (Gough et al., 2000; Li et al., 2014). It was therefore expected that C strategy and resource acquisitive CWM leaf traits would strongly predict both productivity and soil carbon and that this relationship would be present when diversity-productivity relationships are absent or negative.

Many studies looking at relationships between diversity and ecosystem services use manipulated grassland experiments which cannot, by their nature, account for the complexity of natural grassland systems (Tilman et al., 2001; Roscher et al., 2012). Diversity-productivity relationships (hereby used to describe both functional diversity and species diversity), are highly dependent on other factors such as management practices and abiotic conditions (Wang et al., 2022; Ma et al., 2010). Different grassland habitats, that vary in management and environmental conditions, should therefore show different diversity-productivity relationships. This paper aims to define the relationships between species diversity, functional diversity and ecosystem services (productivity and carbon storage) in three Irish semi-natural grassland habitats; dry calcareous and neutral grassland (GS1), dry-humid acid grassland (GS3) and wet grassland (GS4) (Fossitt, 2000). Due to observed differences in grassland habitat types, diversity-productivity relationships were assessed both overall and for each of the three grassland habitat types. The relationship between species diversity and functional diversity metrics was determined and it was assessed, to what degree, species diversity, functional diversity and dominant species strategy predict productivity and soil carbon concentrations.

1.1 - Semi-natural grassland habitats

Irish semi-natural grasslands have been characterised by several studies; each one based on different grassland characteristics (O'Sullivan, 1982). The widely accepted Fossitt (2000) habitat classification is a simple classification system based on geology, soil traits and vegetation composition. The Fossitt (2000) system divides Irish semi-natural grasslands into four habitat types, though only three of the four habitat types are grazed by livestock and considered within this research (GS1, GS3 and GS4).

1.1.1 - Dry calcareous and neutral grassland (GS1)

GS1 grasslands are sites with free-draining mineral soils. The soils on these sites may be calcareous or neutral. GS1 habitats are important from a conservation point of view as they tend to be species rich, and some contain the Priority Annex I - orchid rich *Festuco-Brometalia* (*6210) - habitat (Wallis De Vries and Poschlod, 2002; Wilson et al., 2012). The cover of GS1 grasslands has greatly diminished in the last century due to agricultural intensification (Polus et al., 2007), with nutrient enrichment being the main cause of species loss (Newton et al., 2012). Nutrient enrichment has led to many calcareous grasslands becoming more neutral in pH (Fossitt, 2000). Changes in precipitation patterns, particularly increased long-term drought frequency, have also negatively influenced species richness, both in vegetation and seedbank composition with forbs and sedges being most affected (Basto et al., 2018). GS1 habitats provide a wealth of ecosystem services, including carbon sequestration (Janssens et al., 2005). GS1 grasslands are now mainly restricted to upland areas or shallow soils on limestone pavement that make improvement with farm machinery difficult (Fossitt, 2000).

1.1.2 - Dry meadows and grassy verges (GS2)

Dry meadows in the GS2 classification are infrequently cut, unimproved grassland. This type of habitat is not common due to intensification of agricultural practices (Fossitt, 2000). Grassy verges compose most of the GS2 habitat in Ireland and tend to occur in small areas such as roadsides, church grounds, gardens, manors and demesnes where fertilisation is of little benefit. The lack of grazing leads to the growth of coarse grass species and tall growing herbs.

1.1.3 - Dry-humid acid grassland (GS3)

GS3 grasslands occur on free-draining, relatively acidic soils that vary in soil and topographical characteristics. Some GS3 soils occur in upland areas where the peaty soils are not waterlogged. Others occur in lower elevation areas with mineral rich, acidic soil. The Annex I habitat - Species rich *Nardus* grassland (*6230), can be found in the upland GS3 habitats. These grasslands tend not to be the most species diverse, with dense forms of narrow-leaved grasses and forbs being most characteristic. These grasslands can be subject to high grazing intensities as sheep tend to prefer the vegetation compared to other upland habitats (Williams et al., 2012).

1.1.4 - Wet grassland (GS4)

Wet grasslands include a wide range of grasslands with poorly drained soils that experience periodic inundation. The soil ranges from acidic to alkaline, and can be mineral or organic based. GS4 grasslands sometimes contain the Annex I habitat - *Molinia* meadows (6410) (Fossitt, 2000). These grasslands are distributed throughout the country and can be found on a range of elevations and slopes.

1.2 - Thesis overview

The aim of this thesis is to assess diversity-productivity relationships in three Irish semi-natural grassland habitats. It was hypothesized that the three habitats differ in their abiotic conditions and in the CSR strategies for the different vegetation community assemblages. Based on such observed differences, it was then investigated whether diversity-productivity relationships differ depending on habitat.

This thesis begins with a literature review to provide the reader with a framework of understanding of the ecology of semi-natural grasslands and a basic explanation of functional diversity in terms of its derivations and its relationship with ecosystem functioning. Chapter 3 provides detailed information on the materials and methods used during the fieldwork process, lab analysis and data analysis. Two results chapters are provided, with the first (chapter 4) delving into the differences in CSR strategy, community weighted mean functional traits, functional diversity metrics and soil parameters found between habitat types. The second results chapter (chapter 5) integrates these variables with ecosystem processes by assessing the relationships between diversity, plant strategy, grassland productivity and soil parameters. Chapter 6 reiterates the main results found and suggests causes for the observed patterns while comparing the results with the current literature. The thesis concludes with a summary of the observations made while highlighting the implications of these findings for the current field of knowledge and for future research.

Chapter 2 - Literature review

This review will document the current progress in the literature, as of 2025, of the use of functional traits, functional strategies and functional diversity metrics in grassland ecology research. The merits of each of the suggested functional diversity metrics (FD), as well as their ability to predict and influence ecosystem processes, will be discussed.

2.1 - Functional traits and strategies

The holistic functioning of an individual plant is hard to determine, and it is even more difficult to describe for entire vegetation communities. However, there are many measurable traits based on plant vegetative structure and biochemical composition that are both driven by and drivers of ecosystem processes (De Bello et al., 2013; Diaz & Cabido, 2001). It is pertinent to use traits that have a clear relationship with both plant strategy and community functioning. It is also important to use as wide a range of functional traits as possible, as it makes the multi-trait analysis more representative of the actual multidimensional niche space present in vegetation communities.

2.2 - Measurable functional traits

2.2.1 - Leaf Area (LA)

Leaf area (LA) is a commonly used trait to indicate the state of a grassland's productivity, as a greater surface for CO₂ exchange and light interception potentially allows for greater rates of photosynthesis (Geyger, 1977). As a functional trait, a greater leaf area means a higher competitive ability as it has a larger light capturing area (Pierce et al., 2013). If larger leaves are common in a community, meaning that competition for light is the dominant strategy, then it can be inferred that the environment supports fast growing, resource acquisitive species (Grime, 1977). In a grazed ecosystem, leaf area can be an unreliable indicator as grazing

can decrease leaf size or can minimise the number of leaves that reach their potential size. When this is paired with the fact that selective grazers are more likely to eat the species with greater leaf area (as the faster growing species with large leaf area tend to be more palatable (Dostálek et al., 2020), the relationship between leaf area and productivity becomes distorted.

2.2.2 - Specific Leaf Area (SLA)

Specific leaf area (SLA) is a common leaf trait measurement and is defined as the area of the leaf divided by its dry mass. This measure has been suggested as the best indicator for a plant's position along the leaf economic spectrum (Wright et al., 2004; Wilson, 1999). The leaf economic spectrum is based on a trade-off that exists between nutrient acquisition and nutrient conservation. If a species is acquisitive and participates in active foraging, then its resources are devoted towards growth and further acquisition. For this reason, it cannot be conservative with its resources. A nutrient conservative species can only dominate when resources are scarce or unreliable, and its conservation efforts are redeemable. Since leaf area is indicative of resource acquisition and dry mass is indicative of resource conservation, SLA can be seen as a ratio between opposing strategies. Leaves with a high SLA are generally competitive but short-lived and are therefore best suited to highly productive environments (Dwyer et al., 2014). These fast-growing species tend to have shorter lifespans, lower dry matter content and lower levels of carbon in storage organs (Wright et al., 2004).

2.2.3 - Leaf dry matter content (LDMC)

LDMC can be described as the percentage of dry matter contained within a leaf. This value is determined by the proportion of dry matter obtained by dividing dry matter by fresh matter. The dry matter in a leaf is primarily made of long-lived substances, and so a higher LDMC tends to correlate with longer lived leaves (Garnier et al., 2001). A high dry matter content also indicates that a plant is strategizing more towards resource conservation. Considering that a trade-off exists between nutrient conservation and nutrient acquisition (as both are too energy intensive to occur in unison), LDMC is common in slow-growing species adapted to harsh conditions with unreliable nutrient sources. High LDMC also makes species less palatable to grazers and so they co-exist with other species in a community predominantly via disturbance avoidance (Dostálek et al., 2020).

2.2.4 - Leaf nitrogen content (LNC)

Leaf nitrogen content is another leaf trait which can indicate where a plant is situated along the leaf economic spectrum. In the most comprehensive study of the leaf economic spectrum by Wright et al. (2004), 82% of the variation in leaf nitrogen content and leaf mass area (the inverse of SLA), across a wide range of species, was explained by a single axis. Nitrogen content is positively correlated with greater SLA, and both suggest a more resource acquisitive strategy. Leaf nitrogen content is indicative of high rates of photosynthesis as large amounts of nitrogen are needed for the formation of Rubisco as well as enzymes taking part in the electron transport chain (Toth, 2002). Through its positive effects on photosynthetic rates, leaf nitrogen content is also a good proxy for above-ground primary productivity (Liang, 1995).

2.2.5 - Leaf chlorophyll content (LCC)

As nitrogen is an important component of photosynthetic enzymes, the leaf chlorophyll content is also correlated with leaf nitrogen levels (Toth, 2002). Hence LCC can be insightful

when looking at a plant's resource acquisition. As nitrogen is often the limiting factor in photosynthesis, LCC, by its relationship with leaf nitrogen, can be used as a proxy measure for photosynthetic capacity (Croft et al., 2017). Measuring LCC is also often preferable to leaf nitrogen content as it does not require the destruction of plant matter. There are multiple remote sensing studies, using different approaches, that support a direct relationship between LCC and photosynthetic capacity and vegetation productivity on the ecosystem scale (Schull et al., 2015; Gitelson et al., 2006). Community weighted mean (CWM) values for LCC have also been shown to be positively correlated with productivity (specifically above-ground net primary productivity) (Zhang et al., 2021).

With respect to productivity on the ecosystem scale, a number of factors can influence productivity with little impact on LCC. These include environmental factors such as temperature, CO₂ levels and water availability, as well as physiological factors such as plant water use efficiency or a plant's carbon sink capacity (Lawlor, 1995). This results in a weaker correlation between LCC and productivity in comparison with leaf traits such as LA and SLA.

2.2.6 - Root length density (RLD) and maximum rooting depth (MRD)

Root length density (RLD) is a quantifiable measure for the extent of a given root system. It is calculated as the total length of roots present in a volumetric unit of soil. RLD generally positively correlates with water use efficiency (WUE) and, therefore, is a good indicator of a community's drought tolerance (Wilkinson, 2000). The depth to which root density should be measured is not always clear as factors such as soil depth or texture may influence the feasibility of producing useful, large soil cores. The depth to which root density should be measured is also dependent on the level of aridity experienced in the environment as dry soils tend to have lower RLDs in upper soils and higher RLDs in the lower soils relative to more moist soils (Smucker & Aiken, 1992). The association between RLD and WUE tends to

weaken with dryer soils; however the relationship between maximum rooting depth and WUE is strong (Smucker & Aiken, 1992). Deeper roots can not only access the water from deeper soils during drought but can also cycle water up to the surface soils through hydraulic lift. Therefore, a complementarity effect can exist between deep rooting species and those with shallow root systems (Oram et al., 2018). The indicator traits for drought tolerance are therefore usually limited to RLD values in deeper soil profiles and maximum rooting depth (measures which are not always feasible to derive, especially in the shallow soils of calcareous grasslands).

2.2.7 - Specific Root length (SRL)

Specific root length can be described as the ratio of root length to root mass. Root length is related to resource acquisition as the roots' resources are driven towards active search for soil nutrients and moisture, whereas root mass and width are related to storage and reinforcement of the root structure (Fitter et al., 1991). Because of this, specific root length has been suggested to characterise the economic strategy of a plant root system and is therefore often regarded as the below-ground equivalent of SLA (Ostonen et al., 2007). If a plant can have more resource-inexpensive roots (i.e. high SRL), then it can grow longer, more extensive root systems (i.e. higher RLD). This in turn will make a plant more competitive (Mommer and Weemstra, 2012; Weigelt et al., 2023).

2.4.5 - Above-ground net primary productivity (ANPP)

Above-ground net primary productivity can be measured directly from grasslands by cutting and weighing plant biomass. Indirect proxies such as Normalized Difference Vegetation Index (NDVI) that are measured using remote-sensing methods are more practical when it comes to managed grasslands. NDVI has been shown to be a good proxy for mean annual ANPP

(Gu et al., 2013) as it represents the photosynthetic potential of the vegetation community (Liu et al., 2022).

2.3 - CSR strategies

In relation to defining species by their functional traits, a useful categorization is provided by Grime (1979). Using this approach, plants can be defined by their strategy of survival, tailored to their niche (Pierce et al., 2013). Grime described the three strategies as competitive, ruderal and stress tolerant (CSR). The competitive strategy consists of a high growth rate in favourable conditions where the strong competitor can outperform and, therefore, exclude less competitive species from essential ecosystem services. Highly competitive species tend to have high photosynthetic rates and a high standing biomass (Bonser & Reader, 1995). Such species have evolved to thrive in environments where stress and disturbance levels are low. Ruderal strategists are adapted to more disturbed environments where their short life cycle, nutrient acquisition abilities and high fecundity allow them to easily take advantage of ephemeral niches (Nabe-Nielsen et al., 2021). Ruderal species, especially in grasslands, also tend to perform well in environments where disturbances such as grazing or trampling cause partial destruction of biomass. Stress tolerant species are adapted to environments where stress is high and disturbances are low. While adaptations such as slow growth rate, long leaf life-span and low leaf nitrogen levels do not make them competitive, it allows them to survive more severe environmental conditions. Stress tolerant species tend to be less palatable to grazers, so, where selective grazing occurs, these plants are maintained in the community (Fischer et al., 2019).

2.3.1 - CSR and functional traits

The CSR strategy classification is not clear cut. Instead interspecific and intraspecific variation in a species' strategy exists along gradients. This is due to the axes of trait

variability that define their functional strategy, the variability of which tends to exist due to economic trade-offs occurring on the physiological level. The degree to which these trade-offs occur indicates how the plant is strategizing its investments for survival. One of the greatest trade-offs, that all plants are subjected to, is the balance between investment of energy into acquisition or conservation. This trade-off gives rise to the leaf economic spectrum as mentioned previously (Wright et al., 2004). The software StrateFy (Pierce et al., 2017; Pierce et al., 2013) has been useful as it forms C:S:R ratios for each species using the three plant traits SLA, LA and LDMC (Figure 1) (Pierce et al., 2017). To analyse its value for predicting vegetative strategies concurrent with the surrounding environment, Li and Shipley (2017) used a mixture of community weighted mean (CWM) values of C, S and R percentages for each species, and compared them with the environmental conditions in which the data were collected. CWM values for S were found to increase with increasingly stressful environments. The same was found for ruderals in highly disturbed environments. Li and Shipley (2017) also looked at thirteen other plant traits whose relationship with ecological gradients is understood, and found that CWM values for the CSR strategies correlated with these traits in terms of their relationship with environmental conditions.

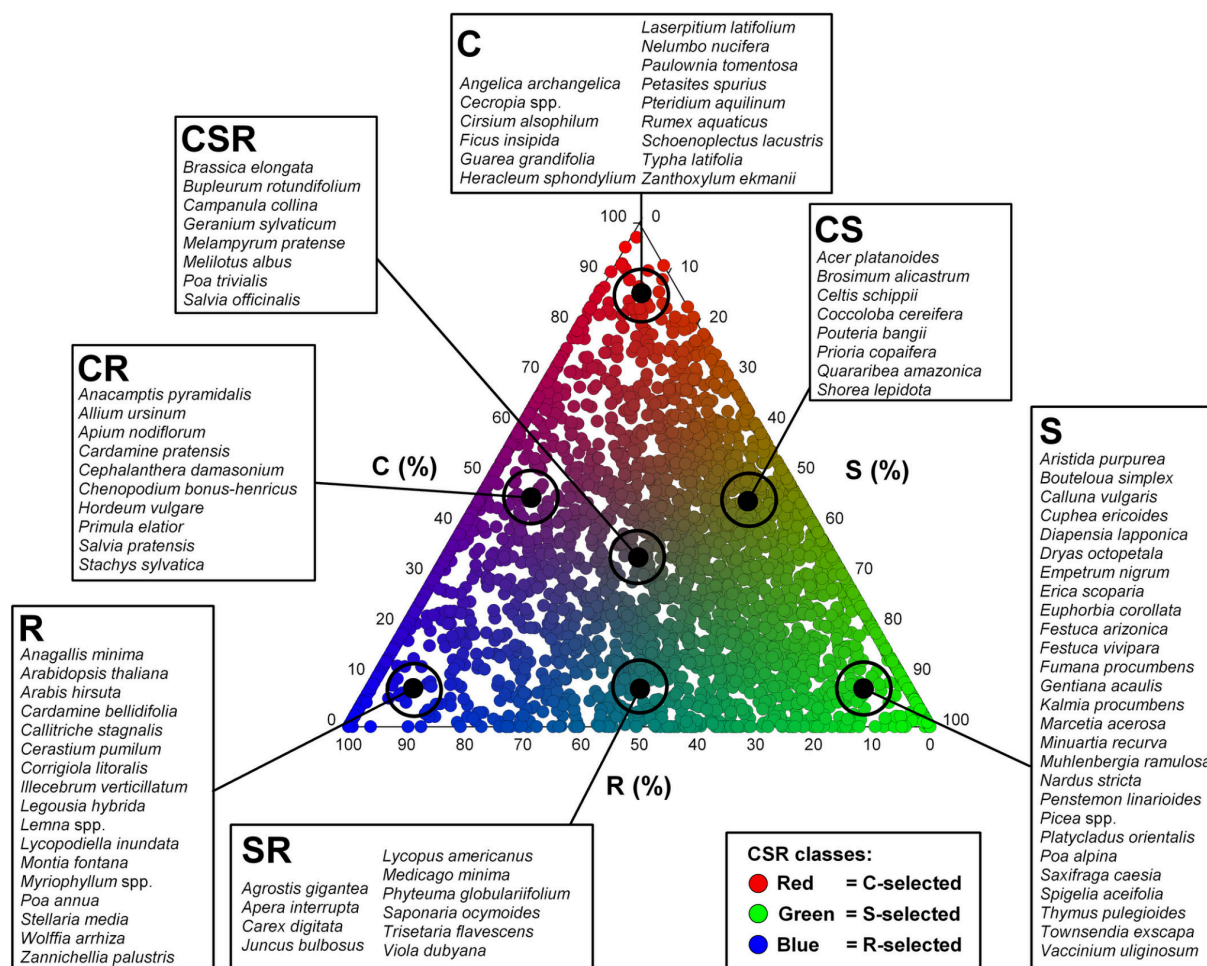


Figure 1. Ternary plot illustrating the variation in plant strategies using Grime's CSR groupings as axes.

Relative proportion (%) of C, S and R-selection using the 'StrateFy' tool. From Pierce et al. (2017).

2.4 - Environmental variables that influence plant functional traits, community composition or productivity

Plant functional traits are not only reflective of a plant's physical and biochemical status but the properties of the wider ecosystem. As seen previously, changes in vegetative traits can suggest changes in vegetation functioning, which in turn can alter ecosystem processes. Plants have the ability to alter function in response to changes in the environment. Therefore there is an observable relationship between plant functional traits and environmental

variables. Discussed below are some of the environmental parameters that provide indications of the greater ecological processes and that affect plant functional traits.

2.4.1 - Soil field capacity

The soil field capacity is the amount of water held in a soil when in a fully saturated state. This value is an important measure from an agricultural perspective as it indicates how well soil may retain moisture, thus influencing how much water is available for plant use (plant available water). If the importance of root morphology and structure is excluded from the importance of plant available water, then the field capacity measurement can be used as an indicator of the available water capacity, which is the amount of plant available water when the soil is fully saturated. This ability for a soil to hold water is dependent on the soil's hydraulic conductivity which in turn is dependent on soil organic matter and soil texture (Lal, 2020).

Increases in available water capacity have been shown to both decrease the frequency and negate the impacts of drought periods (Trnka et al., 2022). Since available water capacity also benefits above-ground net primary productivity, it will have a positive impact on both productivity and yield stability in the future where a country may experience more frequent drought periods (Meresa & Murphy, 2023).

The amount of soil organic matter (SOM) in the soil influences field capacity, as it affects the macroaggregate soil structure which influences the porosity of soil (Hudson, 1994). The organic matter also binds more water through its high cation exchange capacity. The importance of SOM content for water retention also appears to be texture dependent, with coarser soils gaining the greatest water retention benefits from increased SOM content (Rawls et al., 2003; Bauer & Black, 1992).

2.4.2 - Soil organic matter (SOM)

Soil organic matter (SOM) can be described as the amount of organic carbon present in soil. The level of SOM in grasslands is extremely variable and is dependent on ecological and environmental influences. Vegetation can alter SOM by influencing decomposition rates and root exudation (Shen et al., 2020, Breulmann et al., 2012). Mean annual temperatures also influence SOM as lower temperatures slow rates of decomposition more than productivity (Conant et al., 2011). Higher levels of rainfall, up to a threshold, also tend to favour higher levels of productivity in relation to decomposition (Dan et al., 2016). Additionally, SOM is influenced by inherent traits of the soil such as the parent material, age and texture (Plante et al., 2006). The management of grasslands, as with any other agricultural crop, contributes to the amount of organic matter in the soil.

2.4.3 - Soil nitrogen content

The amount of plant available nitrogen in a soil system directly affects the vegetation community present in a grassland (Wedin & Tillman, 1996). Semi-natural grasslands tend to have lower soil nutrient levels (including nitrogen), which often makes soil nutrient availability a limiting factor in the productivity of grassland species (Fay et al., 2015). Interestingly, leaf nitrogen content does not strongly correlate with soil nitrogen content. The vegetation present can influence soil nitrogen content as N_2 -fixing species (leguminous herbs) can actively increase the amount of plant available nitrogen in the soil (Mulder et al., 2002). Grassland productivity not only depends on the availability of nitrogen in the soil, but also on the nitrogen uptake rates and utilisation efficiency of different plant species (Egan et al., 2019; Del Pozo et al., 2000). Nitrogen assimilation rates by plant roots are dependent on precipitation levels and soil moisture content (Polley et al., 2023). Therefore precipitation can influence the relationship between soil nitrogen content and productivity rates (Wang et al.,

2017). A meta-analysis of global grassland research has also shown higher counts of nitrogen-limitation at colder temperatures, with cool temperate latitudes suffering from the lowest nitrogen concentrations (Fay et al., 2015). An increase in species richness (regardless of increase in legume composition) has been shown to increase soil nitrogen content as increased species richness leads to greater productivity and biomass, which in turn has a positive effect on nitrogen retention and nitrogen mineralisation rates (Cong et al., 2014).

2.4.4 - Soil phosphorus content

The amount of phosphorus in soil can often be a significant factor in the productivity of grassland species. The roles of phosphorus and nitrogen on plant growth seem to be intrinsically linked in a way that both nutrients have a synergistic effect of limiting plant growth when both nutrients are not in ample supply (Fay et al., 2015). The loss of species diversity that can occur with nutrient enrichment tends to occur only in the cases where nitrogen and phosphorus are not limited (Van Dobben et al., 2017). Additions of phosphorus without nitrogen, however, tend to have a neutral effect on species richness while still increasing productivity (Soons et al., 2017). An increase in phosphorus can also induce an increase in legume species (DeMalach, 2018).

2.4.5 - Soil pH

Semi-natural grasslands can have a wide range of soil pH values, such that different semi-natural grassland habitats are characterised by their pH and have a species composition associated with different soil pH conditions. Soil pH is one of the most important factors influencing the bioavailability of soil nutrients (Kemmitt et al., 2006). In dry calcareous grasslands, the high pH and porous soils coincide with low nutrient availability (particularly phosphorus which is quickly sequestered by calcium cations) (Bahr et al., 2012). It is also

suggested that drier grasslands will suffer more (i.e. have less of a buffering effect) due to changes in pH than wet grasslands (Liu et al., 2022).

Soil pH influences microbial activity which affects nitrification and nitrogen cycling rates, as well as microbial turnover of soil organic matter (Curtin et al., 1998; Adams & Adams, 1983). Any external nitrogen additions, through deposition or fertiliser application, will affect the soil pH, acidifying it through nitrification processes (Tuyen et al., 2006). pH can also affect plant growth conditions by influencing plant available water. Lower pH soils have a higher water carrying capacity and so provide more water to vegetation (Sujatha, 2016).

2.5 - Impacts of management on functional traits

Like the environmental factors that influence grasslands, management can also alter the properties of an ecosystem which in turn influences the functioning of vegetation (Kahmen & Poschlod, 2008). The two main influences by management are disturbance events (i.e. grazing, mowing, trampling, tillage and reseeding) or alterations to the ecosystem's nutrient and hydrological cycling (i.e. soil improvement or irrigation). Since plant functioning is important for ecosystem services that are beneficial to farmers, the ways in which management influences vegetation functioning is of importance to ecologists and landowners alike.

2.5.1 - Grazing and functional traits

Grazing by herbivores on semi-natural grasslands, is a continuously occurring disturbance event that favours specific plant strategies (Briske, 1996). Two strategies may be adopted in response to grazing - avoidance and tolerance (Rota et al., 2017). The avoidance strategy usually revolves around the species being unpalatable or unfavourable to the grazer. Low

growing species with more basal growth and with small and tough leaves are less likely to be grazed. These species usually have a low specific leaf area (SLA) as they are small and have a high dry matter content. In relation to Grimes' CSR strategies these species would be more S-strategists with their low SLA and leaf area (LA) values (Rota et al., 2017).

Grazing-tolerant species are more likely to have a high SLA and chlorophyll content as this promotes more rapid regrowth after grazing. These may be classed as more C or R-strategists. The balance between these two strategies in response to grazing is based on the ecosystem's ability to promote rapid growth (Cingolani et al., 2005). If nutrient and productivity conditions are favourable then the C-strategists are unimpeded in their continuous regrowth. Therefore the soil nutrient content of these semi-natural grasslands are intimately linked to preferential plant strategy.

The intensity of grazing or manual cutting of vegetation will influence the overall functional strategies of the vegetation community while also influencing taxonomic composition. The link between changes in grazing intensity and the change in relative composition of plant functional traits in communities is unclear as the response differs depending on climatic and environmental factors (Klimesova et al., 2008). The predicted response of different plant functional types in response to changes in grazing intensity also depends on the grazing history of the site (Hallett et al., 2017). Higher intensity grazing has been shown to correlate with a higher number of ruderal strategists in a community (Moog et al., 2005; Busch et al., 2019). In the case of selective grazing, even at high intensity, an increase in competitive species occurred with a decrease in ruderal species (Wang et al., 2018). The soil enrichment caused by defecation from grazing species also tends to promote competitiveness over a ruderal strategy.

Many semi-natural grasslands may be under grazed or, in some cases, abandoned. If the site has had a history of higher grazing intensity, a shift in vegetation strategy tends to occur with higher LDMC and lower SLA (Mori et al., 2013).

2.5.2 - Agricultural improvement and functional traits

The improvement of grasslands, as a management method for increasing productivity, is a common occurrence and its effects on biodiversity are well documented (Grime, 1973). Addition of nitrogen fertiliser has been shown to decrease biodiversity and, in many cases, leads to the complete loss of low-abundance species (Goldberg & Miller, 1990). In many cases a loss of functional diversity can be the driving force for the observed biodiversity loss. Some of the functional diversity loss is due to competition driven trait convergence (i.e. favouring competitive, fast-growing strategies) (Tillman, 1990). The trade-off between above and belowground competitive plant traits is also affected by soil enrichment as shading becomes much more detrimental than a lack of soil resources. The rapidity with which soils are enriched can also have an influence on how much functional trait diversity is lost as fast-growing, resource-acquisitive species can respond quicker to surges in nutrient levels.

Semi-natural Grasslands are unique in terms of their productivity-biodiversity relationship. Unlike other ecosystems where productivity and biodiversity are positively correlated, managed grasslands show a unimodal trend between productivity and biodiversity (Brun et al., 2019). This indicates that both excessive and insufficient management of grasslands can have negative effects on biodiversity and functional diversity.

2.6 - Plant strategy and grassland productivity

2.6.1 - Above-ground net primary productivity

The above-ground net primary productivity (ANPP) in grassland ecosystems is an ecosystem variable important for both landowners and environmentalists as it is part of both the standing biomass as well as carbon sequestration (Pilon et al., 2010). Some plant functional traits, such as leaf area, have been shown to positively correlate with ANPP. Other plant traits, such as leaf carbon:nitrogen ratio, influence decomposition rates of plant litter which in turn influences the lability of the sequestered carbon. Plants with high LDMC values have been shown to produce litter with higher concentrations of such non-labile compounds (Garnier et al., 2004). In comparison to other ecosystems, the variability in grassland ANPP is influenced by precipitation more so than temperature or other factors (Del Grosso et al., 2008). This suggests that drought tolerance/resistance may be the most important factor for maintaining ANPP across growing seasons.

Below ground net primary productivity (BNPP) is just as important as ANPP for a grasslands carbon sequestering abilities as greater root productivity can lead to greater root litter turnover. ANPP and BNPP both respond differently to changes in precipitation (Wilcox et al., 2015). Increases in precipitation, up to a point, make soil nutrients more readily available which then makes above ground resources the most limiting factor. This leads to increases in ANPP but decreases in BNPP.

2.6.2 - Effects of plant strategy on carbon sequestration

The process in which vegetation communities produce and sequester carbon is dependent on the overall strategy of the community (De Deyn et al., 2008). Fast growing species tend to have shorter lifespans, lower dry matter content and lower levels of carbon in storage organs, However, they tend to release larger amounts of root exudates into the soil (Poorter &

Garnier, 2007). Resource conservative species, on the other hand, tend to grow slowly and exude very little carbon into the soil with most of the carbon coming from nutrient poor plant litter (Kazakou et al., 2006). The dominant source of plant-derived carbon will depend on the fertility of the grassland system. Selective grazing can also influence community composition by shifting it towards an overall stress-tolerant, conservative strategy which can influence carbon storage (Zou et al., 2018).

Across the spectrum of plant strategies, root tissues generally tend to be of lower nutritional value than shoots so species with a greater Root:Shoot ratio, RLD and minimum rooting depth may have greater potential for long term carbon sequestration (Bardgett et al., 2005). Root structure (mainly RLD and branching patterns) can also influence the rate of exudate loss from the plants.

2.7 - An introduction to functional diversity

It has been well established that plant traits and strategies can shape ecosystem functions (Loreau et al. 2002, Petchey and Gaston 2006). No plant acts on its own however, so it is essential to assess how the vegetation community, as a whole, influences ecosystem processes.

2.7.1 - Determining functional diversity

Functional diversity has been shown to greatly influence greater ecosystem processes (Clark et al., 2012) and so there have been many attempts to create indices that accurately capture it. Some indices have been formed by dividing species into functional groups however this lacks an appreciation of the complexity and continuity of functional traits (Fonseca and Ganade 2001). The subjective classification used in this method also makes it difficult for reproducible research (Mason et al., 2005). Other methods involve measuring functional

diversity using single functional traits making it unrealistically simplistic. There are also measures for functional diversity that lack an integration of species abundance into their measurements. This is problematic as the effect a species has on overall community functioning is influenced by its abundance (Diaz and Cabido 2001). The main problem with creating indices for functional diversity is that a strict definition of functional diversity does not exist and, therefore, each index differs in relation to how its creator understands the definition (Mason et al., 2005). Another way of looking at functional diversity is as a measurement for niche complementarity. If this is the case then functional diversity can be described by the distribution of individuals across a multidimensional niche space. This approach was taken by Mason et al. (2005), who described the distribution of individuals across niche space using three metrics: Functional richness (FRic), Functional evenness (FEve) and Functional divergence (FDiv). These three measurements are independent of one another and each provides its own insight into ecosystem functioning.

2.7.2 - Community weighted mean values (CWM)

CWM values can be used to test the mass-ratio hypothesis (Grime, 1998). This hypothesis suggests that the impact a given species has on ecosystem level processes is proportional to its relative abundance in that community. It follows that ecosystem processes can then be predicted by assessing the functional traits of the most dominant species. Analysing a grassland system through the scope of the mass-ratio hypothesis puts a greater emphasis on ecosystem functioning and less emphasis on biodiversity as the loss of low abundance species, while detrimental to biodiversity, is relatively inconsequential to ecosystem functioning. If the mass-ratio hypothesis is accepted, the higher CWM values will come from functional traits and strategies that influence ecosystem processes the most. It is for this reason that CWM is often used as a metric for functional diversity in a single trait analysis.

The mass-ratio hypothesis also leads to something called the dominant species effect (Lisner et al., 2022) where species loss only leads to ecosystem function collapse when the more dominant species are affected.

It is important to note that there is evidence accruing that suggests that lower abundance species may have disproportionately large effects on ecological processes (Marriotte, 2014). Lower abundance species have been shown to have big impacts on below-ground microbial communities, nutrient acquisition and carbon/nitrogen storage (De Deyn et al., 2009; De Deyn et al., 2011; Marriotte, 2013a). De Deyn et al. (2009), in their study on grasslands found that two common yet subordinate species (*Trifolium pratense* and *Achillea millefolium*) had disproportionate effects on grassland nutrient cycling. Also since subordinate species tend to be more stress tolerant, and therefore more resource retentive, they tend to have disproportionately larger effects on yield and yield stability during less favourable conditions such as drought (Marriotte, 2013b). Also, since subordinate species may have high frequencies, albeit low abundances, their influences may be far-reaching in relation to ecosystem processes (Marriotte, 2014). This evidence does not appear to disprove the mass-ratio hypothesis but certainly suggests that the relationship is not as clear-cut as it may seem. It is therefore necessary to bear in mind the functioning of individual species when looking at the greater vegetation community.

2.7.3 - Functional richness

Functional richness is a measure of how much multidimensional niche space is filled by the functional traits of a vegetation community. The method used for measuring Functional richness (FRic) is the same one proposed by Cornwell et al. (2006), where a minimum convex hull, that includes all species in the community, is measured from the multidimensional trait space (Figure 2). The volume of the measured convex hull (total space

occupied by all data points) is measured using the Quickhull algorithm (Barber et al. 1996) and is used as an index for FRic. By this approach, it is the species with the most extreme trait values that stretch the convex hull and influence functional richness.

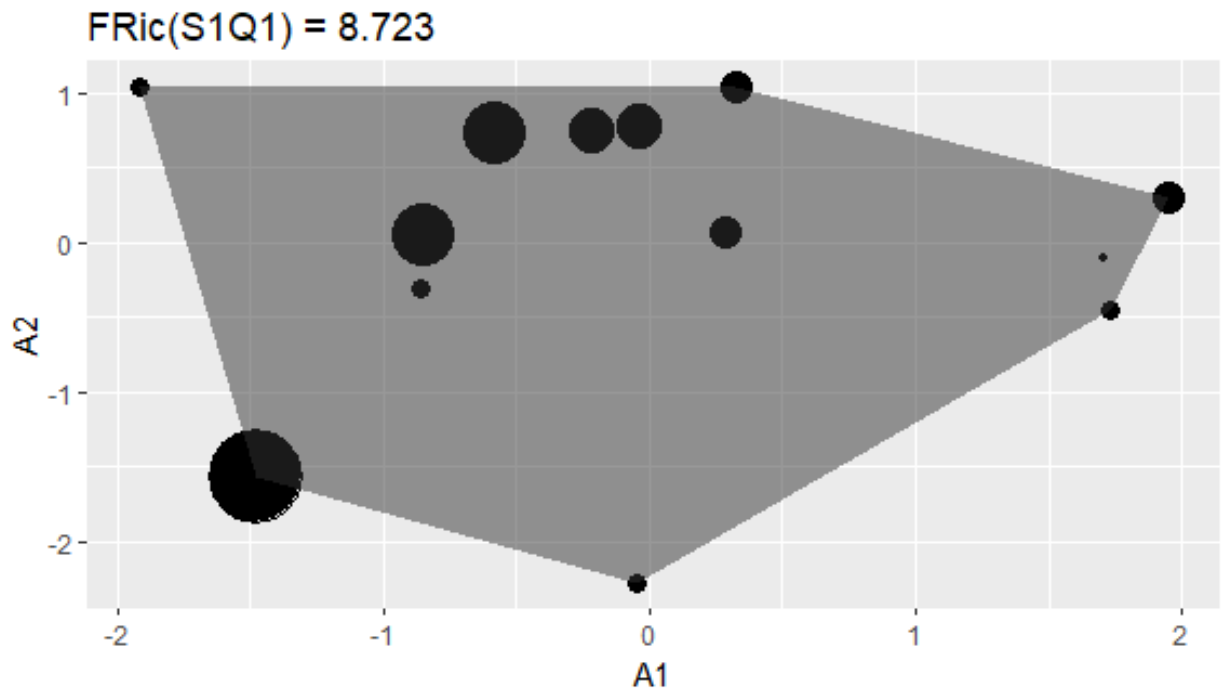


Figure 2. PCA ordination with convex hull volume used to measure functional richness (FRic).

The PCA is simplified to three axes but this figure only shows the two axes explaining the most variation. The black circles are positions of species in multidimensional trait space with the size of the circles indicating abundance. The data used here is based on leaf trait data derived from the 2023 field season used to simply illustrate functional richness.

2.7.4 - Functional evenness

While FRic illustrates the total amount of functional trait space filled by a given community, it only provides information about the extremes at the periphery of trait space. Functional evenness (FEve), however, describes how evenly distributed the abundances of species are across functional trait space. If FEve is high then a community likely has strong niche partitioning and complementarity (Diaz and Cabido, 2001). To measure FEve a minimum

spanning tree (branch pattern connecting all data points with the shortest sum of branch lengths) is calculated (Villéger et al., 2008). This was calculated using pair-wise, abundance weighted distances between species in multi-trait space. The minimum spanning tree is a tree that connects all the species in functional trait space using the shortest accumulative branch length.

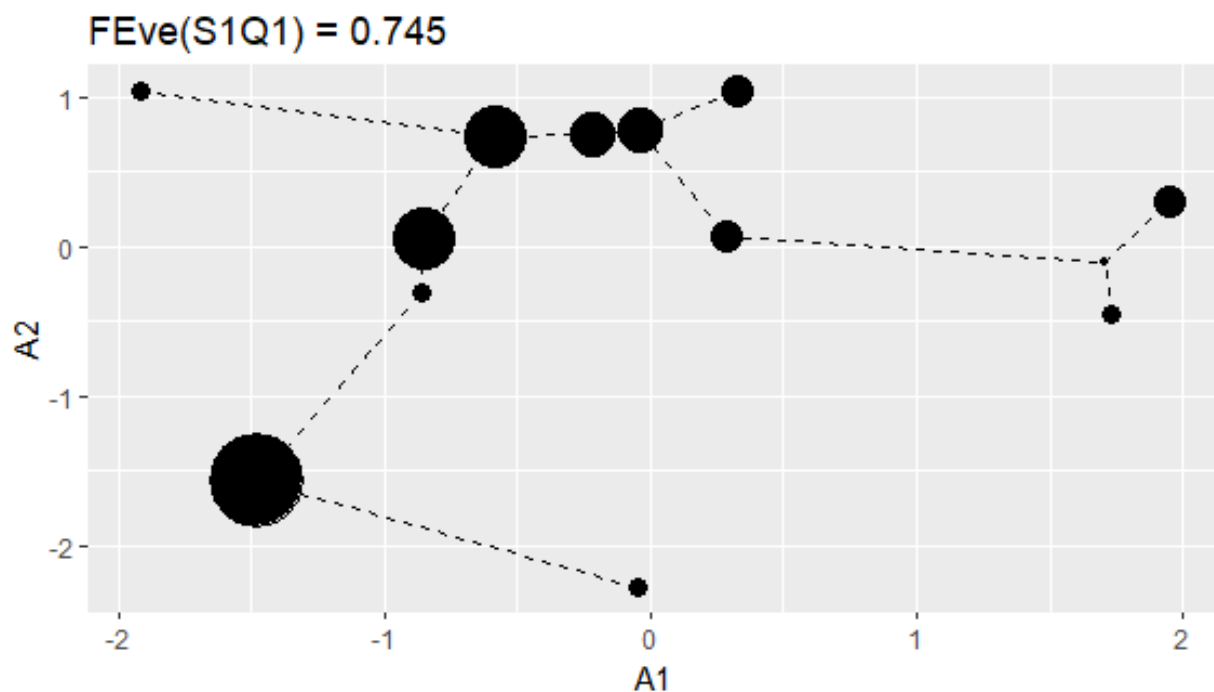


Figure 3. PCA ordination with minimum spanning tree used to measure Functional evenness (FEve).

The PCA is simplified to three axes, but this figure only shows the two axes explaining the most variation. The black circles are positions of species in multidimensional trait space with the size of the circles indicating abundance. The data used here is based on leaf trait data derived from the 2023 field season used to simply illustrate functional evenness.

2.7.5 - Functional divergence

FRic and FEve provide us with the total amount of functional trait space filled by a community as well as how evenly distributed the species are within the trait space. Functional

divergence (FDiv), on the other hand, tells us where the most abundant species are in functional trait space. A high FDiv value indicates that the more dominant species in a community are quite dissimilar (i.e. are further from the centre of functional trait space) (Mason et al., 2003). High functional divergence is indicative of high competition between functionally similar species. This can only occur when environmental constraints are very lenient (Perronne et al., 2017). A high FDiv value is telling of a community with little niche overlap (Mason et al., 2005). If the mass-effect ratio is accepted (where the most abundant species have the greatest effect on community functioning) then a high functional divergence in a community may indicate that no single functional trait is influencing ecosystem processes as the dominant species are functionally dissimilar. It may be the case that, in quadrats with high functional divergence, a relationship between CWM values and environmental variables will be less apparent.

The extent to which trait divergence (the driving force for functional divergence) occurs in an ecosystem has been observed to be scale dependent. Carboni et al. (2014) found that grasslands tended to show more trait convergence on the whole-site scale, but trait divergence was more apparent on a 1m x 1m sample area scale.

2.7.6 - Rao's quadratic diversity (FDq)

FDq is an indicator of the degree of trait differences between the species in a community and can be used to test the role of niche complementarity on functionality (Mason et al., 2005). If FDq values are high, meaning functionally dissimilar species have reached similarly high abundances, it may be the case that complementarity effects are at play. FDq has often been used as a direct indicator of functional diversity as it incorporates both functional distance and functional evenness in its measurements (Botta-Dukát, 2005). Most of the published

research on functional diversity uses only FDq and CWM values for multi-trait and single-trait analysis. Q is calculated as:

$$Q = \sum_{I \neq J}^S P_i P_j d_{ij}$$

Where S is the number of species, P_i and P_j are the relative abundance of two species and d_{ij} is the dissimilarity distance between the two species.

2.8 - Functional diversity and grassland ecology

While much work is done on the response of community functioning to external changes, plant functional traits do not only act as indicators of a changing environment but are also active participants in influencing ecosystem functioning (Diaz & Cabido, 2001).

2.8.1 - Functional diversity and species diversity

It is a presupposition that functional diversity metrics should be independent of species diversity metrics. This was an in-built feature in the design of the previously mentioned functional diversity metrics (Mason et al., 2005) as, otherwise, functional diversity metrics would simply mirror species diversity metrics and so their individual roles in bigger ecological processes would be muddled. However, studies have shown that functional diversity (specifically functional richness) tends to correlate strongly with species richness when assessed in grassland ecosystems (Villéger et al., 2008). This correlation occurs due to shared characteristics between species richness and functional richness even though the equations for FRic do not include species richness.

Studies comparing grasslands across a range of environmental gradients found that relationships between species diversity metrics and functional diversity metrics are either weak or inverted (De Bello et al., 2006). Stress factors such as aridity and low-nutrient levels, for example, greatly decreased species diversity but had negligible or mildly positive effects on functional diversity. Functional diversity metrics also were shown to have an opposite pattern to species diversity across a grazing intensity gradient (only in locations where other environmental conditions were favourable). The lack of covariation between the two measures of diversity is most likely due to the different ecological mechanisms driving plant and functional diversity (Fukami et al., 2005). The nature of the relationship is also very context dependent as the specific environmental conditions will influence how niche space is divided up between the species.

Aspects of functional diversity are important for our understanding of how the biodiversity of a grassland ecosystem may shift in response to climate change (Carboni et al., 2014). The functional composition of a vegetation community can be used to predict ecosystem processes that control community assembly (Mouchet et al., 2010; Mason et al., 2013). So as new environmental conditions shift, the functional composition of species present will influence the rate of species loss/gain.

2.8.2 - Functional diversity and resource use

One mechanism in which greater functional diversity will benefit an ecosystem is by an increase in niche complementarity (Petchey 2003). If a diverse array of functional strategies exist in a plant community, their individual niche spaces are less likely to overlap. In relation to their alpha niche space (i.e. their specific resources used), if there is minimum overlap and high functional evenness, then an optimal level of resources can be assumed, thus maximising the potential productivity of an ecosystem (Cadotte et al., 2011). If other

functional traits that are associated with interactions with the external environment, such as pathogen resistance or drought tolerance, also show great variety, then the ecosystem will benefit from a stronger overall resistance to climatic fluctuations (Chillo et al., 2011).

2.8.3 - Functional diversity and the stress-resource gradient

All grasslands differ in their ecology with variations existing in biotic and abiotic characters, such as variations in resource availability. The relationship that functional diversity metrics have with the stress-resource gradient depends on the ecological processes driving the vegetation community dynamics. In the case of environmental filtering, where the severity of an environment limits the potential number of occupiable niches, variation in functional traits should decrease with increased environmental stress (Mouillot et al., 2005). If competitive processes (such as niche partitioning) are occurring, the more stressful environments will have higher trait variation as niche overlap is less tolerated. Since species in more stressful environments tend to be more stress tolerant than competitive in their strategies, it is presumed that environmental filtering is the more prominent force for shaping community dynamics in stressful environments while competitive interactions such as niche partitioning and limiting similarity are more prevalent in favourable environments. This should provide a general pattern of decreased functional diversity with increased environmental stress; however there are exceptions. For example, experiments done on grasslands along a stress-resource gradient found that a greater functional diversity in communities for SLA and LCC was present in low nutrient environments presumably due to niche partitioning driven by competition for soil resources (Spasojevic & Suding, 2012). For this reason, it may be important to differentiate between above and below ground stress-resource gradients as both can influence functional variation in opposing ways.

2.8.4 - Functional diversity and productivity

Previous studies have found several functional diversity metrics and CWM values that explain high proportions of variance in grassland productivity (Van't Veen et al., 2020; Chanteloup & Bonis, 2013; Roscher et al., 2012). One study found that most variation was explained by CWM values for nutrient preferences with CWM-SLA explaining a significant amount of variation (Van't Veen et al., 2020). According to the mass-ratio hypothesis, the species with greatest abundance have the greatest impact on ecosystem functioning so, if most abundant species show high productivity traits (High CWM-LA or CWM-SLA), there will be a greater positive impact on ecosystem productivity. Models combining both the high productivity CWM traits and FDq have proven to be the strongest predictors of biomass productivity (Roscher et al., 2012).

The “Diversity Hypothesis” as proposed by Tillman (1996) also suggests that ecosystem productivity relies on a wide range in plant traits and strategies that maximise complementarity effects. Functional diversity metrics which indicate minimum niche overlap such as FDq, FDiv, FDis, or the variation in nutrient preferences mentioned above, should all, in theory, explain productivity patterns. The benefit of variety in resource use strategies is dependent on the scarcity of such resources. This suggests that the diversity hypothesis plays a lesser role in fertile habitats.

In these fertile habitats species diversity has mainly been shown to decrease levels of productivity with negative associations with relative growth rate, leaf biomass, leaf chlorophyll content and a positive influence on specific leaf area (De Giorgi et al., 2025).

2.8.5 - Functional redundancy, resilience and yield stability

The resilience of ecosystems to environmental perturbations is of great importance if a stable yield in an unstable climate is to be sustained. A greater functional diversity can aid resilience by increasing the diversity of possible responses to potential shifts in conditions. This is intrinsically tied with the “insurance hypothesis” where a greater number of responses increases the probability of a portion of the vegetation community responding positively to environmental changes (Yachi & Loreau, 1999).

In a study performed by Chillo et al. (2011), arid grasslands were manipulated to look at the effects of a disturbance (controlled grazing) on ecosystem resilience (in this case resilience to species loss). The study found that sites in which diversity within functional groups was highest showed the least amount of species loss in response to disturbance. Sites with more diverse functional groups also showed greater resilience when the intensity and duration of disturbance was increased. Resilience of an ecosystem has been suggested to be disproportionately influenced by less abundant species. Walker et al. (1999) suggested this based on the premise that less abundant species tend to perform the same ecosystem functions as the abundant species, but differ in their ideal environmental conditions. Therefore when the environmental conditions shift the less abundant species will dominate and provide the same ecosystem functions. This is known as functional redundancy and is a good example of how it can provide ecosystem resilience. This is also an example of how functional similarity may be just as important for ecosystem health as functional dissimilarity.

The species diversity within functional groups is also an important factor for resilience as the greater the number of species performing a particular function, the greater the redundancy of an ecosystem function (Mori et al., 2013). If species with similar functional traits respond

differently to environmental perturbations, then this redundancy will increase the likelihood of maintaining ecosystem functioning.

If trait convergence occurs in vegetative communities despite changes in species composition occurring over time, this may suggest functional redundancy and possibly more resilience (Mori et al., 2013). For this reason, it may be true that grasslands with harsher environments, where niche filtering is at play, will be more resilient to environmental changes due to redundancy in functional groups.

Functional redundancy is also an important influence on the relationship between functional diversity and species diversity. If the functional redundancy is high in an ecosystem (i.e. many species share similar functions) then the influence that species diversity has on functional diversity is weaker (Sadeghinia et al., 2023). By this logic, assessing an ecosystem's health through analysis of functional diversity, instead of species diversity, is most important when functional redundancy is high (Sadeghinia et al., 2023).

2.8.6 - Functional diversity and drought tolerance

With the frequency of droughts set to increase in the future (Meresa & Murphy, 2023), the maintenance of normal ecosystem functioning in drought conditions is favourable. Shifts in functional diversity metrics have been observed under manipulated changes in annual precipitation (Hallett et al., 2017). Higher rainfall frequencies have been shown to cause a decrease in functional diversity (FDq) due to convergence of traits towards a competitive strategy while lower rainfall frequencies tend to maintain high functional diversity.

High functional diversity (Rao's functional diversity) and taxonomic diversity have been shown to have a buffering effect on collapses in productivity during extreme to moderate drought (Diaz and Cabido, 2001). This is due to a high diversity of functions begetting a high diversity of reactions to drought conditions. It is also due to an increase in redundancy of similarly functional species which, when species loss occurs due to drought-related stress, will ensure that some species remain to fulfill the same ecological function (i.e. share the same effect traits as the lost species). While this is the case for tolerating drought conditions, the process of recovering from them appears to occur strongest in low-diversity communities dominated by fast-growing species (Bazzichetto et al., 2024). It is important to note, however, that this refers to the restoration of biomass production but does not include restoration of other ecosystem functions that may have been lost. While the loss of dominant species is detrimental to ecosystem functioning, studies have found that grasslands that maintain a high richness of subordinate species, with the cost of losing some abundance of dominant species, showed the least impact in ANPP under drought conditions (Yu et al., 2025).

2.8.7 - Functional diversity and carbon storage

Climate change and increases in atmospheric carbon have led to carbon sequestration becoming the most sought-after ecosystem function. Understanding how functional diversity influences the carbon storage abilities of a grassland system is still in its infancy. The abilities for each species to produce and exude carbon seems to depend on their resource use strategy. Some studies found that higher CWM values related to resource acquisitive traits correlated with higher soil carbon and nitrogen concentrations (Zou et al., 2016; Yang et al., 2019; Sheng et al., 2022)

Functional divergence metrics also correlated positively with carbon storage in some studies suggesting that the niche complementarity effect positively influences carbon storage (Zou et

al., 2016). Yang et al. (2019) found that a multiple regression model using CWM values for resource acquisitive traits as well as FDiv, explained the greatest amount of variation in carbon storage. While different studies found differences in which traits most strongly influence carbon storage, almost all agree that both the mass-ratio hypothesis (influencing CWMs) and the niche complementarity effect (related to FDis) are the key drivers for increased soil carbon storage.

As managed ecosystems, the grazing intensity of semi-natural grasslands is also important to consider as CWM values for high productivity will not necessarily translate to carbon storage if more of the standing biomass is grazed. A study performed by Sheng et al. (2022) found that FRic (total trait variability and related to species richness) best predicted carbon storage in an abandoned grassland. At light grazing intensity CWM-LA became the best predictor for carbon storage. At moderate and high grazing intensities however, FDis showed the most predictive power for soil organic carbon stocks.

2.8.8 - Functional diversity and management/land-use legacies

In the management of grassland ecosystems, a trade-off exists between managing for high yield in optimal conditions and managing for yield stability (or resilience in sub-optimal conditions) (Coté & Darling, 2010). Functional Diversity (FDq and CWM values) has been shown to be higher for sites with moderate grazing levels compared to sites with light grazing levels (Hallett et al., 2017). This suggests that the trade-off between grazing intensities is also important when considering functional diversity.

Grazing practices that promote high functional diversity were also shown to promote higher stability in both vegetation cover and biomass (i.e. yield stability). This correlation between increased functional diversity and increased productivity is only true for well-managed

grasslands as, with abandoned systems, functional diversity decreases when productivity increases (Tardella & Catorci, 2015). Moderate grazing intensities also promote belowground biomass production which positively affects long term productivity and carbon sequestration (Mariotte, 2014).

Soil erosion, caused by trampling of grazers due to overstocking, will also have influences on microhabitat conditions (Bloor & Pottier, 2014). These fine-scale variations in disturbance levels may influence the functional strategies of the vegetation present. The severity of the potential soil erosion is mainly influenced by slope and the aspect (Huang et al., 2020). Increases in nitrogen and phosphorus in grassland soils, by deposition or fertiliser application cause a decrease in functional diversity. In a study by Helsen et al. (2014) nitrogen content was negatively correlated with FDq.

2.9 - Trait selection for functional diversity

Since functional diversity metrics are based on distances of trait dissimilarity between species, traits with higher intraspecific heterogeneity are less useful as species averages are not providing any indication of overall community functioning. Traits that vary on the individual, intraspecific and interspecific scale, are less useful in functional analysis as these plastic traits tend to correlate more with species richness than interspecific trait-based metrics (Clark et al., 2012).

The selection of traits should also be guided by the ecological questions being asked. A study based on grassland productivity will rely on different indicative traits to a study assessing species diversity for example. It is also preferential if the relationship of interactions between certain traits and their surrounding environment is well studied. Several studies have found correlations between community weighted mean values (single-trait,

abundance weighted values) and ecological conditions (i.e. soil conditions, precipitation levels) (Diaz & Cabido 2001; Clark et al., 2012).

It is also important to have a balanced share of above- and below-ground trait measurements as, depending on the environmental conditions, the competitiveness of a species may be apparent either in above-ground traits or below-ground root traits (Wilcox et al., 2015).

An unspoken flaw of functional diversity metrics is the assumption that all traits are equally important in relation to their effects on ecosystem processes (Clarke et al., 2012). The metrics also assume that the variation in traits is equal for all species so that a given amount of variation in seed mass is as ecologically significant as the same amount of variation in leaf chlorophyll content (Clarke et al., 2012). This means that the overall variation in a community observed by determination of functional diversity will be overwhelmingly influenced by the most variable trait. Both assumptions are false in grassland ecosystems, and this must be accounted for when selecting traits and when opting for either single-trait or multi-trait functional diversity indices to explain ecological patterns.

When selecting which functional traits to measure, considerations should be made for the fact that each trait informs about different niches. Different ecosystem processes (assembly processes, competition, complementarity effects) act differently depending on the niche in question. Therefore, finding traits that explain most of the variance in multiple niche axes is paramount. When looking at dissimilarities in traits between species, it has been suggested that traits associated with competitiveness (SLA, leaf area) will tend to be similar in values across communities (functional convergence), while traits associated with resource use (root traits) will show more dissimilarity among species (functional divergence) (Mayfield & Levine, 2010).

2.10 - Intraspecific trait variability

The observed relationship between plant traits and environmental conditions can be attributed to both environmental filtering (where only a select group of species can survive in its environment due to their functional traits) and phenotypic plasticity (where variation in functional traits within a species allows the more plastic individuals to survive in the environment). Both processes act together to refine the trait-environment relationship; however, deciphering the relative effect of each is more difficult.

Trait integration is the pattern (covariation) that exists between different traits between/within species. This occurs due to trade-offs existing between traits (Walker et al., 2017). Plants in more stressful environments tend to have high trait integration as lack of resources calls for a greater optimisation of functions (mainly related to stress tolerance). In low stress environments there is more flexibility in how resources may be invested (Mason et al., 2005).

Low stress environments may allow for - a) more inter-specific trait variability (as more species, with alternating strategies may co-exist), b) species diversity (due to functional diversity being accommodated by species diversity) and c) intraspecific diversity as individuals can show more plasticity in functional traits without an environmental constraint.

2.11 - Incorporating plant functional diversity into conservation and management

To integrate functional diversity into management practices it is important to first understand how the different functional diversity metrics can predict different ecosystem processes. For example, if it is understood that an even partitioning of niche space among species is optimal for a given ecosystem function such as resistance towards invasive species, then the FEve metric should be used as a predictor when assessing how strong a particular grassland is in

warding off invasive species. Fortunately, there are several studies that have analysed which of the number of functional diversity indices are best suited at predicting ecosystem functions (Mouillot et al., 2011; Clark et al., 2012). In a study performed by Clark et al. (2012), native species were sown in managed plots. The study was attempting to find the predictive power of different functional diversity indices for above-ground biomass productivity. Out of all the metrics the abundance weighted functional diversity (a measurement very similar to FDq) , FEve and FDiv had the strongest correlation with productivity. Mouillot et al. (2011) also found that a combination of FDiv, FEve and FRic was consistent in predicting decomposition rates, nutrient turnover and productivity. FDiv appears to be the most predictive metric for ecosystem processes especially in regions with greater variation in plant strategies as the spacing within functional trait space is more important than the sheer volume of trait space occupied (Clark et al., 2012).

In many cases the functional diversity of an ecosystem can be more important than species diversity for conservation purposes as it pertains to the functioning of the ecosystem and the maintenance of its services. Conservation of services therefore relies heavily on conservation of functional diversity. Any changes in management of grassland ecosystems should be assessed based on the resulting influence on functional diversity as, in many cases, land-use change can negatively influence functional diversity more than species diversity (Flynn et al., 2009).

2.12 - Conclusion

As there is abundant evidence that the functional composition of a vegetation community and the external ecosystem processes are intrinsically linked, the next step involves using certain elements of functional diversity to gain insights into the current state of our semi-natural grasslands. It is also important to note that functional diversity and species diversity are both

important factors when considering the state of grassland systems. Also, since both are independent of each other, the use of species and functional diversity in tandem will be very useful when analysing ecosystem health. It is important that farmers are informed about the functional composition of their grassland as not only does it influence their ANPP, yield stability, resilience and recovery rates but it is also heavily influenced by land-use legacies and disturbance/ abandonment periods.

Chapter 3 - Materials and Methods

3.1 - Site selection and surveying

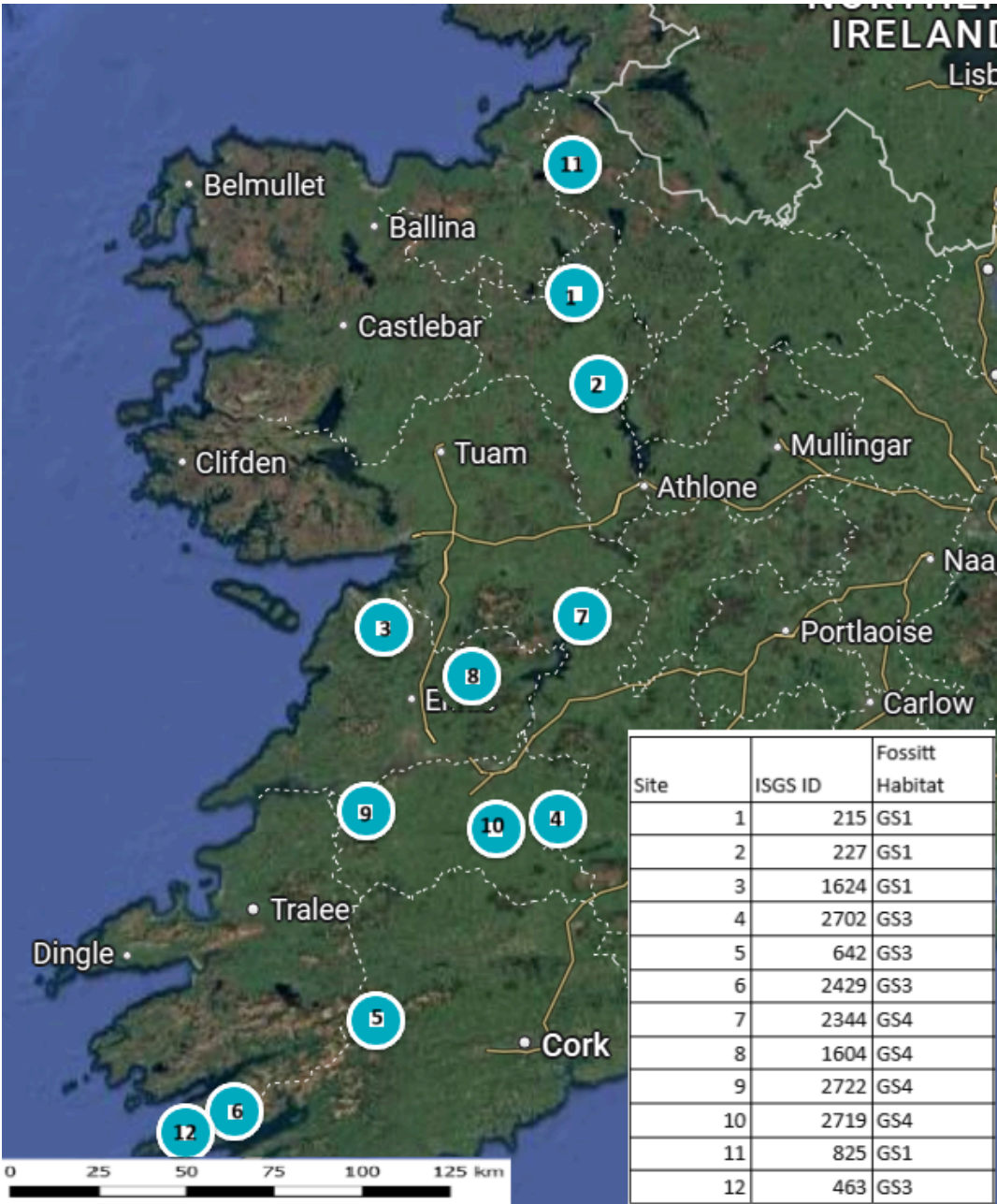


Figure 4. Map of Irish western coastline with all 12 sites.
The table provides the identification number given to each site by the ISGS survey as well as the prescribed Fossitt habitat classification.

Twelve semi-natural grassland sites were selected for this study, four sites for each of the three Fossitt semi-natural grassland habitats (Fossitt, 2000): GS1 Dry calcareous and neutral grassland, GS3 Dry-humid acid grassland and GS4 Wet grassland. Previously studied sites from the Irish semi-natural grassland study (ISGS) (O'Neill et al., 2013) provided a choice of multiple semi-natural grasslands however site selection was confined to the western part of Ireland. All GS3 sites are located in mountainous regions in southern Ireland (Cork, Kerry and Limerick). One GS3 site (site 12) is located on the old copper mines in Urhan, west Cork. The GS1 sites are located on limestone pavements with three in the Roscommon/Leitrim region and one in the Burren in north Clare. Two of the GS4 sites are located in Limerick on relatively flat terrain. Site 7 (GS4) is on the banks of lough Derg in Portumna and is in close proximity to alkaline fen habitat. The last GS4 site (site 8) is in Glendree, east Clare, an area with relatively mountainous terrain. The mean annual precipitation and temperatures also varied between the sites and habitats (Table 1).

Table 1. Location and climatic details for all twelve sites.

The climatic details were taken from Met Eireann historical grid data from the year of surveying. These values have a resolution of one kilometre squared (within which they are the relevés for the sites). Monthly rainfall and temperatures were averages for the twelve months (<https://www.met.ie/climate/available-data>).

Site	ISGS ID	Fossitt	Location	County	Irish Grid Reference	Mean monthly rainfall (mm)	Mean annual temperature (°C)
1	215	GS1	Boyle	Roscommon	G 182500 301400	104.58	9.83
2	227	GS1	The Plains	Roscommon	M 187700 274900	95.81	10.22
3	1624	GS1	Cragballyconnol	Clare	M 125254 200909	134.30	10.22
4	2702	GS3	Barna	Limerick	R 184850 124237	130.84	9.34
5	642	GS3	Kilcaskan	Cork	W 121319 080511	170.52	8.67
6	2429	GS3	Canagullen	Kerry	V 076302 054261	226.03	10.16
7	2344	GS4	Portumna	Galway	M 186313 204265	73.33	10.84
8	1604	GS4	Glendree	Clare	R 153123 187045	110.79	10.22
9	2722	GS4	Ballyhahill	Limerick	R 120388 144482	118.23	11.01
10	2719	GS4	Lough Gur	Limerick	R 160614 140960	84.60	11.06
11	825	GS1	Sracummer	Leitrim	G 182159 338391	123.18	9.18
12	463	GS3	Urhin	Cork	V 61087 047069	147.19	11.04

The categorization of relevés into habitat types was based on the habitat description assigned to each relevé during the botanical survey (Lynch-Milner, 2024). This designation was opted over the overall site level habitat classification (provided by the ISGS survey in 2012) as many relevés, particularly in GS1 sites, were clearly GS4 habitat. The vegetation survey was performed by Oliver Lynch-Milner (University of Galway) who also provided the species diversity data for the productivity-diversity analysis presented in this thesis (Lynch-Milner, 2024).

3.2 - Observations on grassland habitats and management

The management and grazing intensity imposed on the grasslands under study was not assessed quantitatively, however observations were made on variations in management practice between habitats:

GS1 sites were most often grazed by sheep and sometimes by cattle. The intensity of grazing never reached a point where any poaching or damage to soil or vegetation was observable. No seeding or tilling was performed on these sites mainly due to the often present limestone pavement and shallow soil which made accessibility to farm machinery difficult.

GS3 sites were only grazed by sheep and never by cattle. Like GS1 these sites were never managed in relation to tilling or seeding due to the gradient of the landscape. Selective grazing occurred to a large extent on these sites with grass and forb species kept very low by the livestock. Some of these sites were commonage areas that had been left under grazed or sometimes were completely abandoned. These sites include some relevés from site 5 and all relevés in site 12. These relevés consisted of a few tussock forming grass species as well as heather and other heathland associated vegetation (*Eriophorum angustifolium*, *Narthecium ossifragum*, etc.).

GS4 grasslands, when stocked, were predominantly grazed by cattle as the soils were too wet for sheep. These sites were often fertilised with slurry. Many of these sites were not grazed and instead were let grow and cut twice annually for fodder. Many sites had clear signs of trampling and poaching by cattle in the wet soils which damaged vegetation.

The abiotic conditions which dictate the ease of survival for grassland communities also varied between habitat types (Table S1). GS1 grasslands were generally in hilly landscapes with shallow sandy soils. GS3 sites were predominantly in mountainous areas at steep gradients with high wind exposure. GS4 sites were mainly situated in low land areas where the landscape and weather conditions, and precipitation were never too extreme.

Another factor that needs some consideration is that, while all sites were situated along the southwest and west regions of the country, the habitat types differed in their latitude and locality (Figure 4). GS1 sites were predominantly in the north west part of the country (Leitrim, Roscommon) and one site was in the Burren in north Clare. GS4 sites were situated in north east Clare and Galway and across the county Limerick. GS3 sites were the most southerly with one in the Galtees, county Limerick and the other three near the Beara Peninsula. This latitudinal gradient along with observed differences in mean monthly temperatures and precipitation should, therefore, also be considered when looking at variations between the habitat types (Table 1).

All the aforementioned variables and factors will be considered when commenting on the observed patterns of variation in grassland habitats and providing possible explanations for said patterns.

3.3 - Collection of leaf samples and storage

Leaf samples were collected during the months May to July with sites from different habitats visited every week (for example a GS1 habitat in week 1, GS3 in week two and GS4 in week 3) to evenly disperse any seasonal variation in sampling times between habitat types. Leaf samples were taken from each 2m x 2m relevé recorded for each of the twelve sites. Samples were only taken from individuals with healthy (non-blemished) leaves. When

possible, five leaf samples were taken per species with a leaf taken from each individual. To ensure sample collection was reflective of the relevé's species composition and abundance, samples were collected from enough species that a collective 85-90% of relative species abundance (for all higher plants) was represented. Samples were collected with the petiole/rachis still intact. Immediately following collection, the chlorophyll content of each leaf was measured using a Chlorophyll Meter SPAD-502Plus. This method was followed for all species with leaves large enough to be measured. Specimens were then labelled, wrapped in wet tissue paper and stored in ziplock bags which were refrigerated on-site using a cooler box. When same day lab-analysis was not possible (i.e. on multi-day field trips), samples were refrigerated at 4°C overnight. Leaves were fully rehydrated in the laboratory (Garnier, 2001b).

3.4 - Determination of leaf traits

Before measurements were taken, petioles were removed from the base of leaves. In the case of compound leaves, all leaflets were measured together. The fresh leaves were then weighed for leaf fresh weight. To measure leaf area (LA) a scanner was used to print high quality images of the leaves with a ruler to scale. These images were run through ImageJ software where LA was measured. The samples were then placed into a fan-assisted oven at 60°C for 72 hours. All leaf samples were taken out of the oven and stored in a desiccator until their measurements could be taken. Samples were then weighed for their leaf dry weight (LDW). These values, along with LA and LFW were then used to calculate specific leaf area (SLA) and leaf dry matter content (LDMC). SLA was measured as leaf area over leaf dry weight and LDMC was measured as leaf dry weight over leaf fresh weight.

3.5 - Classification of CSR strategies

Competition-stress tolerance-ruderality (CSR) functional strategies were determined from the community weighted mean leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC) using the StrateFy tool (Pierce et al. 2017) (StrateFy software). StrateFy works based on the assumption that CWM-LA indicates competition, CWM-LDMC indicates stress tolerance and CWM-SLA indicates ruderality. Using the CWM values, StrateFy provides relative proportions for each of the three CSR strategies (given in percentages).

3.6 - Determination of functional diversity metrics

To derive metrics for functional diversity the R package FD (Laliberté & Legendre 2010), downloaded through R statistical package version 2.15.0 was used to analyse the trait data. By providing the dbFD function with individual abundance and trait matrices for each relevé, the dbFD function provides multiple indices associated with functional diversity including: FRic (an indice for functional richness), FEve (functional evenness), FDiv, FDis (two indices for functional divergence) (Botta & Dukát, 2005; Villéger et al., 2008; Petchey and Gaston, 2006). These indices were calculated for each relevé and compiled into a single data frame. The rao.diversity() function from the R package SYNCSA was also used to calculate Rao's functional diversity (FDq) (a measure of functional divergence) as well as functional redundancy (FRed) which is a measure of the difference between species diversity and the trait divergence of species (FDq) (de Bello et al. 2007).

3.7 - Soil sampling and analysis

Soil samples were collected over a two week period in the later half of July. When collecting soil samples for soil analysis, an open-tube soil sampler with 2.5 cm diameter was used. For each relevé, four samples were taken roughly one metre apart in a square shape. When

possible, the sampler was buried ten centimetres into the soil. The upper layer containing litter and plant matter was removed and all four cores were mixed together. Soil samples were stored and transported in two layers of ziplock bags. These were then stored in a cold room. The soils were then sub-sampled with one portion sent off to IAS laboratories. These samples were then tested for the following; soil inorganic carbon, total carbon, total nitrogen, carbon nitrogen ratio, organic matter, soil organic carbon and organic carbon stock. The rest of each sample was used to measure pH in the laboratory. Samples were first air-dried. Roots were then removed from the sample by passing through a 2 mm sieve and then removing roots from the sieved soil with a tweezer for no more than 10 minutes. 10 grams of dried soil were then added to beakers containing 50 ml of deionized water. The water and soil were then stirred for one minute. After leaving the soil particles to settle for an hour, the pH was measured using a calibrated pH probe.

3.8 - Determination of root length density

Soil samples were also collected from each relevé for root trait analysis. These samples were collected in late September/early October. Samples were only taken from GS3 and GS4 sites as the GS1 sites were found mainly on limestone pavement and rarely had more than 10 cm of soil. A split tube sampler was used to extract intact soil cores 40 cm in length and 5 cm across. A single core was taken from each relevé. The split tube sampler was hammered to a depth of 40 cm where possible, however, most soils did not reach such depths. In those cases the soil sampler was hammered down till it met with resistance from rock, gravel or dense clay layers. Each soil core sample was then split by hand at 10 cm intervals. Images were taken of the cross sections on either side of the breaks. Using the core break method (Van Noordwijk et al., 2000), the tally of roots visible on either side of the cross section provided a value for root length density (RLD). The counting of roots in each soil break was performed using ImageJ software.

3.9 - UAV (unmanned aerial vehicle) surveys to determine NDVI

UAV surveys were conducted by Dr Samuel Hayes (University College Cork). A DJI Mavic 3 Multispectral quadcopter (<https://ag.dji.com/mavic-3-m>), was used to capture high resolution imagery of the study sites. Surveys were conducted in June and July of 2024 at times ranging from 10.50 am to 6.26 pm, depending on location and weather conditions (Table S1).

Most flights were pre planned to capture imagery at a height above ground of 120 m and with 70% side and front overlap. However, some sites had highly variable and steep terrain, requiring the UAV to vertically track a digital elevation model to maintain a consistent height above ground. The small mismatches between the actual terrain and the digital elevation models introduced some variability in the overall ground resolution, which ranged from 5.0 cm to 6.1 cm across the sites. Measurements were not taken for every relevé so any analysis performed in relation to productivity included a reduced dataset. Sites 6, 7, 8 and 11 were not surveyed and so one GS1, one GS3 and two GS4 grasslands are excluded.

Orthomosaics were generated in Agisoft Metashape Professional 1.7.5 and the projection set to Irish Transverse Mercator. Normalised Difference Vegetation Index ($NDVI = \frac{\text{near infrared-red}}{\text{near infrared} + \text{red}}$) maps were then created before being exported as geotiff images for further analysis. Settings and filters used in generating the orthomosaics are available in the Supplementary Table S2.

3.10 - Data analysis

The leaf trait values taken from the five samples of each species in a given relevé were averaged. The resulting values were multiplied by the species relative abundance, as the proportionate effect a functional trait has on its community is influenced by its abundance

(Diaz and Cabido 2001). These weighted values were then averaged across all selected species in each relevé to determine the community weighted mean values (CWM's) using the following sum:

$$CWM = \sum (P_i \times T_i) / i$$

Here the relative abundance (P) of species "i" is multiplied by a specific trait value (T_i).

To search for relationships between overall functional strategy in each relevé and the associated environmental variables, a correlation test using the non-parametric Spearman rank method was performed between the CWM values and environmental measurements. Correlation tests were also performed for functional diversity and species diversity metrics. Relationships were analysed between FD metrics, species diversity, soil metrics and NDVI values. When analysing correlations with pH and other parameters a nonlinear correlation test was performed using the `nlcor()` function in R if the graphed relationships appeared to be more quadratic than linear.

Analysis of differences in leaf traits and environmental metrics was performed on a site and habitat scale. The variables were tested for normal distribution (Shapiro-Wilk test) and equal variance between groups (Bartlett test). Most of the variables broke the assumptions of an ANOVA test so a Kruskal-Wallis test (the non-parametric equivalent of an anova) was performed. Post hoc, Wilcoxon tests were performed afterwards to assess which sites/habitats differed from each other.

Analysis of individual species and the relationship between their abundance, functional traits and environmental metrics was also performed. Functional strategies for each species were visualised using ternary diagrams. To assess intraspecific variation in leaf traits, the coefficient of variation (CV) was calculated using the leaf trait measurements from each

relevé for a given species. These relevé values were averaged values from the five leaf samples taken.

To visualise how functional diversity metrics and community strategies varied in relation to each other and across habitats, a non-metric multidimensional scaling (NMDS) ordination plot was produced using dissimilarity matrices derived from species abundance data. The functional diversity metrics and Competition-Stress tolerance-Ruderality (CSR) strategies were plotted onto the NMDS plot using the `enfit()` function.

Chapter 4 - Plant functional traits in relation to grassland types

This chapter focuses on site and habitat variations in plant functional traits and strategies including leaf traits, root length density and CSR strategies to determine if the grassland habitats show significant abiotic variations. Dominant community strategies were also analysed. Abiotic measurements taken from each site (i.e. soil measurements) were analysed and their relationship with community functional traits was investigated. It was hypothesized that the three grassland types would vary significantly in their abiotic conditions which, in turn, would lead to significant differences in their leaf and root traits.

4.1 - Soil parameters

Before analysing variation of soil metrics between sites and habitats, Shapiro-Wilk tests were performed to test for normality in the soil parameters. Bartlett tests were also performed to assess whether there was even variance between each site/habitat. Only total nitrogen and pH values were normally distributed. Therefore the non-parametric Kruskal-Wallis test was chosen for analysis of variance. Kruskal-Wallis tests were performed using both site and habitat as the categorical variable for each of the soil measurements (with every relevé being a replicate). With the exception of inorganic carbon, total carbon and organic matter content, all soil measurements differed significantly between the three habitat types.

4.1.1 - Soil pH

Soil pH differed significantly between sites ($p < 0.0001$) (Figure 5b). There was little within-site variation in soil pH with the narrow boxes indicating a narrow interquartile range. Outlier relevés were present in site 2, 9 and 11. From the boxplots it is clear that the three grassland habitat types differed significantly in pH levels ($p < 0.0001$) with GS1 being most alkaline (pH = 6.94), GS4 slightly more acidic (pH = 6.6) and GS3 being most acidic (pH = 5.71) (Figure

5a). This is expected since the Fossitt habitat classification includes soil pH in describing habitat type. Both GS1 and GS4 habitats differed significantly from the GS3 habitat however the difference between GS1 and GS4 was insignificant. Site 7 is exceptional as it is a GS4 habitat yet it had the highest average pH levels of all sites (pH = 8.24).

Figure 5c & d show the inorganic carbon content for sites and habitats. Site 7 is an unmanaged site that is in close proximity to alkaline fen habitat and has some areas of *Molinia* meadows (Annex habitat 6410). Although recorded as GS4, the site is becoming more akin to a GS2 habitat (dry and grassy verges) which often occurs in under-grazed sites. The high inorganic carbon content in these sites is likely due to carbonates as would be expected with its proximity to alkaline fen. The only other relevé outside of those from site 7, with significant inorganic carbon content was a relevé in site 2. Though site 2 was predominantly a GS1 habitat, relevé two was present in a very damp, under-grazed GS4 habitat. The vegetation, dominated by *Filipendula ulmaria* and graminoid species, is quite similar to that of site 7 relevé 2 and was also located near fen habitat.

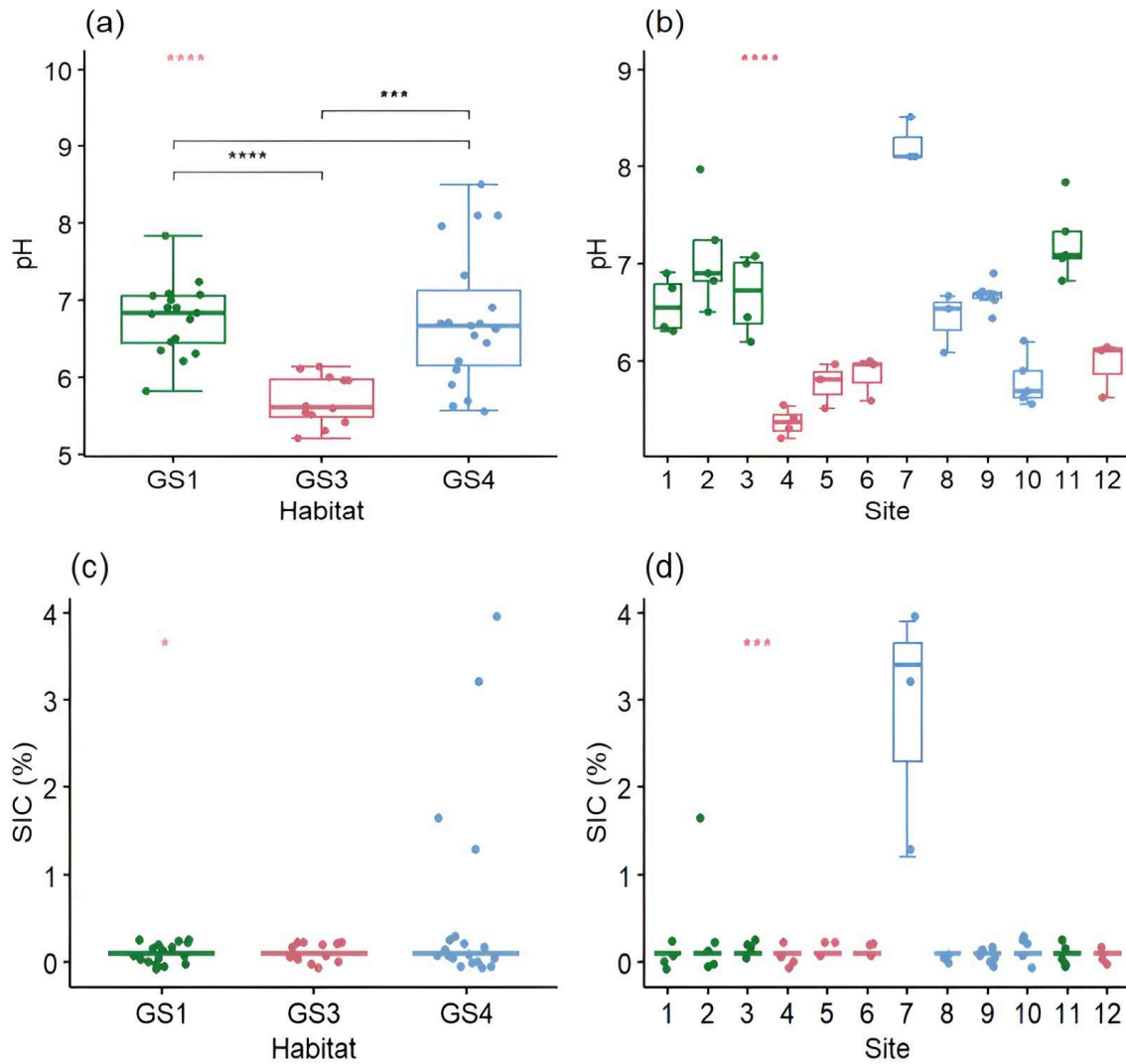


Figure 5. Differences in pH between habitat (a) and sites (b) as well as variation between habitat (c) and site (d) in soil inorganic carbon (SIC), ($N = 48$).

Habitats are categorised by the colouration of boxplots (GS1 = green, GS3 = red, GS4 = blue). The length of the box indicates the interquartile range. The band in the middle of the box represents the median value. The whiskers either side of each box indicate minimum and maximum values with values beyond these points considered outliers. Coloured dots represent data points (these points are scattered for visual purposes). The significance of the differences between categorical variables (Kruskal-Wallis) is indicated by the number of red asterisks in the top left corner ($p < 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$, $< 0.0001^{****}$) and the significance of differences between individual habitats (Wilcoxon test) is indicated by the black asterisks above the brackets linking each habitat type.

4.1.2 - Soil carbon and nitrogen content

Soil organic matter content differed significantly between sites ($p < 0.01$) but not between habitats. GS1 and GS4 differed significantly in their soils' organic matter content (Figure 6a). Site 12 had the highest organic matter content however there was a high amount of variability among the site 12 relevés. Site 10 had the lowest SOM content. GS1 sites had the highest average SOM content followed by GS3 and GS4. Though site 12 was exceptionally carbon rich compared to other GS3 sites, the average of the GS3 sites excluding site 12 was still higher than that of the GS4 sites.

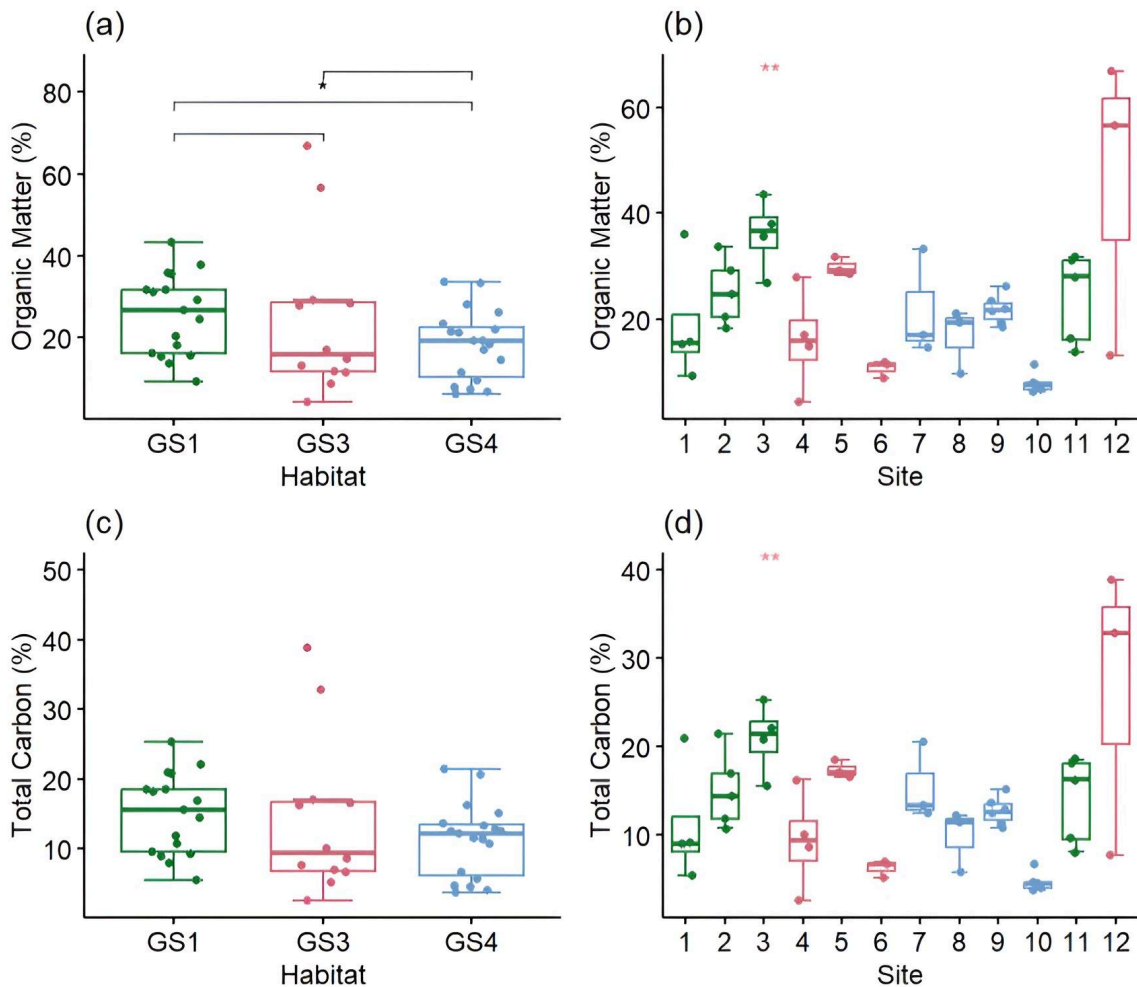


Figure 6. Differences in organic matter content between habitat (a) and sites (b) and differences in total carbon content between habitats (c) and sites (d), ($N = 48$).

Habitats are categorised by the colouration of boxplots (GS1 = green, GS3 = red, GS4 = blue). The length of the box indicates the interquartile range. The band in the middle of the box represents the median value. The whiskers either side of each box indicate minimum and maximum values with values beyond these points considered outliers. Coloured dots represent data points (these points are scattered for visual purposes). The significance of the difference between categorical variables (Kruskal-Wallis) is indicated by the number of red asterisks in the top left corner ($p < 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$, $< 0.0001^{****}$) and the significance of difference between individual habitats (Wilcoxon test) is indicated by the black asterisks above the brackets linking each habitat type.

Total nitrogen content differed significantly both between sites ($p < 0.001$) and habitat type ($p < 0.01$). Site 3 had the highest soil nitrogen concentration. Site 10 had the lowest soil nitrogen concentration. GS1 habitats had the highest average soil nitrogen concentration followed by GS3 and GS4. GS3 and GS4 habitats did not show significant differences in nitrogen content (Figure 7a). The ratio between soil carbon and nitrogen content was highest for GS3 habitats and differed significantly between all habitat types (Figure 7c). GS1 habitat had the lowest C:N ratio with very little variation across relevés.

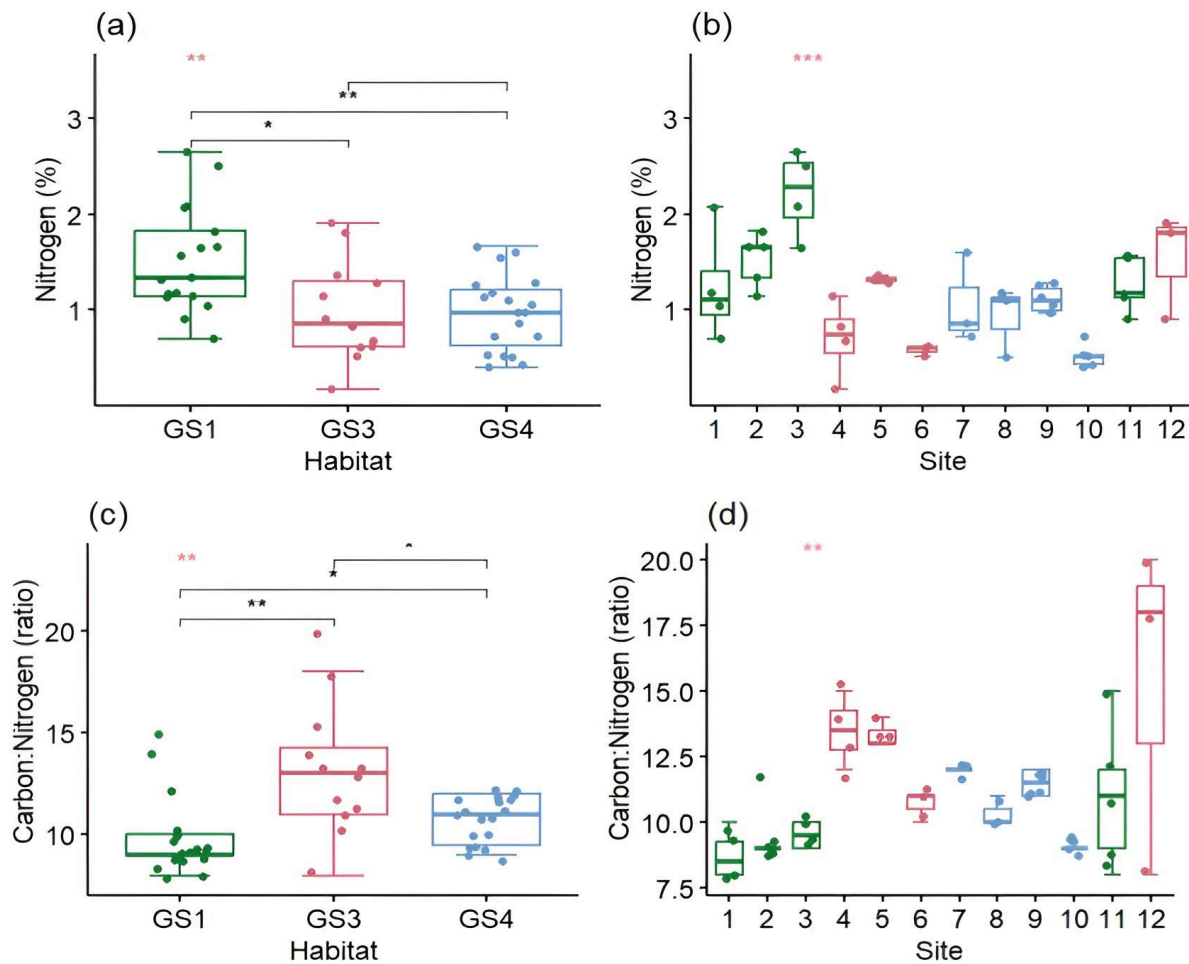


Figure 7. Differences in nitrogen (N) content between habitats (a) and sites (b) and differences in carbon nitrogen ratios (C:N) between habitats (c) and sites (d), ($N = 48$). Habitats are categorised by the colouration of boxplots (GS1 = green, GS3 = red, GS4 = blue). The length of the box indicates the interquartile range. The band in the middle of the box represents the median value. The whiskers either side of each box indicate minimum and maximum values with values beyond these points considered outliers. Coloured dots represent data points (these points are scattered for visual purposes). The significance of the difference between categorical variables (Kruskal-Wallis) is indicated by the number of red asterisks in the top left corner ($p > 0.05$, $< 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$, $< 0.0001^{****}$) and the significance of difference between individual habitats (Wilcoxon test) is indicated by the black asterisks above the brackets linking each habitat type.

4.2 - Above-ground net primary productivity (NDVI)

NDVI values differed significantly between sites ($p < 0.01$) and between habitat types ($p < 0.05$) (Figure 8). GS4 relevés had the highest average NDVI followed by GS3 and then GS1. GS4 was significantly different from both GS3 and GS1 habitats (Figure 9a). Site 3 and Site 12 (GS1 and GS3 respectively) had the lowest NDVI with site 9 and 10 (GS4) having the highest average NDVI values (Figure 8b).

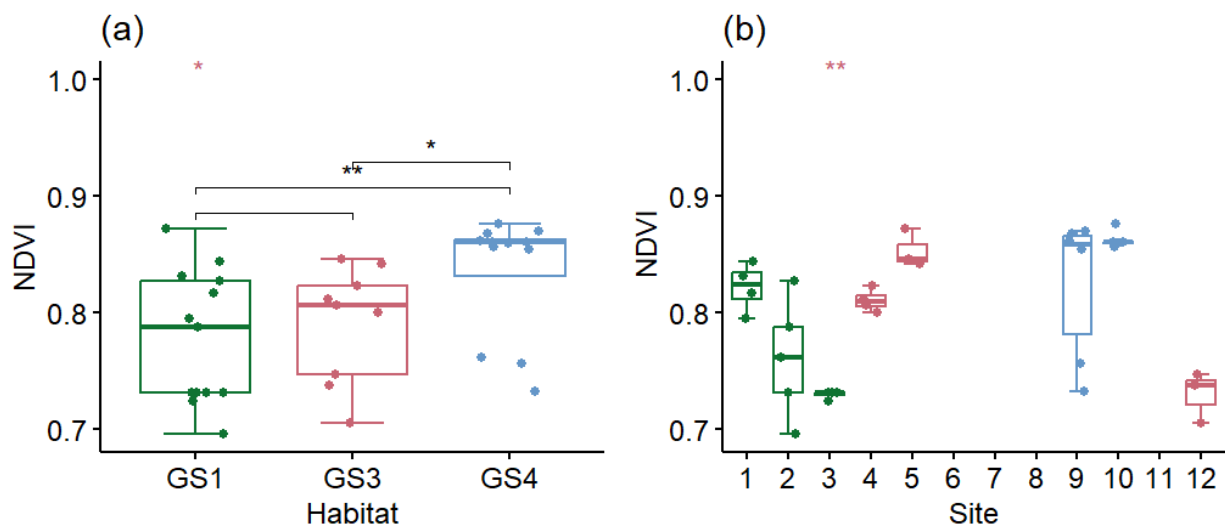


Figure 8. Differences in NDVI values between habitats (a) and sites (b), ($N = 30$).

The Fossitt habitat is indicated by the colouration of boxplots (GS1 = green, GS3 = red, GS4 = blue). The length of the box indicates the interquartile range. The band in the middle of the box represents the median value. The whiskers either side of each box indicate minimum and maximum values with values beyond these points considered outliers. Coloured dots represent data points (these points are scattered for visual purposes). The significance of the difference between categorical variables (Kruskal-Wallis) is indicated by the number of red asterisks in the top left corner ($P > 0.05$, $< 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$, $< 0.0001^{****}$) and the significance of difference between individual habitats (Wilcoxon test) is indicated by the black asterisks above the brackets linking each habitat type.

4.3 - Root length density

Root length density (RLD) could not be measured for GS1 relevés as soil depths were consistently shallow. Root length density (RLD) differed between the soil cores taken from the GS3 and GS4 sites (Figure 9). Soil depth was highly variable and many relevés had soil depths of 10 cm or less. Therefore, values for RLD that were comparable for all quadrats were limited to the first 10 cm. Site 7 had the greatest variation in RLD in sampled soil cores which is likely due to the stark differences in vegetation composition between relevés. RLD varied significantly between the GS3 and GS4 habitats with GS3 sites having an average RLD of 17 roots cm^{-2} compared to 10 roots cm^{-2} in GS4 sites. GS3 sites also varied more in their RLD values, whereas GS4 sites had consistently low RLD. Site 5 (GS3) had consistently high RLD density with increasing soil depth. Site 12 (GS3) also had high RLD at lower depths though to a lesser degree.

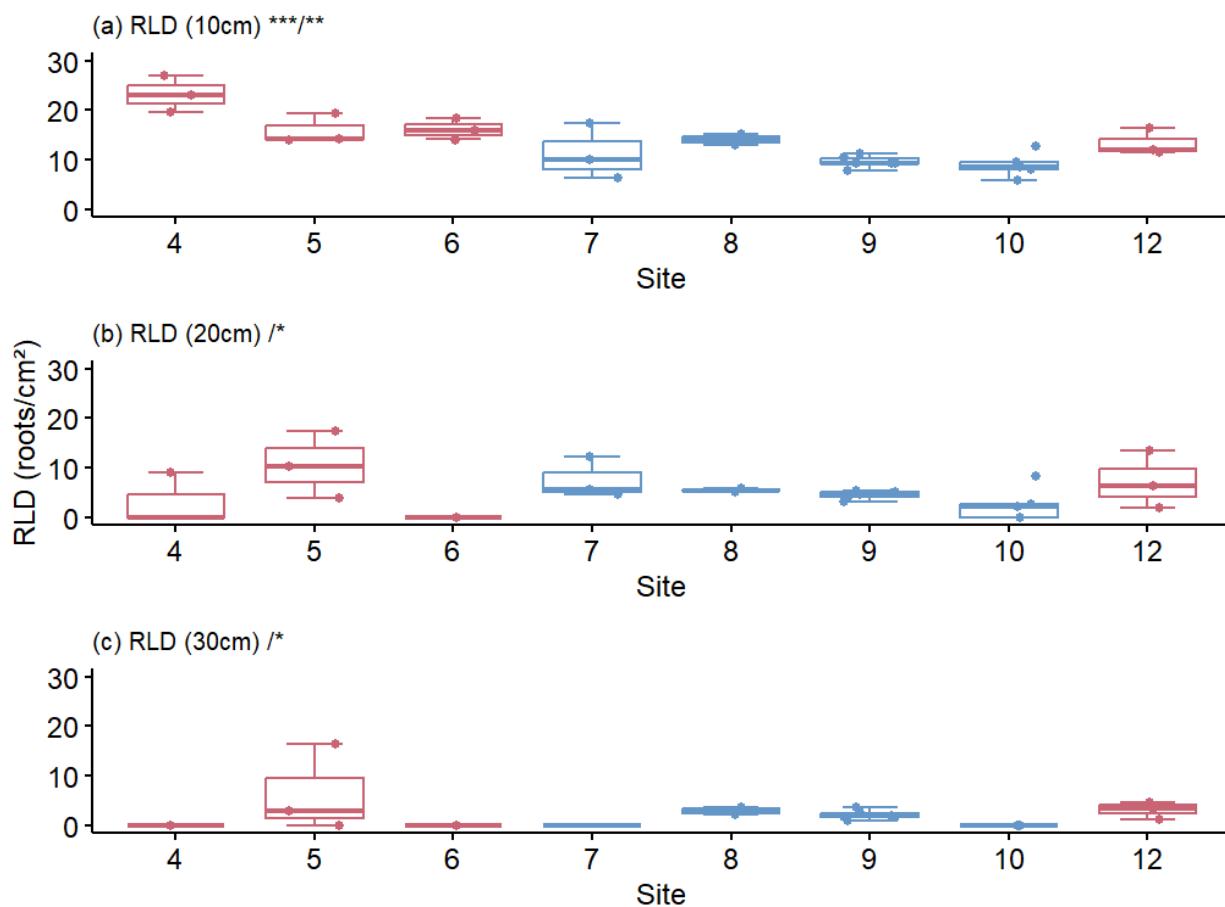


Figure 9. Differences in root length density for site, ($N = 28$).

The box plots show RLD at different soil depths, 10 cm (a), 20 cm (b) and 30 cm (c). The Fossitt habitat is indicated by the colouration of boxplots (GS3 = red, GS4 = blue). The length of the box indicates the interquartile range. The black band in the middle of the box represents the median value. The whiskers either side of each box indicate minimum and maximum values and the white dots indicate outlier values. The significance of difference in RLD values between sites and habitat types is indicated in the titles where asterisks represent significance values ($p < 0.05$ = blank, $< 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$, $< 0.0001^{****}$) for habitat/sites.

4.4 - Leaf traits

The three grassland habitat types showed significantly different abiotic conditions. This suggests that the habitats differ in terms of the stresses imposed on vegetation communities. This should therefore lead to significant differences in plant functional traits and strategies as such traits are heavily influenced by environmental conditions.

4.4.1 - Intraspecific variation in leaf traits

Differences in functional traits found within species were measured using the coefficient of variation (CV) measurement which is a standardised measure of the variation found for each species among different vegetation communities. For this reason singleton species were not included. Figure 10a illustrates that leaf area was the most variable trait seen among grassland species. The two species with the most variable leaf area were high productivity grass species *Lolium perenne* and *Cynosorus cristatus*. After these are two large leaf forbs that are common in GS4 grasslands (*Filipendula ulmaria* and *Ranunculus repens*). Following them are a number of forbs and grass species common to GS1 and GS4 grasslands. No sedge or rush species, or any species common to GS3 grasslands, showed such high variability in leaf area. Forb species were, on average, more variable in their leaf area than graminoids.

The species with the highest amount of SLA variation were predominantly acid grassland species such as *Elyochaeis multicaulis*, *Galium saxatile*, *Festuca rubra* (Figure 10b). *Galium verum*, a species found only in the GS1 communities, also showed very high SLA variation. Forb species tended to be more variable in their specific leaf area in comparison to graminoids.

Leaf dry matter content was the least variable plant trait among species (Figure 10c). *Galium saxatile*, a common species in GS3 communities, showed the greatest variation in LDMC. Other species associated with the GS3 habitat, such as *Potentilla erecta*, *Sesleria caerulea*, *Agrostis canina* and *Festuca rubra*, showed similarly high LDMC variation. Both forb and graminoid species showed similar variation in LDMC values.

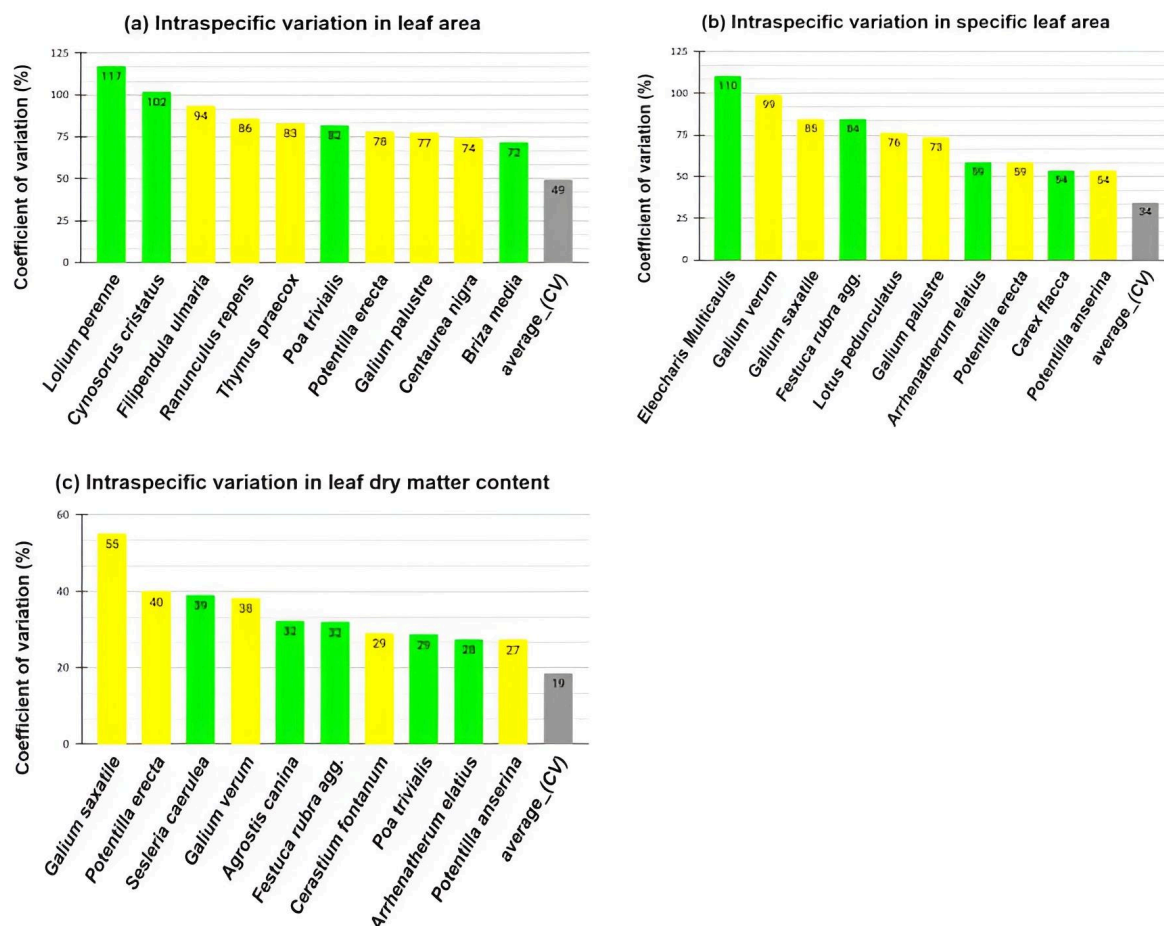


Figure 10. Intraspecific variation in leaf area, specific leaf area and leaf dry matter content.

Intraspecific variation in leaf area (a), specific leaf area (b) and leaf dry matter content (c). Intraspecific variation is measured by the coefficient of variation (CV) which provides a standardised value for variation within a species across relevés. The ten species present are the species with highest CV values and the eleventh grey value is the average CV value among all species. Species are colour coded green for graminoid species and yellow for forb species.

4.4.2 - Leaf area

Community weighted mean Leaf area (CWM-LA) values did not have a normal distribution across all relevés and lacked even variance between habitats and sites. Therefore a Kruskal-Wallis test was performed. The test indicated a significant difference in CWM-LA between sites. A Wilcoxon test performed post Kruskal-Wallis test showed that Site 7 differed most significantly from other sites. Site 7 had the highest mean leaf area with the highest CWM-LA value measured from an unmanaged, fen-like, GS4 relevé. Site 7 also had the highest amount of variance between its relevés. Site 6 had the smallest average CWM-LA. A significant difference was also found in CWM-LA values between habitat types. Figure 11 shows that GS4 habitat had the highest leaf area followed by GS1 and GS3. A Wilcoxon test between habitat types (Figure 11a) indicated that all habitats differed significantly from each other with the GS4 and GS3 habitats differed most significantly in terms of leaf area. GS3 habitats had the lowest amount of variance between relevés with site 12 having the most consistent CWM-LA values across the site.

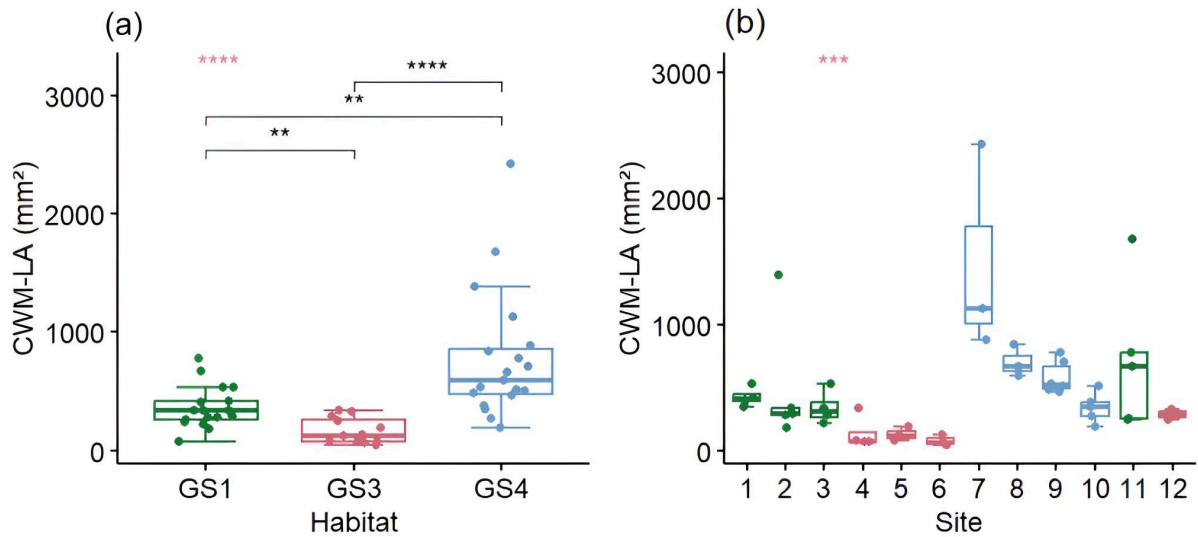


Figure 11. Differences in community weighted mean leaf area between habitats (a) and sites (b), ($N = 48$).

The Fossitt habitat is indicated by the colouration of boxplots (GS1 = green, GS3 = red, GS4 = blue). The length of the box indicates the interquartile range. The band in the middle of the box represents the median value. The whiskers either side of each box indicate minimum and maximum values with values beyond these points considered outliers. Coloured dots represent data points (these points are scattered for visual purposes). The significance of the differences between categorical variables (Kruskal-Wallis) is indicated by the number of red asterisks in the top left corner ($p > 0.05$, $< 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$, $< 0.0001^{****}$) and the significance of difference between individual habitats (Wilcoxon test) is indicated by the black asterisks above the brackets linking each habitat type.

4.4.3 - Specific leaf area

The CWM-SLA values showed a normal distribution across relevés. Variance within sites and habitats, however, were uneven, therefore making ANOVA unsuitable for analysis of variance. A Kruskal test found no significant differences on the site and habitat scale for CWM-SLA. In the case of inter-site variation (Figure 12) this is likely due to large within site variability. Site 5 had the highest levels of variation while site 8 had even CWM-SLA values across all relevés (Figure 12c). GS3 habitats had the greatest range in values with the lowest

average values found in site 12 and the highest values found in site 5. The GS4 relevés had the least variation in CWM-SLA. The highest average CWM-SLA was found in GS1 habitats (Figure 12a).

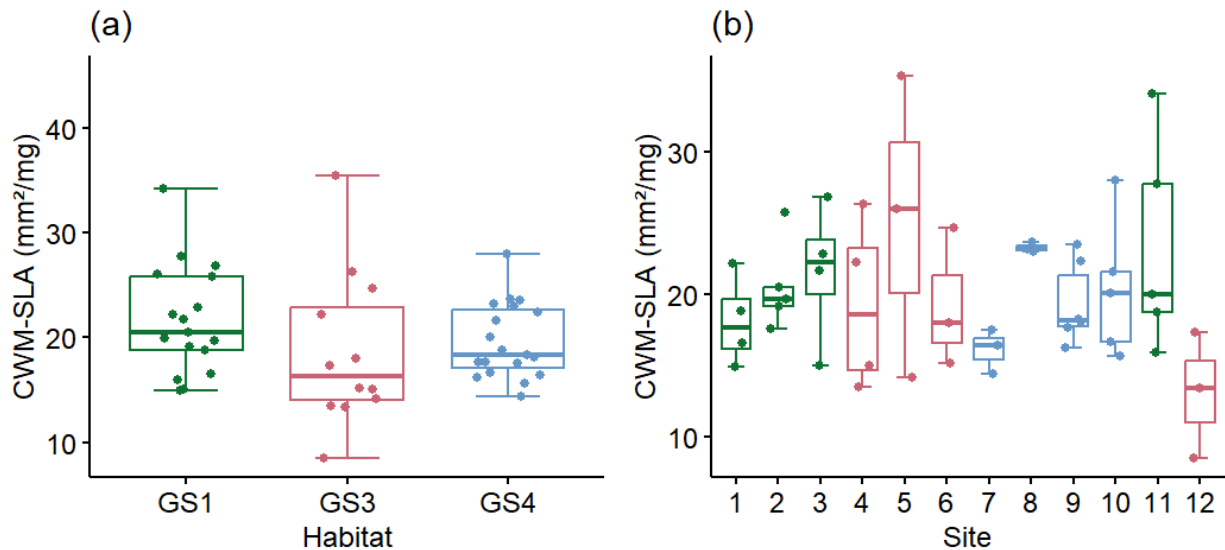


Figure 12. Differences in community weighted mean specific leaf area between habitats (a) and sites (b), ($N = 48$).

The Fossitt habitat is indicated by the colouration of boxplots (GS1 = green, GS3 = red, GS4 = blue). The length of the box indicates the interquartile range. The band in the middle of the box represents the median value. The whiskers either side of each box indicate minimum and maximum values with values beyond these points considered outliers. Coloured dots represent data points (these points are scattered for visual purposes).

4.4.4 - Leaf dry matter content

A Shapiro test was performed to assess the distribution of CWM-LDMC values across all sites and the results indicated normality. Uneven levels of variance were found between habitat types and sites, breaking the assumptions of an ANOVA test. Therefore, a Kruskal-Wallis test was performed and significant differences were found in CWM-LDMC values between sites and habitats (Figure 13). The boxplot in Figure 13b, suggests that site 12 is the biggest outlier in terms of average CWM-LDMC values (which is also suggested by

a Wilcoxon test). GS3 habitats had the highest level of variation in values with the highest average values in site 12 and the lowest in site 5. GS4 sites consistently had the lowest average values.

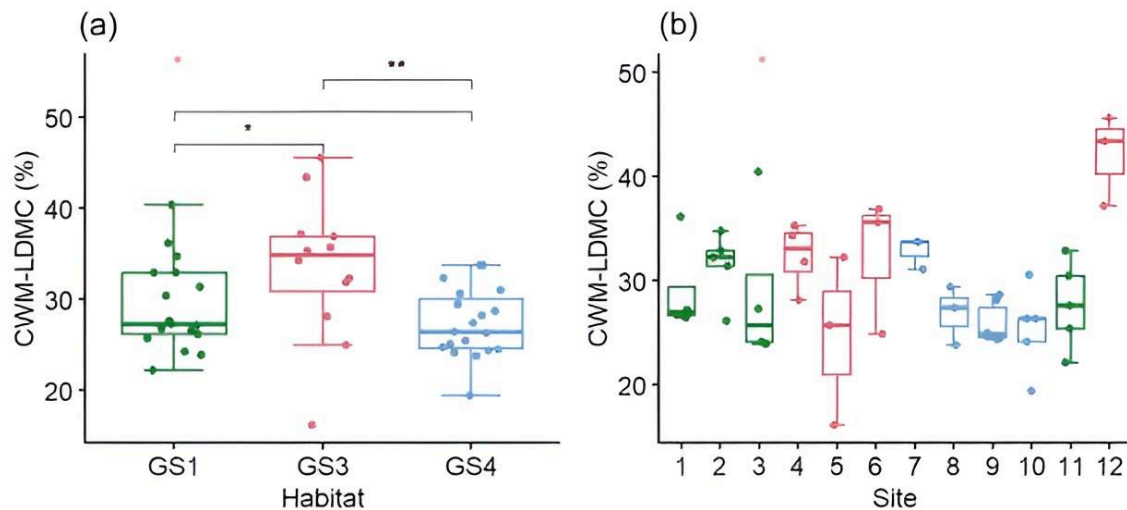


Figure 13. Differences in community weighted mean leaf dry matter content between habitats (a) and sites (b), ($N = 48$).

The Fossitt habitat is indicated by the colouration of boxplots (GS1 = green, GS3 = red, GS4 = blue). The length of the box indicates the interquartile range. The band in the middle of the box represents the median value. The whiskers either side of each box indicate minimum and maximum values with values beyond these points considered outliers. Coloured dots represent data points (these points are scattered for visual purposes). The significance of the differences between categorical variables (Kruskal-Wallis) is indicated by the number of red asterisks in the top left corner ($p > 0.05$, $< 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$, $< 0.0001^{****}$) and the significance of differences between individual habitats (Wilcoxon test) is indicated by the black asterisks above the brackets linking each habitat type.

4.4.5 - Leaf chlorophyll content

CWM-LCC SPAD values did not show a normal distribution therefore a Kruskal Wallis test was performed to assess variation between site and habitat types. The Kruskal Wallis test did

not show significant inter-site and inter-habitat differences however a Wilcoxon test found significant differences in CWM-LCC SPAD values between GS3 and GS4 relevés (Figure 14a). Site 8 had the highest average LCC values at 44 SPAD units while site 6 had the lowest at 28 (Figure 14b). Site 4 had the greatest amount of variation in CWM-LCC levels between relevés whereas site 7 had the most consistent values across all relevés. The GS4 habitat had the highest average CWM-LCC values. GS1 and GS3 were similar however GS3 grasslands had the lowest average CWM-LCC.

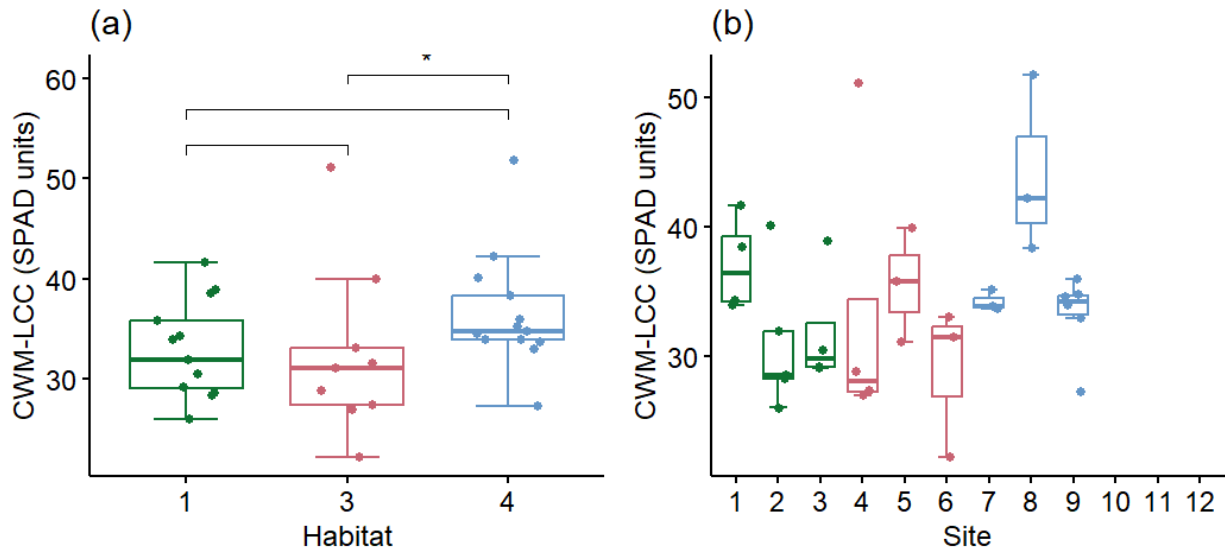


Figure 14. Differences in community weighted mean leaf chlorophyll content between habitats (a) and sites (b), ($N = 35$).

The Fossitt habitat is indicated by the colouration of boxplots (GS1 = green, GS3 = red, GS4 = blue). The length of the box indicates the interquartile range. The band in the middle of the box represents the median value. The whiskers either side of each box indicate minimum and maximum values with values beyond these points considered outliers. Coloured dots represent data points (these points are scattered for visual purposes). The significance of differences between individual habitats (Wilcoxon test) is indicated by the number of black asterisks above the brackets linking each habitat type ($p > 0.05$, $< 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$, $< 0.0001^{****}$).

4.5 - Plant strategies

4.5.1 - Species analysis

The points on the ternary diagram below (Figure 15) are measures of relative CSR strategy derived by taking average, non-weighted functional trait values for each species and using the StrateFy tool to derive percentages of competitiveness (C), stress tolerance (S) and ruderality (R). This diagram illustrates the disparity of functional strategy between individual species. The more stress tolerant, less competitive species are mainly graminoid and heath scrub species with a few hardy, small leaved perennial forbs (*Thymus praecox*, *Galium verum*). Ruderal species appear to be perennial herbs with more succulent leaves (*Bellis perennis*, *Lotus pedunculatus*, *Mentha aquatica*, *Potentilla reptans*). The most competitive species (with the exception of *Iris pseudocorus*) are mainly forb species with large basal rosettes (*Cirsium palustre*, *Plantago lanceolata*, *Centaurea nigra*, *Jacobea vulgare*, *Hypochaeris radicata*).

If the consideration of intraspecific phenotypic plasticity is excluded, the communities in which species with strong strategy preferences are at high abundance should also present the same functional strategy. For example, competitive species such as *Cirsium palustre*, *Centaurea nigra*, *Plantago lanceolata* and *Iris pseudocorus*, are usually abundant in GS4 grasslands which, as noted previously, appear to be the most competitive habitat of the three.

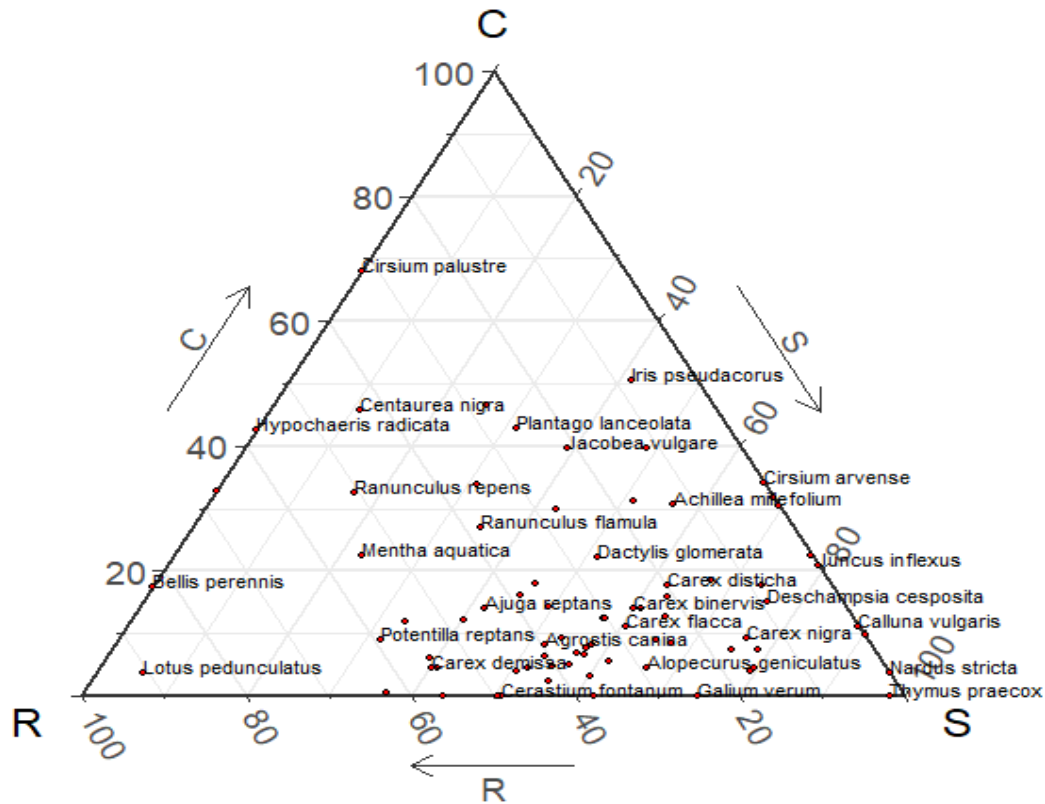


Figure 15. CSR strategy of each species based on average leaf trait values, ($N = 90$).

The ternary diagram above illustrates the wide range of strategies among the grassland species. The values were calculated by averaging the trait values of each species across all sites. StrateFy was then used to transform these leaf trait values into CSR strategies. Each red dot is a species with the corresponding species name present directly to its right.

4.5.2 - CSR and grassland habitats

Figure 16 below provides a visual representation of the dominant strategies present in all the vegetation communities surveyed. The strategies were measured using community weighted mean values of leaf traits (CWM-LA for C, CWM-SLA for R and CWM-LDMC for S). It is clear from the ternary diagrams that all habitats had predominantly stress tolerant species. GS3 had communities that range widely on the stress tolerance-ruderality axis; however competitiveness does not appear too prevalent in these communities (Figure 16b). One

relevé in site 5 (GS3) was calculated at 90% ruderal in strategy (with 0% stress tolerance). This vegetation community consists of only three species above 3% cover, all of which are generalist grass species (*Anthoxanthum odoratum*, *Holcus lanatus* and *Agrostis capillaris*). The vegetation community with the highest stress tolerance value was the first relevé in site 12 (GS3). This community was dominated by sedge and heather species and, when analysed using the Irish vegetation classification system (IVC), appears more similar to a HE4B community which is a transient vegetation community somewhere between grassland and heathland and, as a commonage site, may well be under grazed. The GS4 communities tended not to vary in terms of community strategy with the exception of a community in site 10 (Figure 16c). This site was the first surveyed and some grass species were not yet present, however such species would likely be more stress tolerant and would tip the overall community strategy in that direction. GS1 and GS4 grassland communities had similar strategies with GS4 vegetation being slightly more competitive (Figure 16a). The competitiveness strategy differed significantly between the three habitats ($p < 0.0001$) (Figure 16d). GS4 communities were the most competitive followed by GS1 and GS3. Significant differences were also found in stress tolerance strategy with GS3 being the most stress tolerant followed by GS1 and GS4 (Figure 16e). Ruderality did not differ significantly between habitat types (Figure 16f).

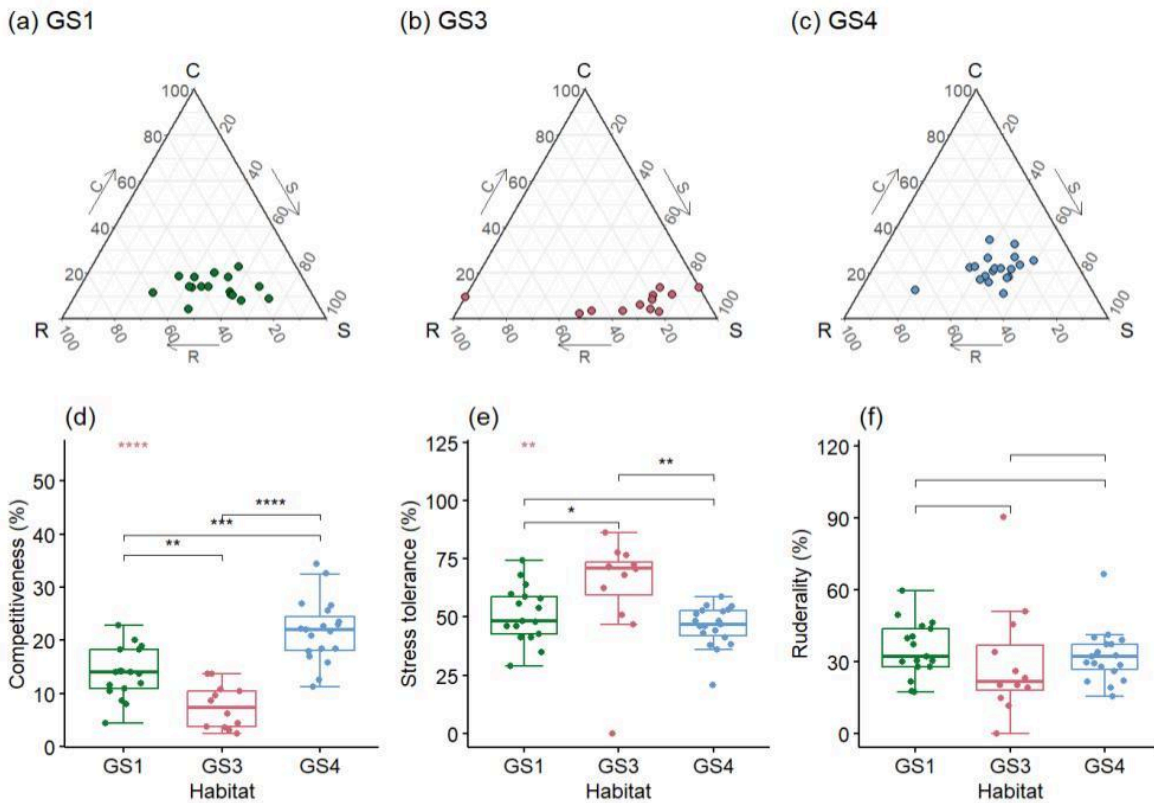


Figure 16. CSR strategies in each habitat type and variation in community strategies between habitats, (N = 48).

The ternary diagrams (a, b & c) illustrate the strategies for all relevés in GS1, GS3 and GS4 habitats respectively. In the boxplots below (d, e & f) The Fossitt habitat is indicated by the colouration of boxplots (GS1 = green, GS3 = red, GS4 = blue). The length of the box indicates the interquartile range. The band in the middle of the box represents the median value. The whiskers either side of each box indicate minimum and maximum values with values beyond these points considered outliers. Coloured dots represent data points (these points are scattered for visual purposes). The significance of the differences between categorical variables (Kruskal-Wallis) is indicated by the number of red asterisks in the top left corner ($p > 0.05$, $< 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$, $< 0.0001^{****}$) and the significance of differences between individual habitats (Wilcoxon test) is indicated by the black asterisks above the brackets linking each habitat type.

4.6 - Above-ground vs below ground traits

Root length density (at 10 cm depth) showed a significant negative relationship with community weighted mean leaf area ($p = 0.002$). Root length density at 10 cm sharply decreased with increasing leaf area in GS3 grasslands (Figure 17a). Interestingly, in GS3 habitat, RLD at 20 cm showed a significant positive relationship with CWM-LA ($p = 0.051$) (Figure 17b). GS4 sites showed no correlation between RLD and CWM-LA. Specific leaf area showed no correlation with root length density overall but in GS3 relevés, the positive correlation between RLD-10 and CWM-SLA was near significant ($p = 0.071$) (Figure 17c). At a depth of 10 cm, CWM-LDMC showed an overall near significant positive correlation with root length density at 10cm (Figure 17e), however this pattern was not apparent within the habitat types.

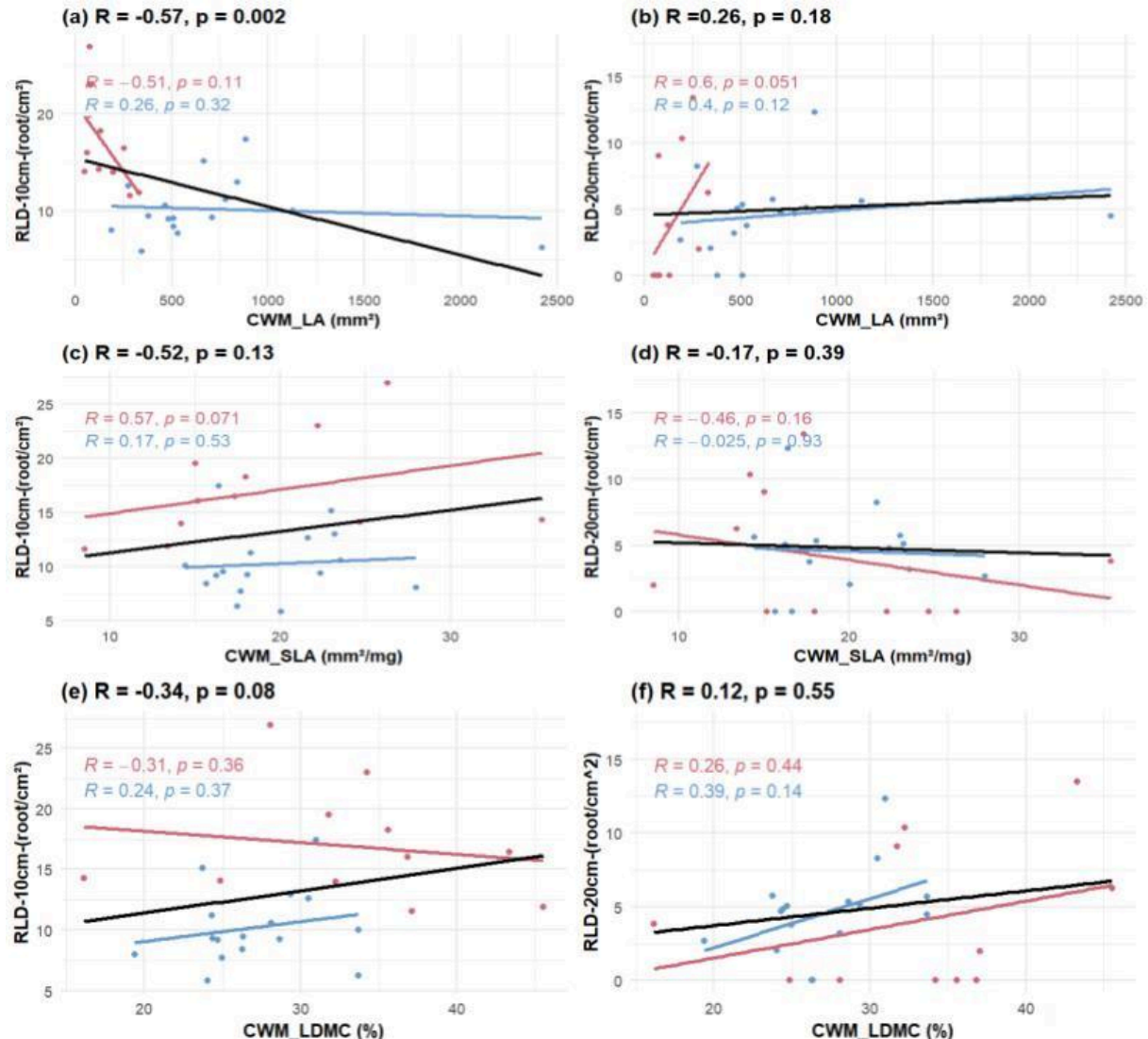


Figure 17. Relationship between community weighted mean leaf traits and root length density, ($N = 28$).

Relationship between the below-ground RLD measurements at 10cm and 20cm soil depth and above-ground CWM-LA (a & b), CWM-SLA (c & d), CWM-LDMC (e & f). The overall regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests. Data points present relevés with the same colour associations as the linear model lines.

4.7 - Functional diversity

The functional diversity metrics measured were based on the three leaf trait measurements for each vegetation community. These metrics include functional richness, Rao's quadratic entropy (Rao's quadratic diversity), functional redundancy, functional divergence, functional dissimilarity and functional evenness.

4.7.1 - Functional richness, evenness and divergence

Functional richness (FRic) differed significantly between the three grassland habitats. The non-parametric Kruskal-Wallis provided significant results for inter-site and habitat differences (Figure 18a). Further post-hoc analysis was performed using a Wilcoxon test and found that a significant difference in FRic was found between GS3 and the two other grassland habitats; however no significant difference was observed between GS1 and GS4 (Figure 18a). GS4 grassland was most significantly different from GS3 despite GS1 having the highest average FRic. GS1 grassland showed the greatest variation in the functional richness of its vegetation communities particularly in site 3 (Figure 18b). A Kruskal-Wallis test found no significant difference in FEve or FDiv values between grassland habitats and sites (Figure 18).

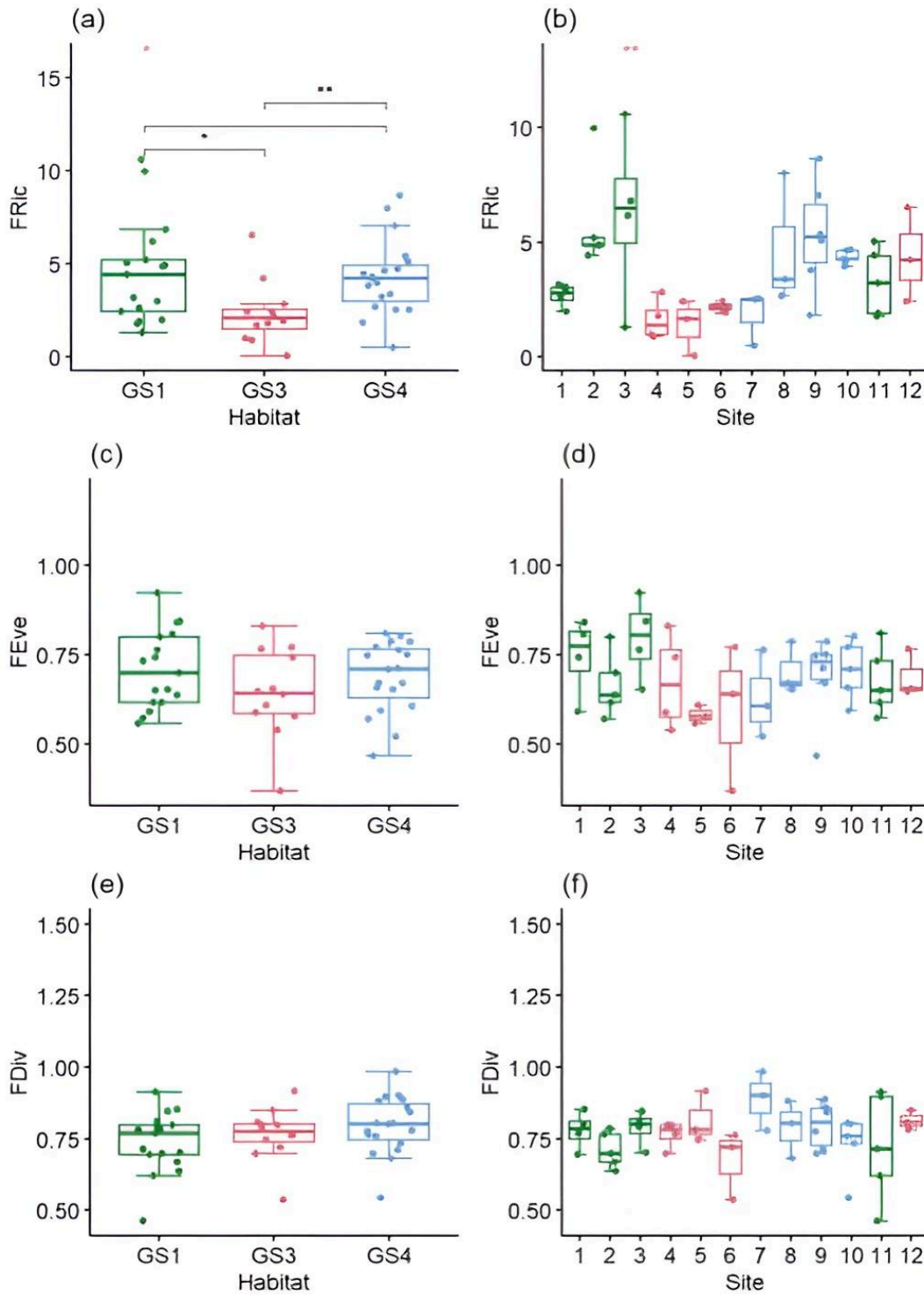


Figure 18. Difference in community functional richness (FRic) (a & b), functional evenness (FEve) (c & d) and functional divergence (e & f) between habitats and sites, ($N = 48$).

The Fossitt habitat is indicated by the colouration of boxplots (GS1 = green, GS3 = red, GS4 = blue). The length of the box indicates the interquartile range. The band in the middle of the box represents the median value. The whiskers either side of each box indicate minimum and maximum values with values beyond these points considered outliers. Coloured dots represent data points (these points are scattered for visual purposes). The significance of the difference between categorical variables (Kruskal-Wallis) is indicated by the number of red asterisks in the top left corner ($p > 0.05$, $< 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$, $< 0.0001^{****}$) and the significance of differences between individual habitats (Wilcoxon test) is indicated by the black asterisks above the brackets linking each habitat type.

4.7.2 - Rao's quadratic entropy and functional redundancy

The measurement of Rao's quadratic entropy (FDq) did not differ significantly between habitats or sites. There was little variation found within sites and habitats for FDq (Figure 19a, b) with very few outlier values. The consistency of FDq metrics across sites and habitats suggests an absence of any trends in this functional diversity metric. The functional redundancy (FRed) did not differ significantly across all habitats however it did differ significantly across sites (Figure 19c, d). A Wilcoxon test also showed that there was significant difference in FRed between GS1 and GS3 vegetation communities. Site 5 had the lowest amount of FRed with site 1, 2 and 3 all having high FRed values. GS4 sites had similarly high FRed values with the exception of site 7 that had little functional redundancy.

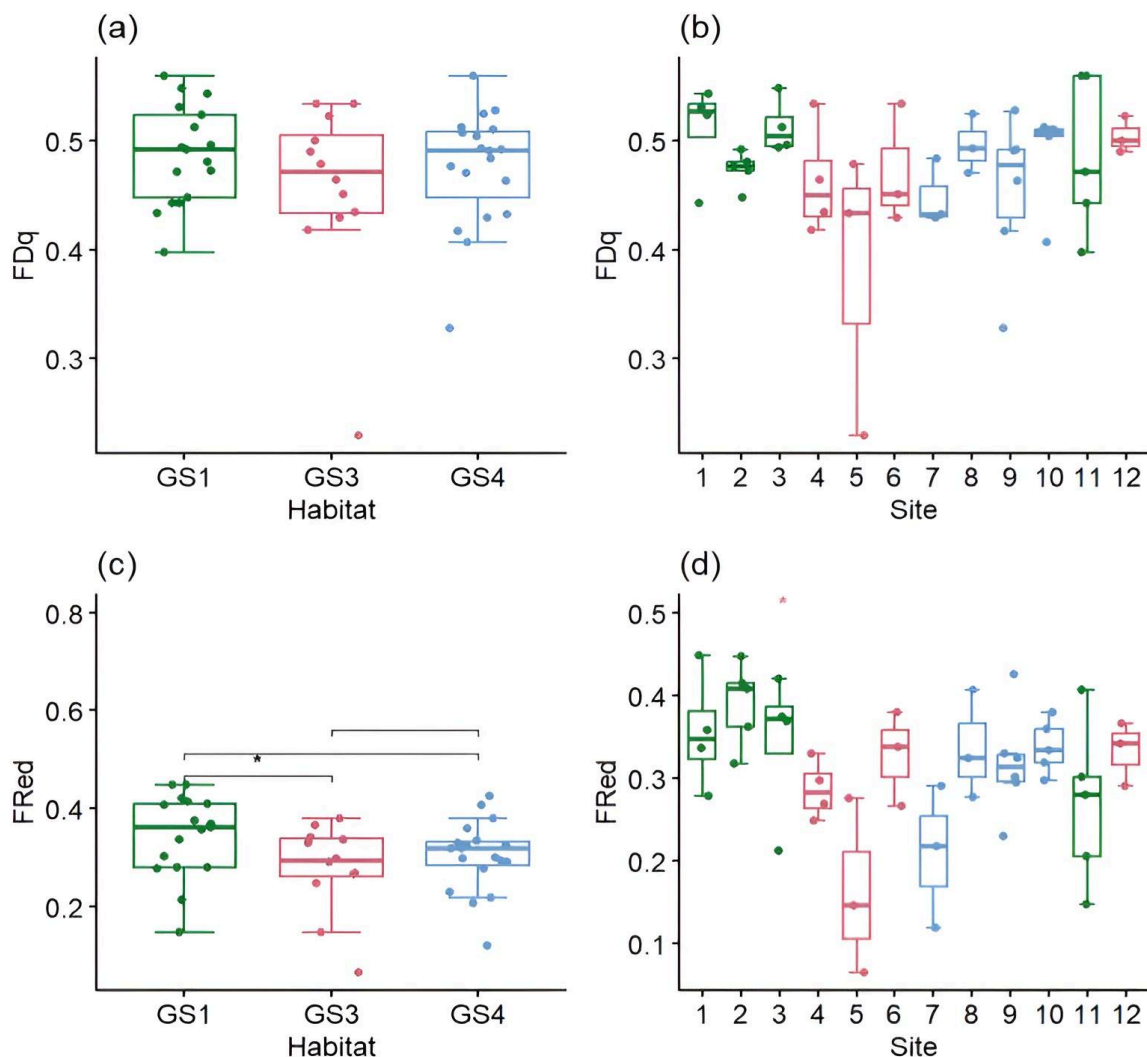


Figure 19. Differences in Rao's functional diversity (FDq) (a & b) and functional redundancy (FRed) (c & d) between habitats and sites, ($N = 48$).

The Fossitt habitat is indicated by the colouration of boxplots (GS1 = green, GS3 = red, GS4 = blue). The length of the box indicates the interquartile range. The band in the middle of the box represents the median value. The whiskers either side of each box indicate minimum and maximum values with values beyond these points considered outliers. Coloured dots represent data points (these points are scattered for visual purposes). The significance of difference between categorical variables (Kruskal-Wallis) is indicated by the number of red asterisks in the top left corner ($p > 0.05$, $< 0.05^*$, $< 0.01^{**}$, $< 0.001^{***}$, $< 0.0001^{****}$) and the significance of difference between individual habitats (Wilcoxon test) is indicated by the black asterisks above the brackets linking each habitat type.

4.8 - Association of functional diversity metrics and functional strategies with habitat

FDiv appears to increase in opposite direction to the other functional diversity metrics with GS4 and GS3 sites having higher levels of functional divergence (Fig. 20). The GS4 sites had the greatest competitiveness. Functional richness was most associated with the GS1 and GS4 habitats. FRed, FEve, FDq and ruderality were more associated in GS1 habitats. Functional evenness (FEve) and Rao's functional diversity were greatest in GS1 grasslands. Stress tolerance was more associated with GS3 habitats.

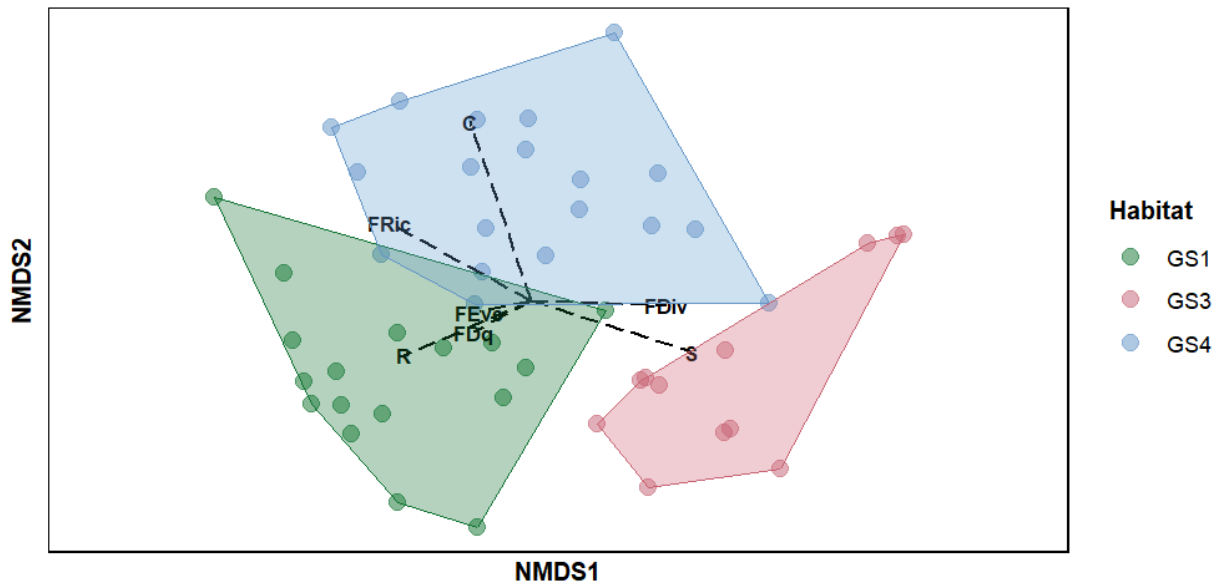


Figure 20. Relationship between functional diversity metrics, CSR strategies and the three grassland habitats, ($N = 48$).

This ordination plot is based on non-metric multidimensional scaling (NMDS) where patterns in species abundances in each relevé are analysed. The two axes that explain most of the variation in abundances are plotted here (NMDS1 & NMDS2). The data points represent individual relevés and are coloured based on their Fossitt habitat. The area of multidimensional space taken up by each habitat is represented by the convex hulls, each of which are also coloured based on habitat. The dotted lines represent the functional diversity metrics with the direction of the line indicating the directionality of the vector (i.e. higher FDiv

in GS3 relevés) and with the length of each line indicating how strongly the FD metric correlates with the ordination axes.

4.9 - Functional traits and variations in soil pH

4.9.1 - Leaf traits and soil pH

An overall correlation of increased CWM-LA with soil pH is apparent and was statistically significant ($p < 0.001$) (Figure 21a). Each habitat also shared this pattern though GS4 had the only statistically significant correlation ($p = 0.015$). The repeated pattern in each habitat removes the possibility of the correlation between CWM-LA and pH only being present due to discrepancies between the habitat types (which are apparent as seen in the boxplots previously). The CWM-SLA values do not correlate significantly with soil pH across or within habitat types (Figure 21b). In the case of CWM-LDMC (Figure 21c), no overall correlation exists with soil pH but GS4 grasslands have a strong pattern of increasing CWM-LDMC with soil alkalinity ($p = 0.0061$). GS3 has the same pattern, but this was insignificant. GS1 grassland appears to be uninfluenced by soil pH in this regard. In fact, the leaf traits of plants in GS1 grasslands appear to be completely unaffected by soil pH variation.

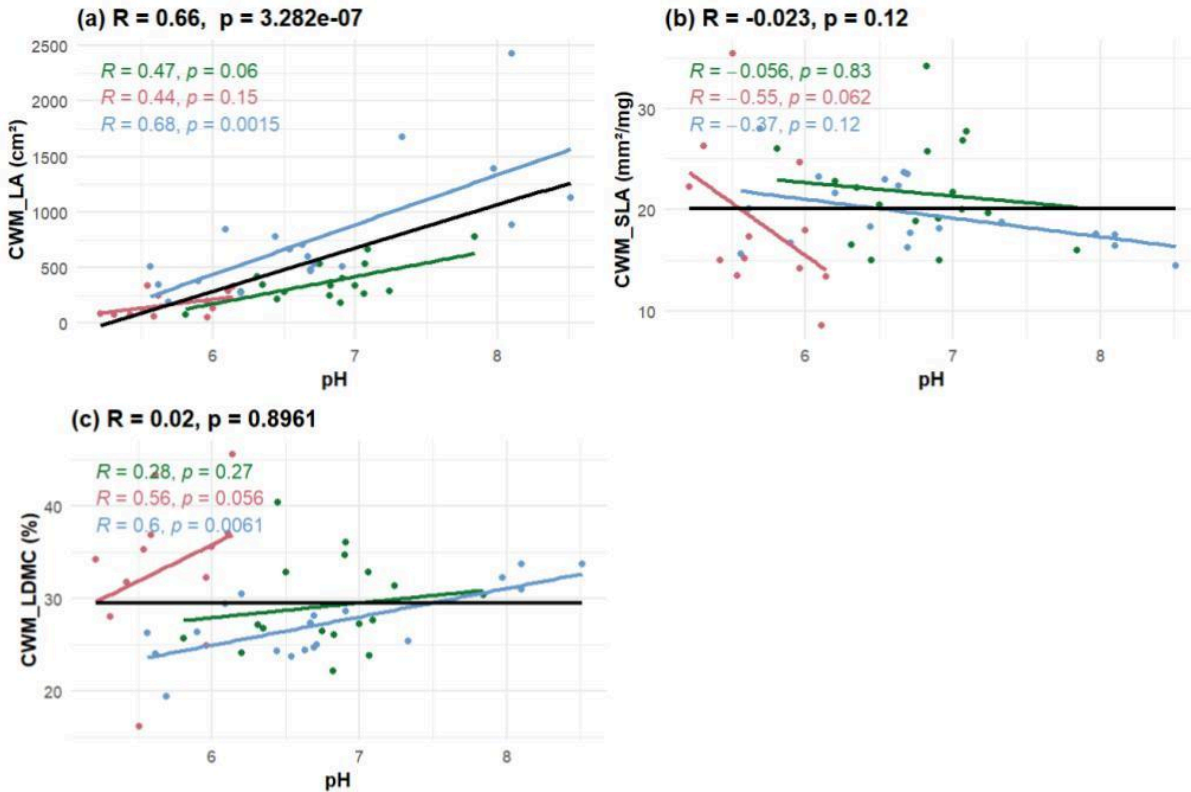


Figure 21. Relationship between community weighted mean leaf traits with soil pH, ($N = 48$).

Relationship between CWM-LA (a), CWM-SLA (b) and CWM-LDMC (c) with soil pH. The overall regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests with the same colour associations as the linear model lines. Data points, representing relevés, are also coloured based on habitat.

4.9.2 - Root traits and soil pH

While communities in GS3 and GS4 habitats show an above-ground increase in leaf area and dry matter content with soil pH, the root length density at 10 cm depth had a significant negative correlation with soil pH ($p = 0.01$) (Figure 22a). The overall pattern suggests that root length densities were higher for communities in more acidic soils; however this pattern is only evident within GS3 grasslands ($p = 0.0027$) whereas GS4 grasslands showed no

correlation. At 20 cm soil depth a positive relationship existed between RLD and pH (Figure 22b). This correlation was significant in the case of GS4 relevés ($p = 0.024$).

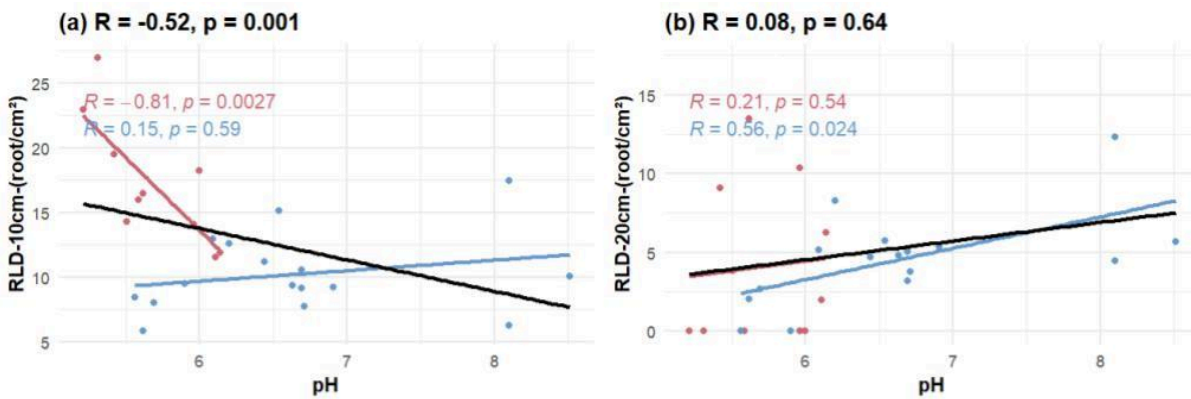


Figure 22. Relationship between root length density with soil pH, ($N = 28$).

Relationship between RLD at 10cm (a) and 20cm (b) with soil pH. The overall regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests with the same colour associations as the linear model lines. Data points, representing individual relevés, are also coloured based on habitat.

4.9.3 - Functional diversity metrics and soil pH

None of the relationships between pH and functional diversity were significant across all habitats (Figure 23). GS4 grasslands showed a significant negative correlation between pH and functional evenness ($p = 0.00075$) and functional redundancy ($p = 0.015$) (Figure 23b, e).

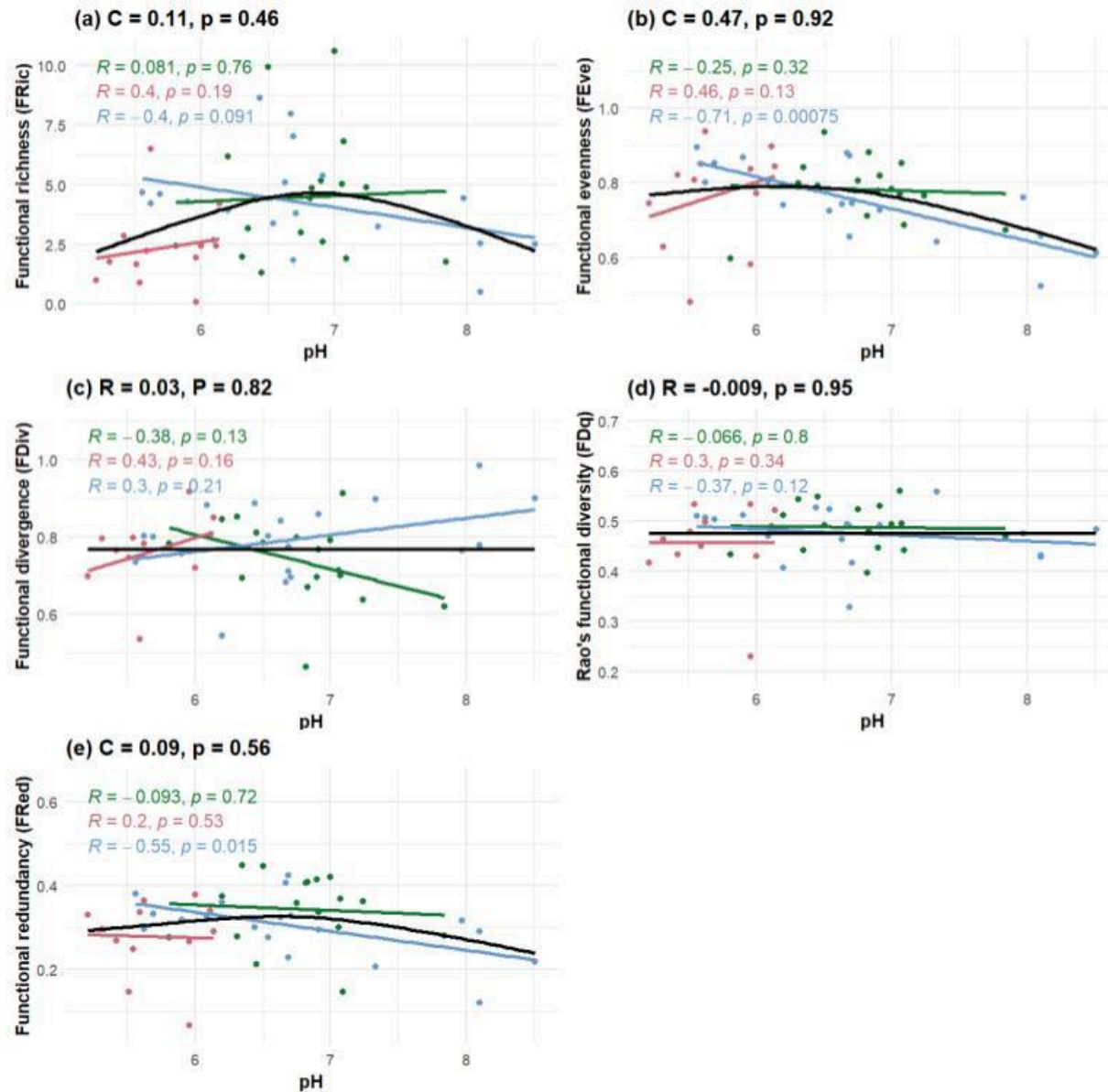


Figure 23. Relationship between functional diversity metrics and soil pH, ($N = 48$).

Relationship between soil pH and Functional richness (a), functional evenness (b), functional divergence (c), Rao's functional diversity (d) and functional redundancy (e). The overall linear regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests. When the line of best fit appeared nonlinear, a nonlinear correlation analysis was performed instead. Data points, representing individual relevés, are also coloured based on habitat.

4.9.4 - Species diversity and pH

All species richness metrics were highest at neutral pH (6-7 pH) (Figure 24). Simpson evenness showed a negative correlation with pH (Figure 24c). This was significant in both GS4 and GS3 relevés ($p = 0.00072$ and 0.044 respectively). GS4 communities, which were generally more alkaline, showed a negative correlation between Shannon diversity and pH ($p = 0.0013$) (Figure 24b). GS3 communities, which were more acidic, showed an increase in species richness towards more neutral pH levels. Species diversity in GS1 communities appeared to be unaffected by soil pH and tended to be quite rich in diversity metrics across all relevés.

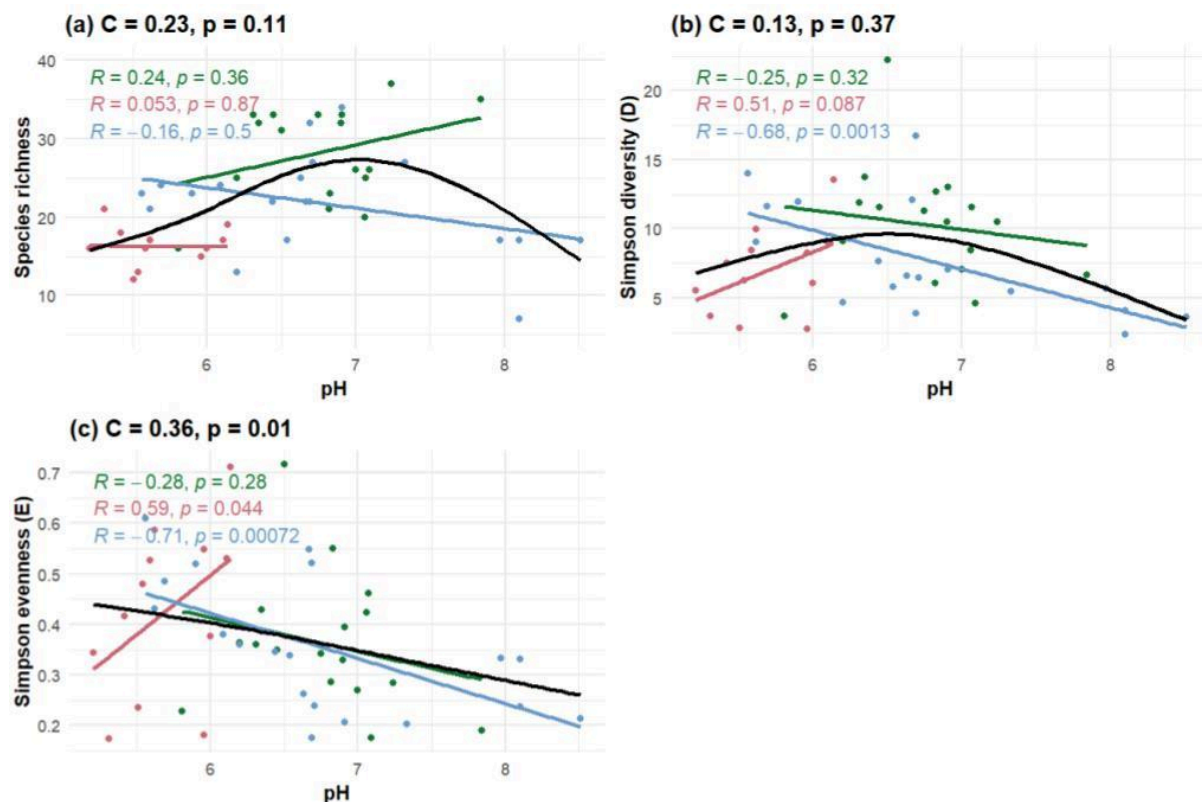


Figure 24. Relationship between species diversity metrics and soil pH, ($N = 48$).

Relationship between soil pH and species richness (a), Simpson diversity (b) and Simpson evenness (c). The overall regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests. When the

line of best fit appeared nonlinear, a nonlinear correlation analysis was performed instead. Data points, representing individual relevés, are also coloured based on habitat.

Chapter 5 - Relating functional diversity metrics, species diversity metrics and grassland productivity

Functional diversity has been hypothesized as a cause for the positive relationship observed between species diversity and grassland productivity (Petchey et al., 2004). The aim of this chapter is to assess how species diversity relates to functional diversity in the grasslands studied. Both species diversity and functional diversity were compared with grassland carbon storage and productivity. Models using species diversity or functional diversity were used to see which facet of diversity better predicts ecosystem processes (productivity and soil fertility).

5.1 - Functional diversity vs species diversity metrics

Functional diversity and species diversity metrics are not inherently covariate (with the exception of FRic and species richness which tend to correlate (Villéger et al., 2008)). This aspect was considered important when metrics for describing aspects of functional diversity were proposed (Mason et al., 2005). It would be expected, however, for increases in species diversity to lead to increases in some functional diversity metrics (functional richness or functional evenness) as a greater number of species could lead to greater variety in functional traits as well as more evenly spaced trait variation (greater niche partitioning).

5.1.1 - FRic and species diversity

Functional richness showed a significant positive correlation with all species diversity metrics (Figure 25), with Simpson diversity being the most correlated ($p = 0.0001$) (Figure 25b). GS4 communities showed a significant positive correlation between FRic and all species diversity metrics. For GS1 communities the relationship between FRic and species diversity was insignificant and, in the case of species richness, appeared to be a negative relationship

(Figure 25a). GS3 communities had a positive correlation between FRic and species diversity.

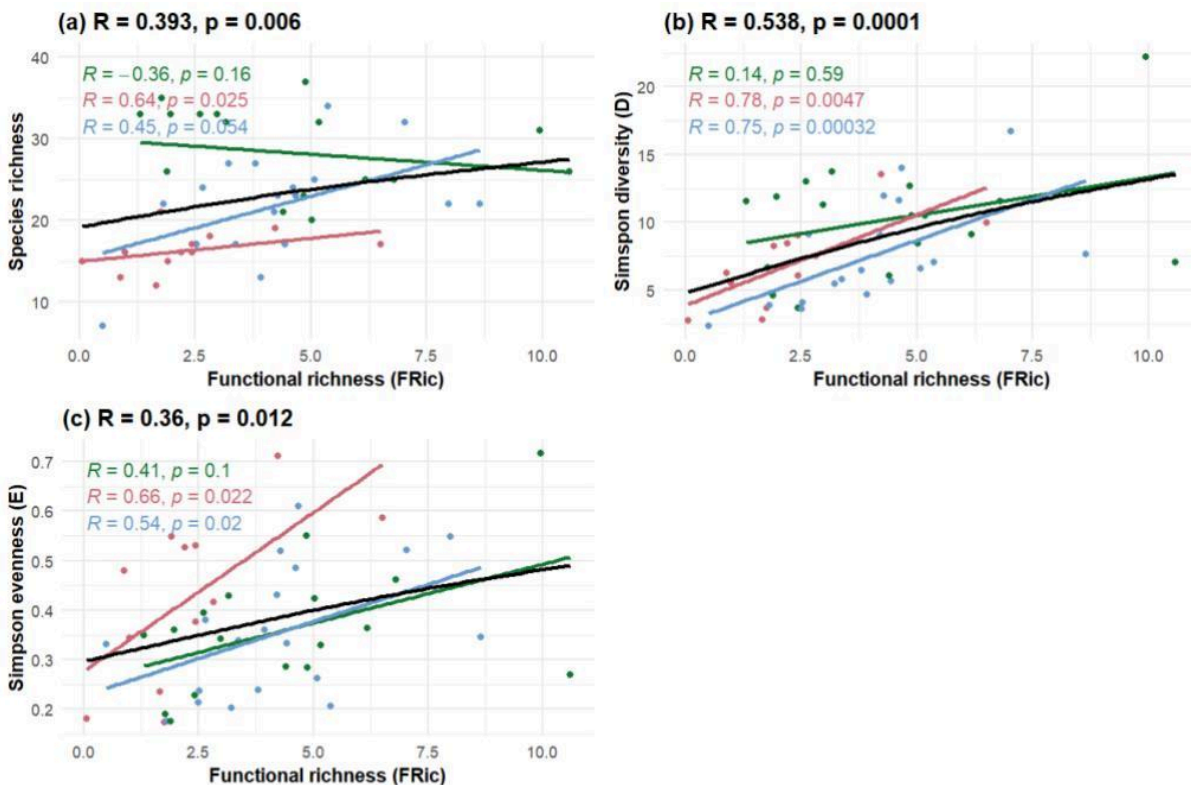


Figure 25. Relationship between functional richness and species diversity, ($N = 48$).

Relationship between FRic and species richness (a), Simpson diversity (b) and Simpson evenness (c). The overall regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests with the same colour associations as the linear model lines. Data points, representing individual relevés, are also coloured based on habitat

5.1.2 - FEve and species diversity

Functional evenness correlated strongly with all species diversity metrics when no distinction was made between habitat types (Figure 26). In the case of species richness, only GS4 relevés showed a significant, positive correlation with functional evenness ($p = 0.04$) (Figure 26a). All habitats showed a positive correlation between functional evenness and Simpson

diversity but only the GS3 relevés were significantly correlated ($p = 0.043$) (Figure 26b). Since Simpson evenness and functional evenness are both based on evenness of abundance distributions, it is unexpected that GS4 relevés showed no relationship between the species evenness and functional evenness metrics.

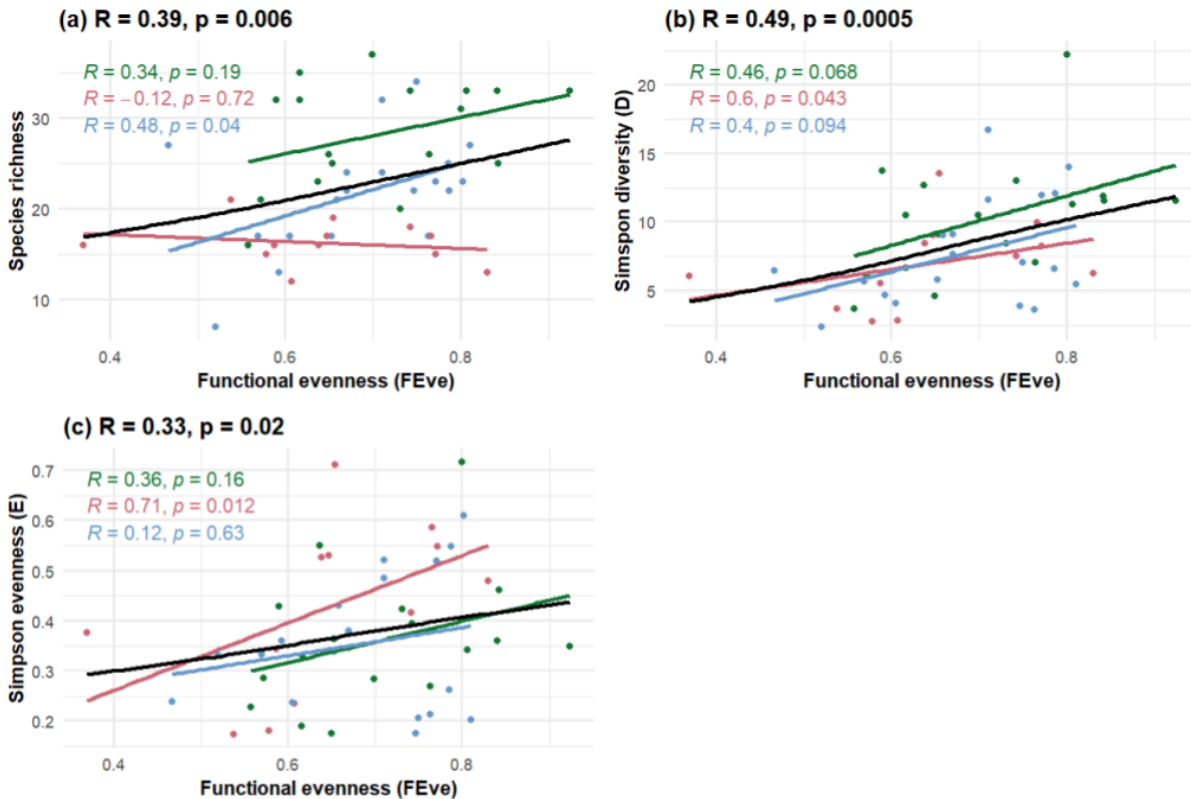


Figure 26. Relationship between functional evenness and species diversity, ($N = 48$).

Relationship between FEve and species richness (a), Simpson diversity (b) and Simpson evenness (c). The overall regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests with the same colour associations as the linear model lines. Data points, representing individual relevés, are also coloured based on habitat.

5.1.3 - FDiv and species diversity

Functional divergence is a measure for describing how distant species are from each other in terms of their functional traits. There was no overall significant relationship between functional divergence and any species diversity metrics (Figure 27). GS4 relevés, however, showed a significant negative correlation with Simpson evenness ($p = 0.043$) (Figure 28c).

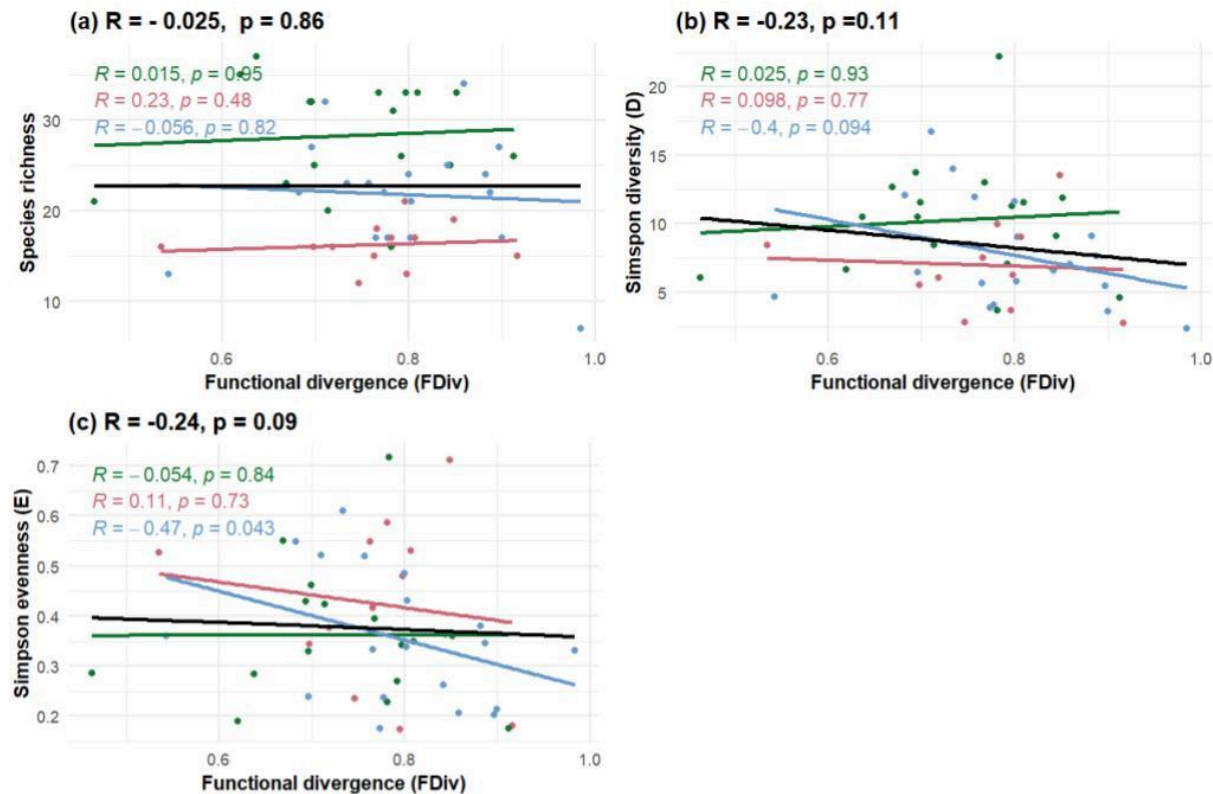


Figure 27. Relationship between functional divergence and species diversity, ($N = 48$).

Relationship between FDiv and species richness (a), Simpson diversity (b), and Simpson evenness (c). The overall linear regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The Statistics are derived from Spearman-Rank tests with the same colour associations as the linear model lines. Data points, representing individual relevés, are also coloured based on habitat.

5.1.4 - FDq and species diversity

FDq had a positive relationship with species richness; however it was not statistically significant (Figure 28a). FDq showed a strong positive correlation with both Simpson diversity ($p = 0.0004$) and Simpson evenness ($p = 0.0004$) (Figure 28b and c respectively). GS3 and GS4 relevés showed significant correlation with Simpson diversity, while GS1 relevés did not (Figure 28b). Only GS3 communities showed a significant positive correlation with Simpson evenness ($p = 0.019$) (Figure 28c).

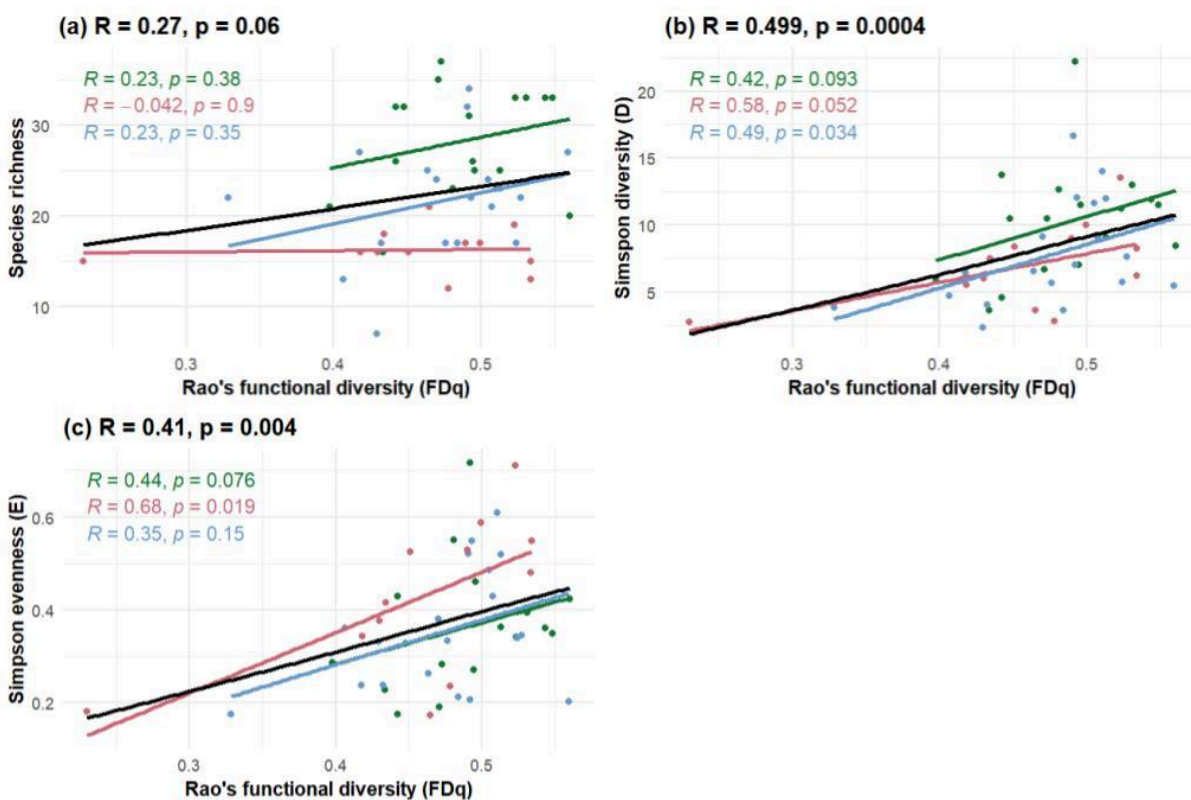


Figure 28. Relationship between Rao's functional diversity and species diversity, ($N = 48$).

Relationship between FDq and species richness (a), Simpson diversity (b) and Simpson evenness (c). The overall regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests with the same colour associations as the linear model lines. Data points, representing individual relevés, are also coloured based on habitat.

5.1.5 - CWM-LA and species diversity

As can be seen in Figure 29a CWM-LA had an overall significant negative correlation with species richness ($p = 0.04$). In GS4 grasslands there was a significant decrease in CWM-LA in relation to all species diversity metrics. GS1 communities showed no relationship between species diversity and community weighted mean leaf area.

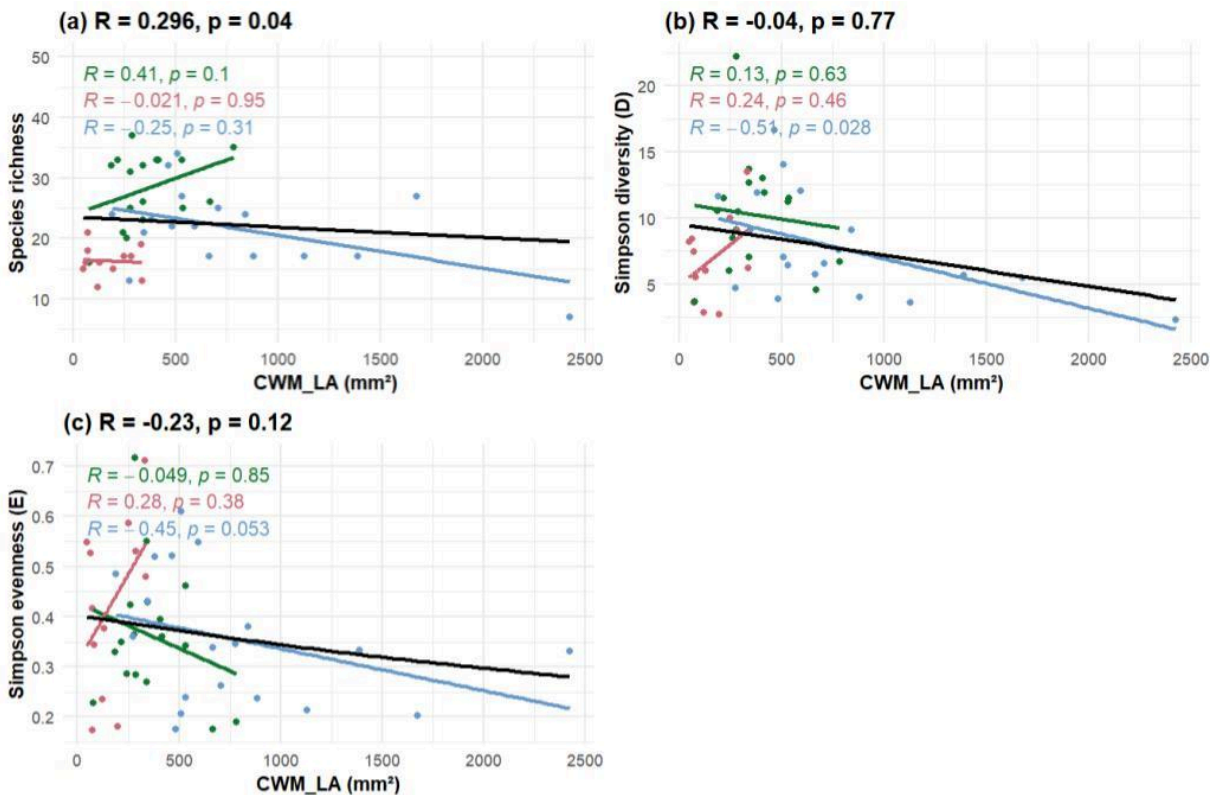


Figure 29. Relationship between CWM-LA and species diversity metrics, ($N = 48$).

Relationship between CWM-LA and species richness (a), Simpson diversity (b) and Simpson evenness (c). The overall regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests with the same colour associations as the linear model lines. Data points, representing individual relevés, are also coloured based on habitat.

5.1.6 - CWM-SLA and species diversity

CWM-SLA showed starkly different relationships with species diversity in the three grassland habitat types (Figure 30). There was no overall relationship between CWM-SLA and species metrics. The general trend across the biodiversity metrics was that GS4 relevés showed an increase in specific leaf area with increasing diversity whereas GS1 and GS3 grasslands showed a decrease in CWM-SLA with increasing diversity. This in turn resulted in no apparent trends across the three grasslands combined. In GS1 relevés, CWM-SLA was strongly negatively correlated with species richness ($p = 0.00029$) (Figure 30a). GS4 relevés showed a significant positive correlation with Simspon diversity ($p = 0.0039$) and a near significant positive correlation with Simpson evenness ($p = 0.073$) (Figure 30b, c).

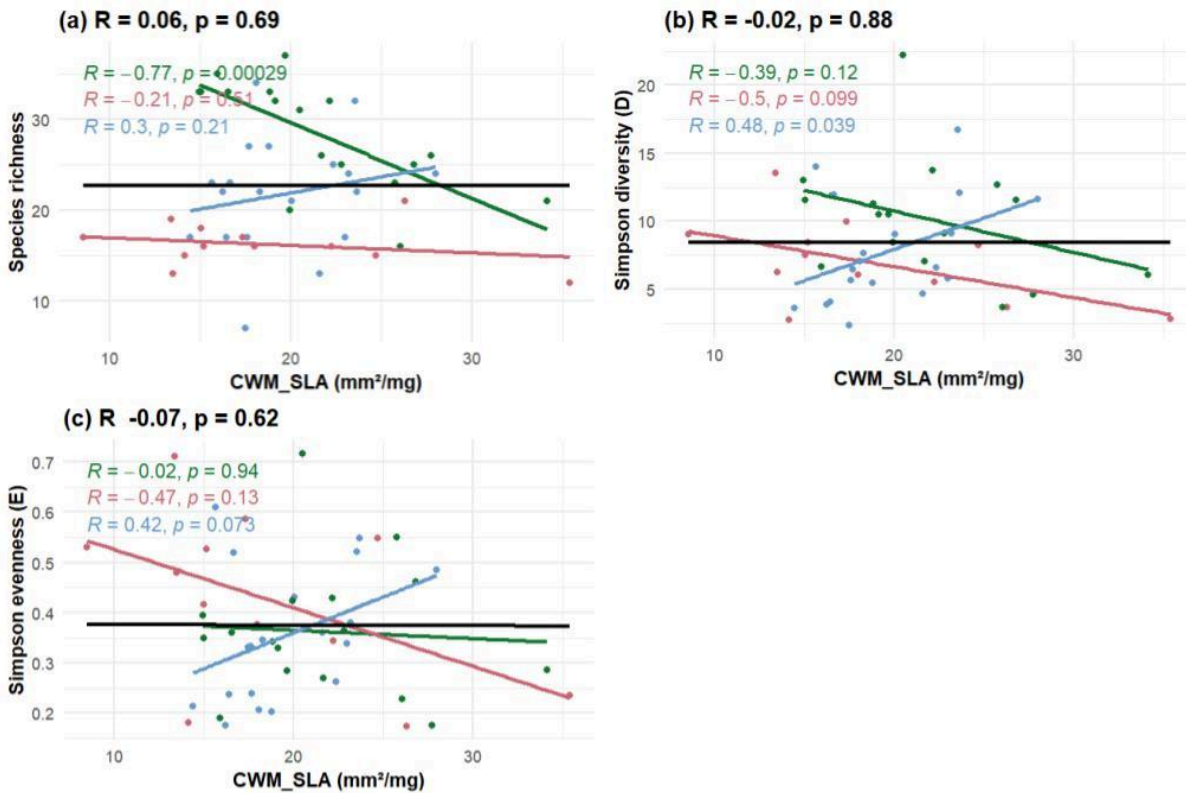


Figure 30. Relationship between CWM-SLA and species diversity, ($N = 48$).

Relationship between CWM-SLA and species richness (a), Simpson diversity (b) and Simpson evenness (c). The overall linear regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests with the same colour associations as the linear model lines. Data points, representing individual relevés, are also coloured based on habitat.

5.1.7 - CWM-LDMC and species diversity

CWM-LDMC showed no overall correlation with species diversity (Figure 31). GS1 relevés showed a significant positive correlation with CWM-LDMC and species richness ($p = 0.032$) (Figure 31a). GS3 communities showed the strongest correlation between CWM-LDMC and species diversity metrics. leaf dry matter content was positively correlated with Simpson

diversity ($p = 0.0091$) and evenness ($p = 0.026$) in GS3 communities (Figure 31b, c). GS4 communities showed a general decrease in CWM-LDMC with increased species diversity however none of these relationships were significantly correlated.

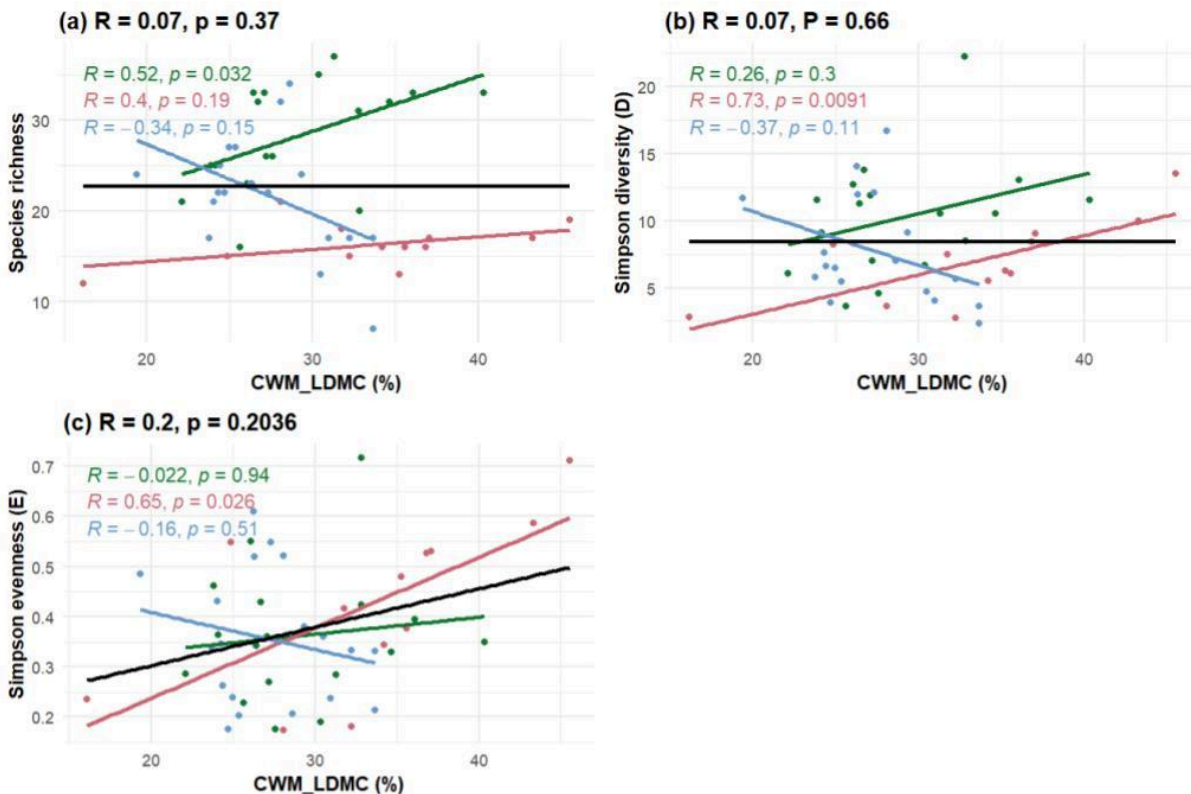


Figure 31. Relationship between CWM-LDMC and species diversity, ($N = 48$).

Relationship between CWM-LDMC and species richness (a), Simpson diversity (b) and Simpson evenness (c). The overall linear regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The Statistics are derived from Spearman-Rank tests with the same colour associations as the linear model lines. Data points, representing individual relevés, are also coloured based on habitat.

5.2 - Functional diversity and carbon storage

5.2.1 - Community weighted mean leaf traits and carbon storage

CWM-LA showed no overall significant correlation with soil carbon content; however GS4 grasslands showed a significant positive correlation between CWM-LA and total carbon content ($p = 0.00051$) (Figure 32a). The same pattern was observed for soil nitrogen content which also had a significant positive relationship with CWM-LA in GS4 relevés ($p = 0.0054$) (Figure 32b). CWM-SLA showed no pattern in relation to changes in soil carbon or nitrogen levels (Figure 32c, d). This was the case both overall and for each habitat type. CWM-LDMC was not significantly correlated with soil carbon content (Figure 32e). Only GS4 relevés showed a significant positive correlation with CWM-LDMC and carbon content ($p = 0.031$). Soil nitrogen content had no correlation with CWM-LDMC (Figure 32f).

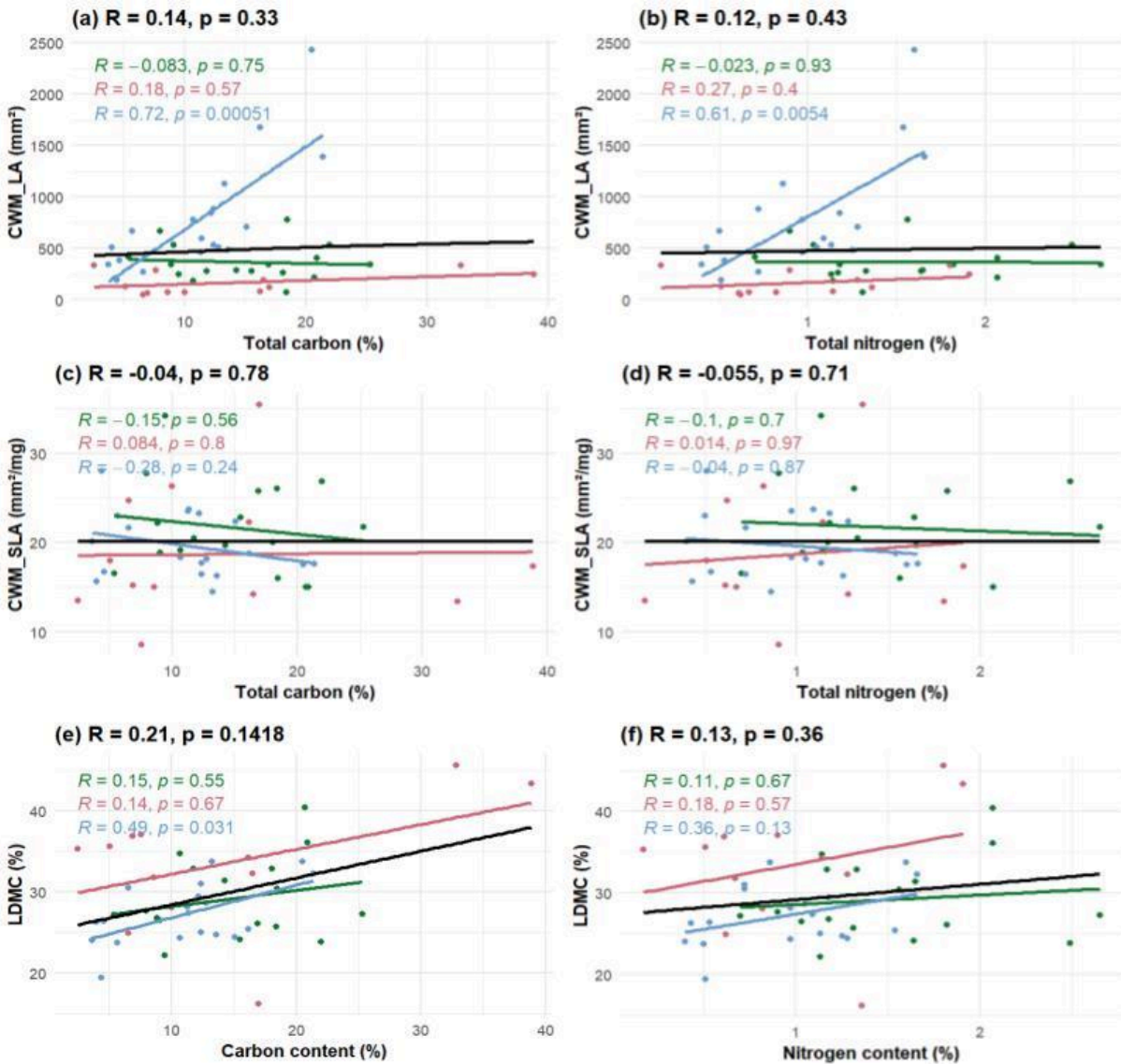


Figure 32. Relationship between community weighted mean leaf traits and soil fertility, (N = 48).

Relationship that CWM-LA has with total carbon content (a) and total nitrogen content (b), the relationship that CWM-SLA has with total carbon content (c) and total nitrogen content (d) and the relationship that CWM-LDMC has with total carbon content (e) and total nitrogen content (f). The overall linear regression between the two variables is indicated by the black line and the relationship based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests with the same colour associations as the linear model lines. Data points, representing individual relevés, are also coloured based on habitat.

5.2.2 - CWM-LCC and carbon storage

Leaf chlorophyll content showed no significant relationship with any of the soil metrics (Figure 33).

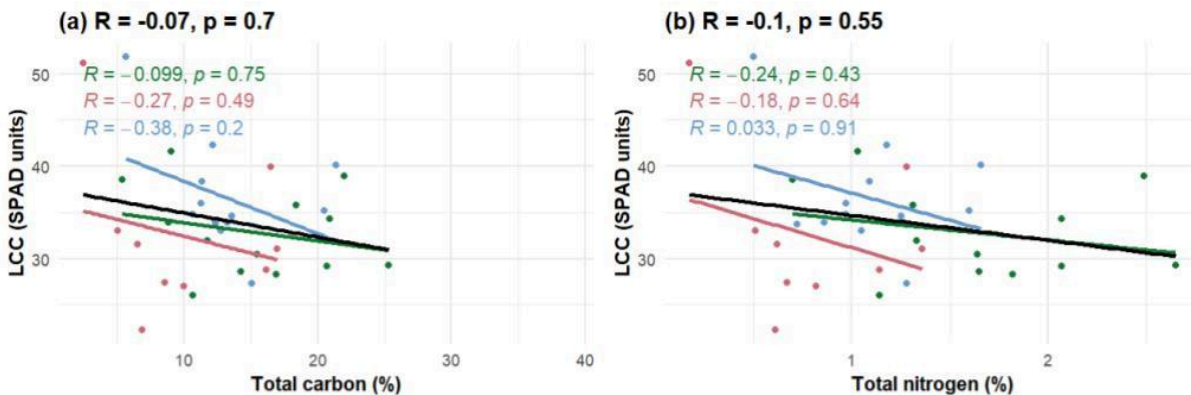


Figure 33. Relationship between community weighted mean leaf chlorophyll content and soil carbon content, ($N = 48$).

Relationship between CWM-LCC and total carbon content (a) and nitrogen content (b). The overall linear regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests with the same colour associations as the linear model lines. Data points, representing individual relevés, are also coloured based on habitat.

5.2.3 - RLD and carbon storage

Root length density at 10 cm soil depth had no correlation with carbon and nitrogen content. This is true both overall (across all habitats) and for the two habitat types (Figure 34a, c). At 20 cm soil depth there was a strong positive correlation between RLD and carbon content ($p = 0.003$) and nitrogen content ($p = 0.01$) (Figure 34c, d). This relationship was significant overall and for GS3 grassland communities but not for GS4.

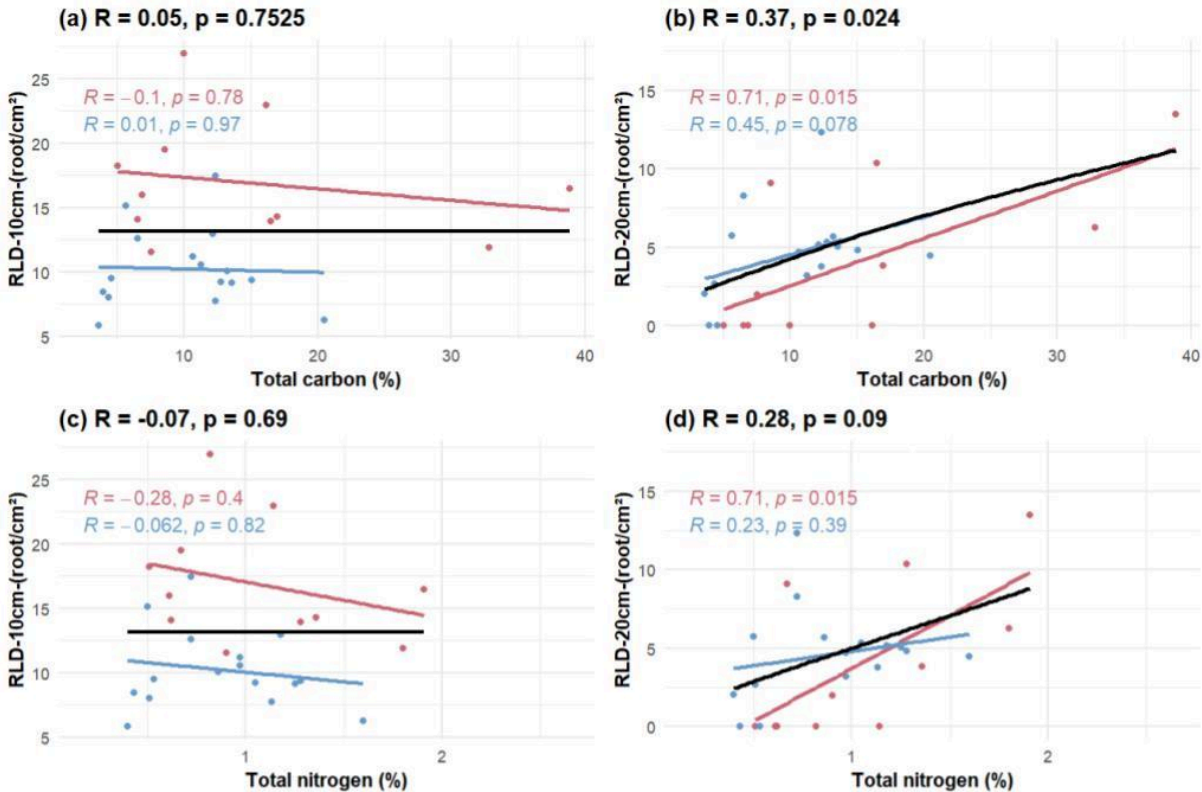


Figure 34. Relationship between root length density with soil carbon and nitrogen content, ($N = 28$).

Relationship between RLD at 10cm and 20cm with soil carbon content (a & b respectively) and soil nitrogen content (c & d respectively). The overall linear regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests with the same colour associations as the linear model lines. Data points, representing individual relevés, are also coloured based on habitat.

5.2.4 - Functional richness, evenness and divergence

Figure 35 below shows the relationship between FRic, FEve and FDiv with soil carbon and nitrogen content. There were no significant correlations between any of the three functional diversity metrics and carbon or nitrogen content. This was true for overall patterns and for the individual grassland habitats.

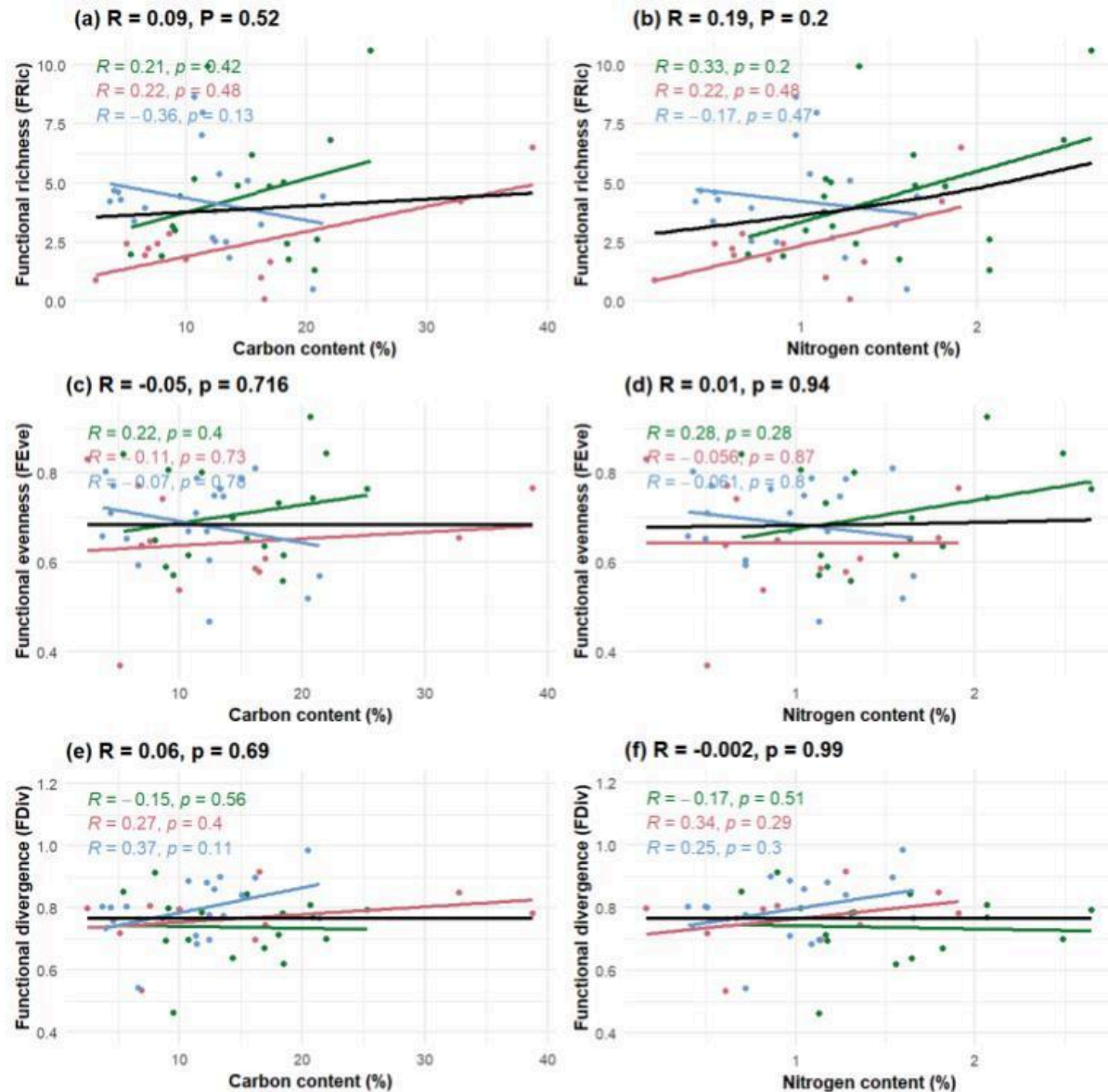


Figure 35. Relationship between functional diversity metrics and soil C and N content, ($N = 48$).

Relationship between carbon content and nitrogen content with functional richness (a & b respectively), functional evenness (c & d) and functional divergence (e & f). The overall linear regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests with the same colour associations as the linear model lines. Data points, representing individual relevés, are also coloured based on habitat.

5.2.5 - Rao's functional diversity and functional redundancy

There was no correlation, across all relevés, between FDq or FRed with either soil carbon or nitrogen content (Figure 36). There was, however, a negative correlation between FRed and carbon content in the GS4 habitat ($p = 0.03$) (Figure 36c). FDq also showed a negative trend however it was insignificant (Figure 36a)

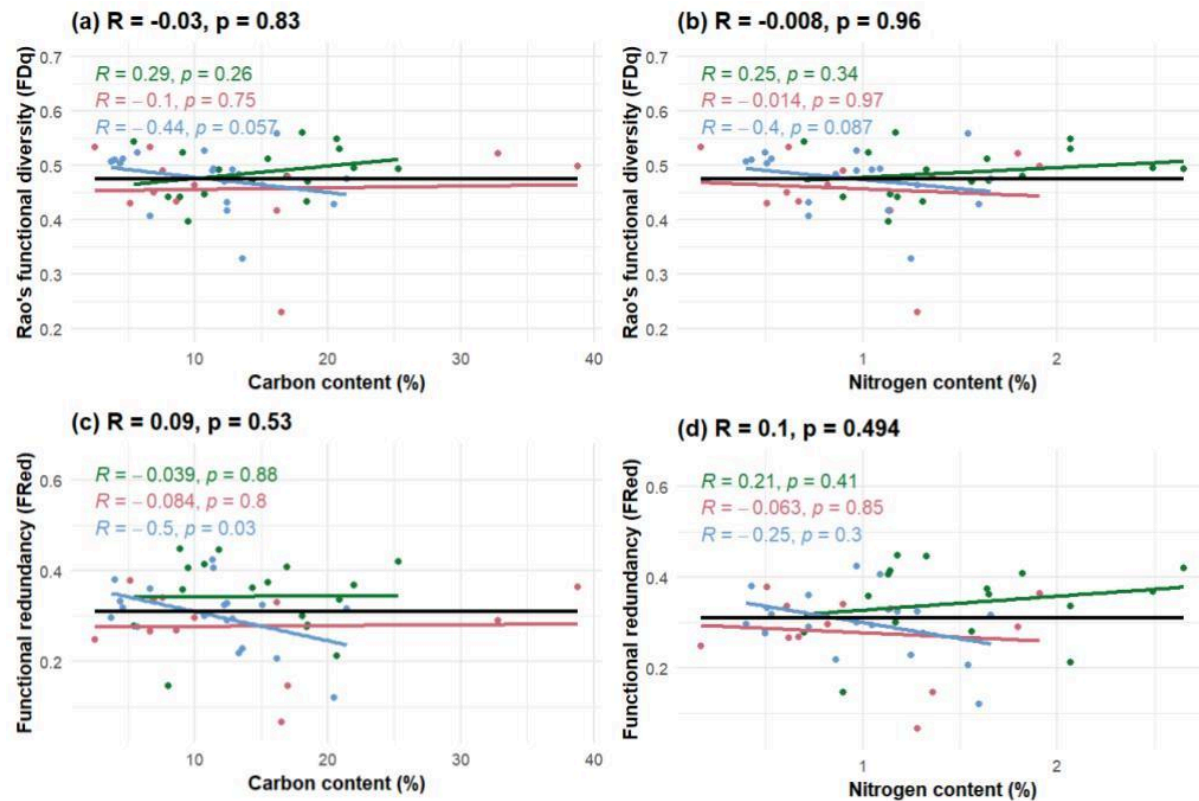


Figure 36. Relationship between FDq and FRed and soil C and N content, ($N = 48$).

Relationship between carbon content and nitrogen content with Rao's functional diversity (a & b respectively) and functional redundancy (c & d). The overall linear regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests with the same colour associations as the linear model lines. Data points, representing individual relevés, are also coloured based on habitat.

5.3 - Functional diversity and productivity

Greater functional diversity should theoretically lead to higher levels of productivity. Increased functional diversity has been proposed as one of the main causes for positive relationships found between biodiversity and productivity (Petchey et al., 2004). Community weighted mean values of leaf traits associated with productivity (CWM-LA, CWM-SLA), should also indicate higher levels of overall productivity due to the mass-ratio hypothesis.

5.3.1 - Community weighted mean leaf traits and productivity

CWM-LA showed no relationship with NDVI values (Figure 37). This is unexpected as higher leaf areas suggest greater above-ground productivity and the mass ratio hypothesis suggests that a greater CWM-LA would suggest greater overall productivity. As well as no overall correlations existing between CWM-LA and NDVI there were also no correlations found for individual habitat types (Figure 37a). CWM-SLA showed no significant correlation with NDVI values (Figure 40b). CWM-LDMC showed a significant negative correlation ($p = 0.002$) with NDVI values (Figure 37c). This negative relationship was significant in GS3 grasslands ($p = 0.034$) but not in GS1 or GS4. GS1 and GS4 showed no correlation between NDVI values and any of the leaf traits.

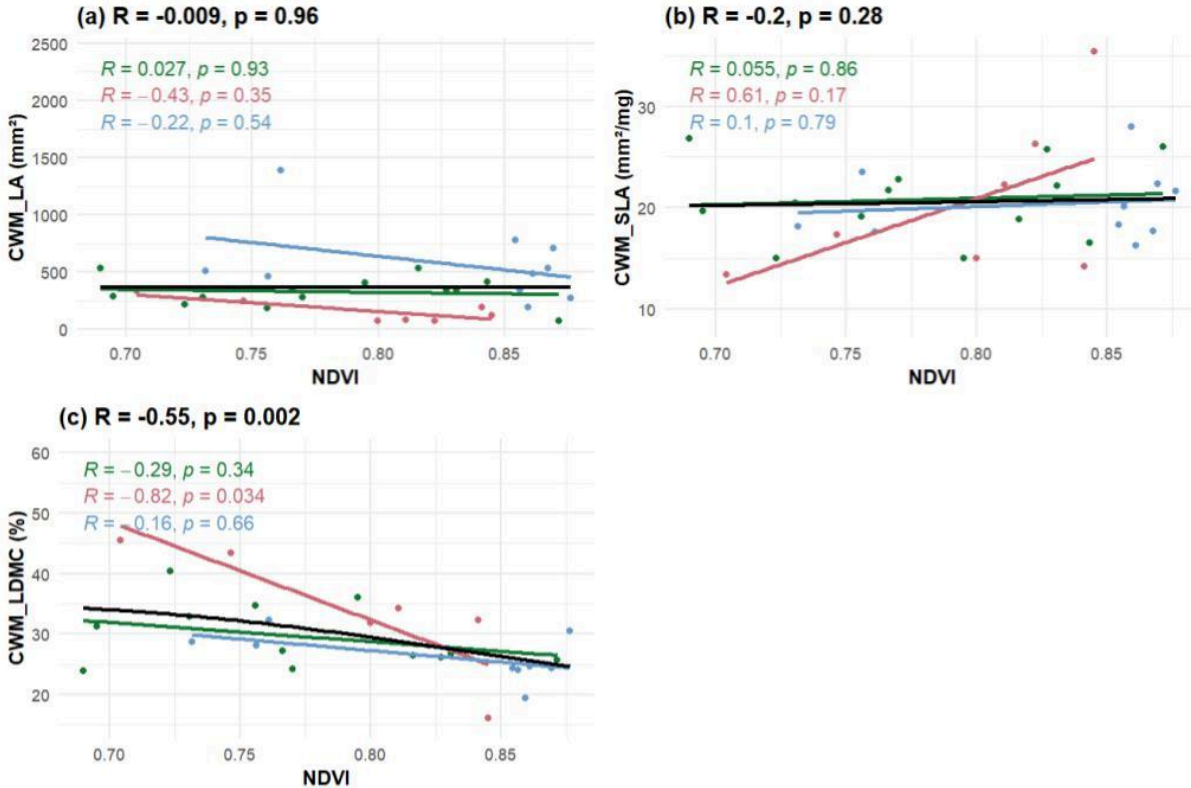


Figure 37. Relationship between community weighted mean leaf traits and grassland productivity, ($N = 30$).

Relationship between grassland yield (NDVI) and CWM-LA (a), CWM-SLA (b) and CWM-LDMC (c). The overall linear regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests. Data points present individual relevés also coloured based on habitat.

5.3.2 - Functional richness, evenness and divergence

Functional richness showed a significant negative correlation ($p = 0.04$) with NDVI (Figure 38a). There was a significant negative correlation between functional richness and NDVI in GS3 grassland ($p = 0.049$). FEve showed a significant negative correlation with NDVI values when looking at all relevés ($p = 0.03$) but no significant correlation existed within habitats (Figure 38b). FDiv showed no correlation with NDVI values (Figure 38c). This was the case for all habitats combined and for individual habitats.

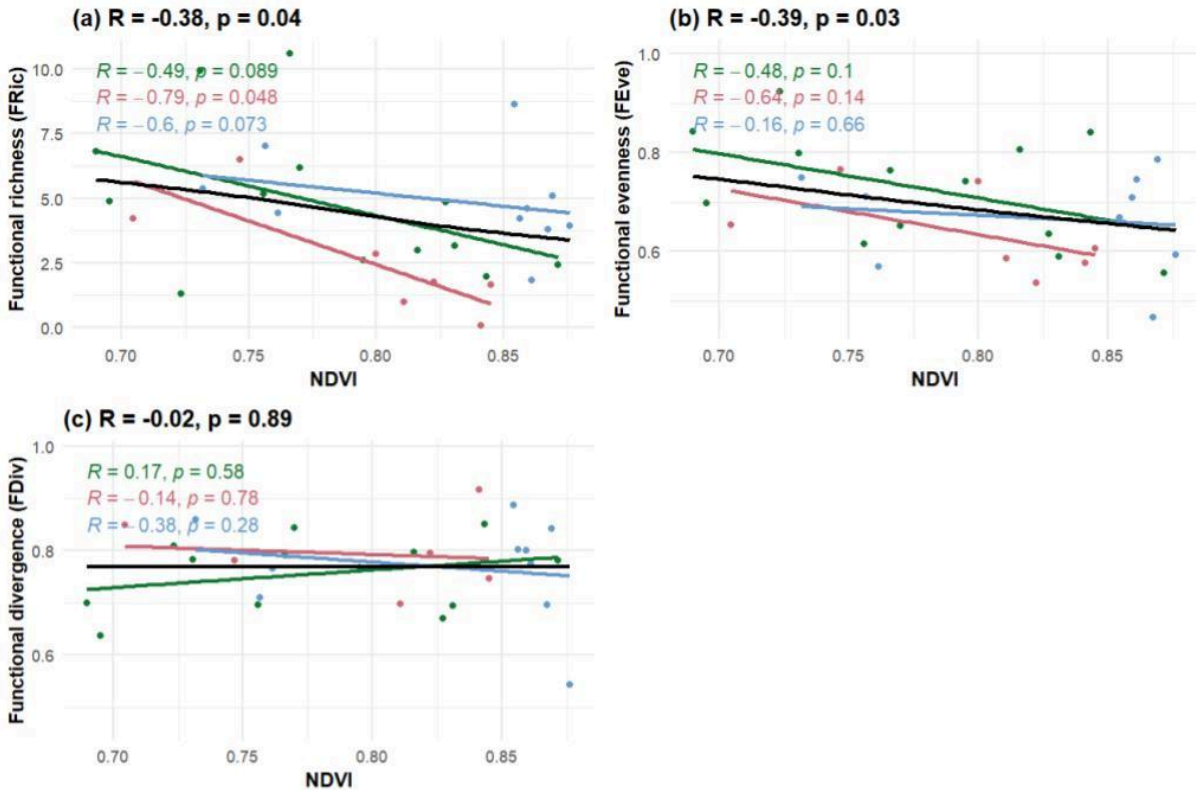


Figure 38. Relationship between functional diversity metrics and grassland productivity, ($N = 30$).

Relationship between grassland yield (NDVI) and FRic (a), FEve (b) and FDiv (c). The overall linear regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests. Data points present individual relevés also coloured based on habitat.

5.3.3 - Rao's functional diversity and functional redundancy

Rao's functional diversity showed a significant negative correlation ($p = 0.038$) with NDVI values (Figure 39a). However, this was not statistically significant for individual habitat types. Functional redundancy had no significant correlation with NDVI (Figure 39b).

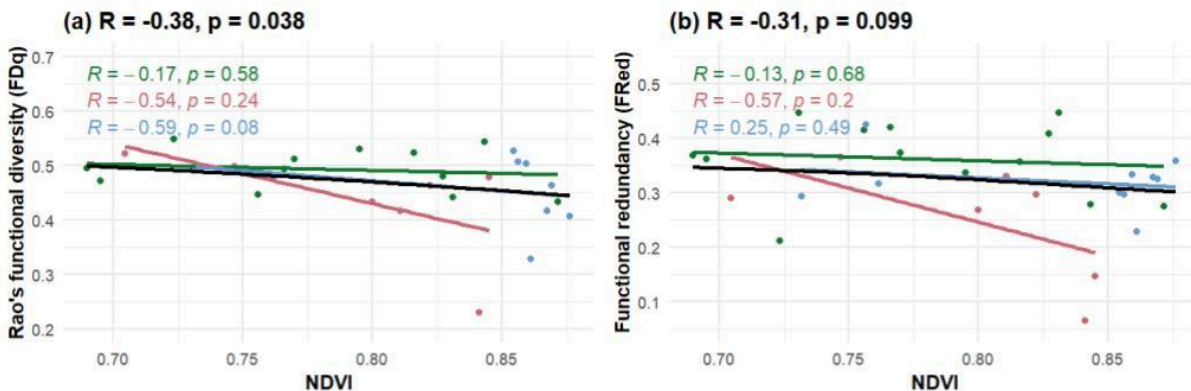


Figure 39. Relationship between FDq and FRed and grassland productivity, ($N = 30$).

Relationship between grassland yield (NDVI) and FDq (a) and FRed (b). The overall linear regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests. Data points present individual relevés also coloured based on habitat.

5.4 - CSR strategies and productivity

The competitive strategy showed no correlation with NDVI values (Fig. 42a). However, stress tolerance strategy showed a significant negative correlation with NDVI (Fig. 42b). GS3 grasslands were the only habitat to also show this significant negative correlation. The ruderal strategy showed an overall significant positive correlation with NDVI; however there was no significant pattern present within the habitats (Fig. 42c).

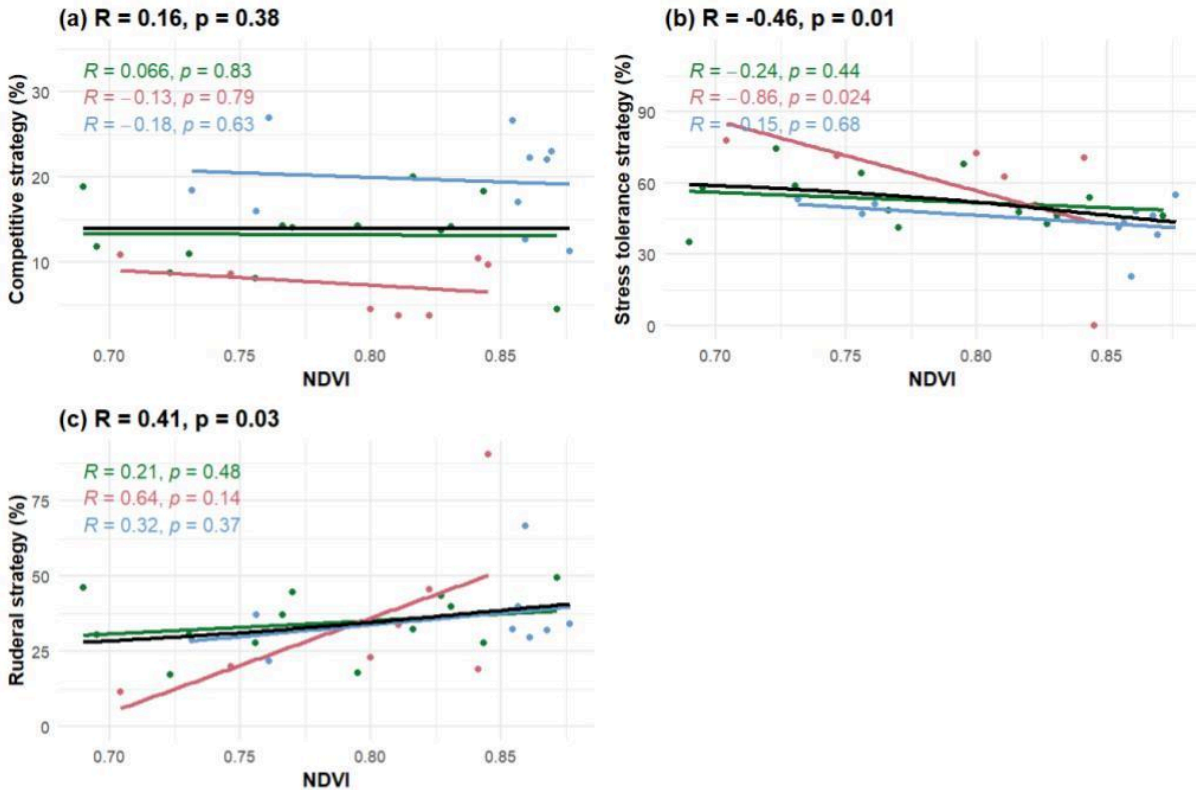


Figure 40. Relationship between CSR strategy and grassland productivity, ($N = 30$).

Relationship between grassland yield (NDVI) with competition strategy (a), stress tolerance strategy (b) and ruderal strategy (c). The overall linear regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests. Data points, representing individual relevés, are also coloured based on habitat.

5.5 - Species diversity and carbon storage

5.5.1 - Species diversity

Species richness showed no correlation with soil carbon content (Figure 41a). A positive correlation was found in species richness and nitrogen content ($p = 0.04$); however it is apparent, from Figure 41b, that this trend is due to significant variations between habitat types in terms of richness and nitrogen content as there is no correlation within each habitat type. When looking at overall patterns of variation across all habitats Simpson diversity showed no overall correlation with carbon or nitrogen content (Figure 41c, d). Simpson diversity in GS4 relevés showed a significant negative correlation with carbon content ($p = 0.0032$) (Figure 41c). Simpson evenness did not show an overall correlation with soil carbon and nitrogen content (Figure 41e, f). Within the GS4 habitat however, Simpson evenness had a significant negative correlation with carbon content ($p = 0.00042$) and nitrogen content ($p = 0.0029$).

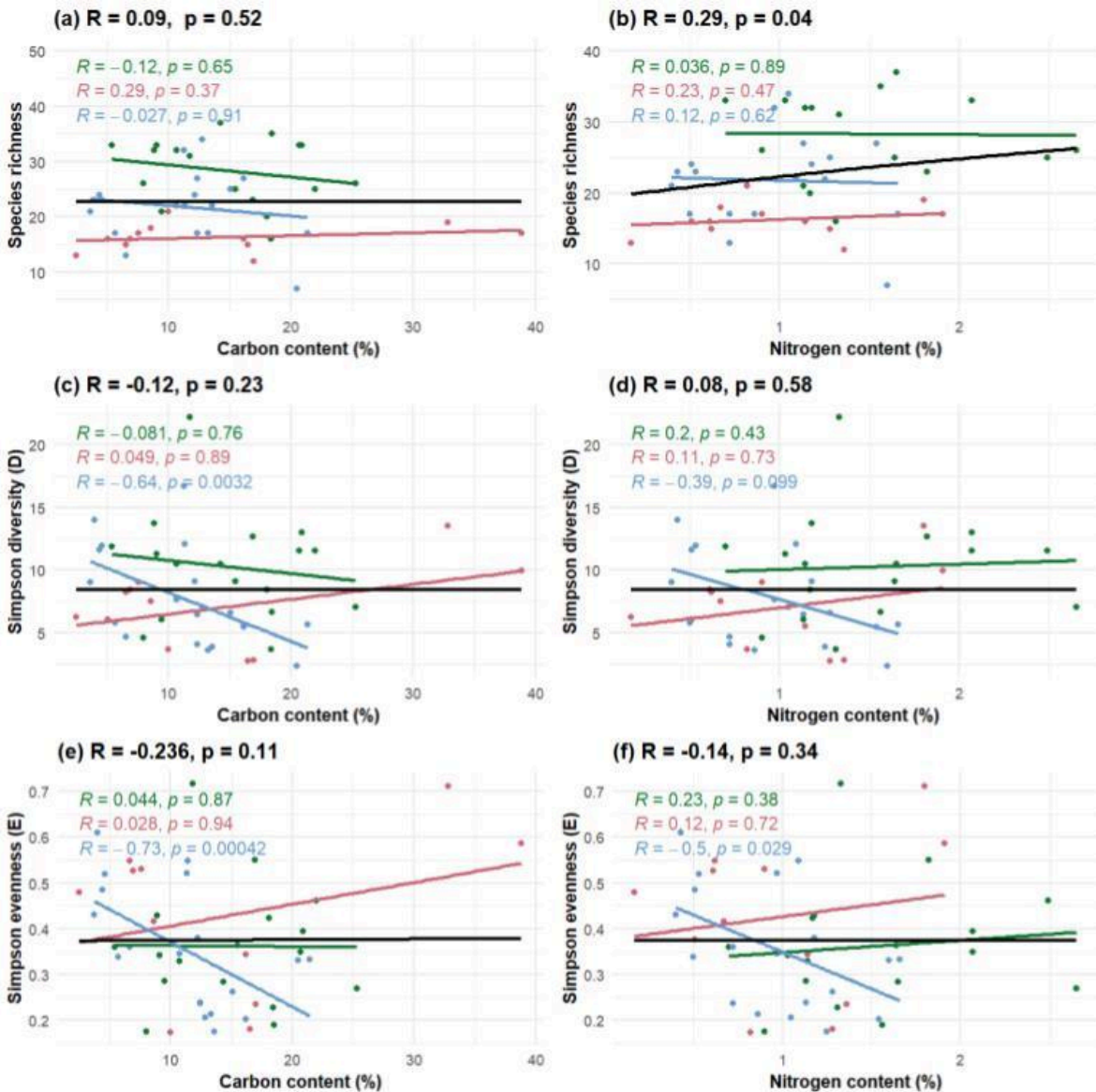


Figure 41. Relationship between species diversity metrics and soil carbon and nitrogen content, ($N = 48$).

Relationship between carbon content and nitrogen content with species richness (a & b respectively), Simpson diversity (c & d) and Simpson evenness (e & f). The overall linear regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests with the same colour associations as the linear model lines. Data points, representing individual relevés, are also coloured based on habitat.

5.6 - Species diversity and productivity

Diversity-productivity relationships have previously been observed in grassland ecosystems (Nie et al., 2024). This has given rise to the widely used “complementarity effect” where multispecies swards show a higher yield than monocultures (Prieto et al., 2015). The causes for this include greater resource partitioning, facilitation by altering the environment and positive feedback between species and other organisms in the ecosystem (Barry et al., 2019). The extent to which each of these processes can influence the species diversity-productivity relationship depends on other environmental factors. All these aspects may be influenced by functional diversity (especially resource partitioning). It can be hypothesised therefore that species diversity will lead to an increase in yield in a similar way that functional diversity does.

5.6.1 - Species diversity metrics and productivity

The species diversity metrics showed a range of patterns with NDVI values (Figure 42). Species richness ($p = 0.03$) and Simpson diversity ($p = 0.008$) showed significant negative correlation with NDVI (Figure 42a, b). Within GS3 communities these negative correlations were also significant. While the overall correlation between Simpson evenness and NDVI was not statistically significant ($p = 0.07$), GS3 habitats showed significant declines in NDVI at higher species evenness ($p = 0.002$) (Figure 42c).

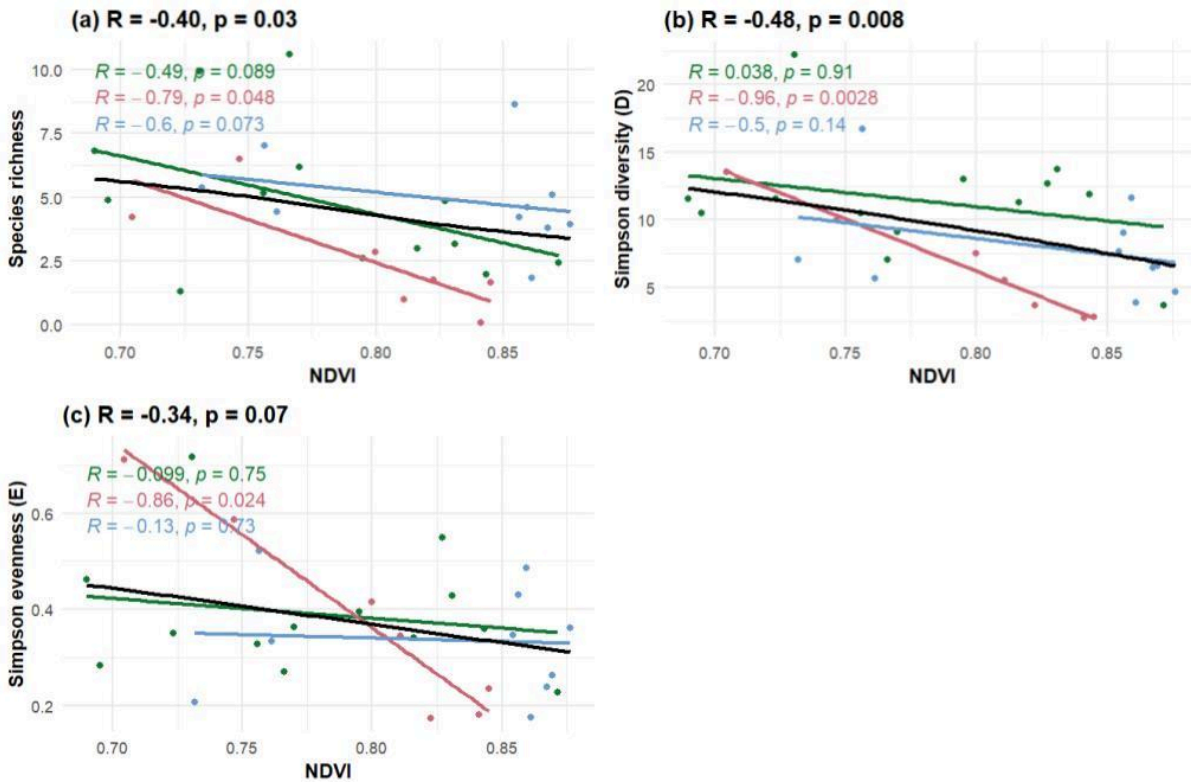


Figure 42. Relationship between species diversity metrics and grassland productivity, ($N = 30$).

Relationship between grassland yield (NDVI) with species richness (a), Simpson diversity (b) and Simpson evenness (c). The overall linear regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests. Data points, representing individual relevés, are also coloured based on habitat.

5.7 - Soil carbon and nitrogen and productivity

Significant negative correlations were found between NDVI and both soil C and N contents (Figure 43). This was the case overall but relationships within habitats were insignificant with the exception of GS1 relevés which showed a near significant negative correlation between soil N and productivity (Figure 43b).

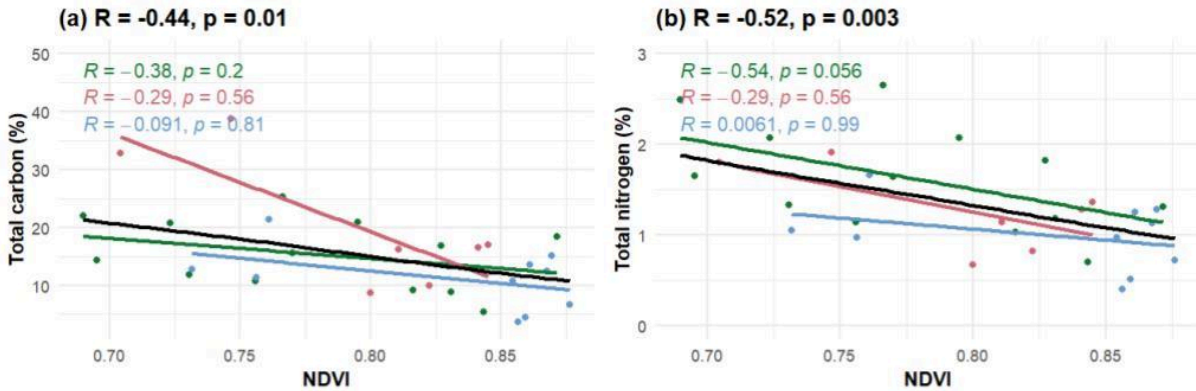


Figure 43. Relationship between productivity and soil carbon and nitrogen content, ($N = 30$).

The relationship between NDVI values and soil C (a) and N (b) concentrations in the three grassland habitats. The overall regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests with the same colour associations as the linear model lines. Data points, representing individual relevés, are also coloured based on habitat.

Chapter 6 - Discussion

The three Fossitt habitat types differed significantly in abiotic conditions (soil pH, soil N and productivity) (Figure 5, Figure 7 and Figure 8, respectively). Significant differences in CSR strategy and functional richness were also found between the habitat types (Figure 16, Figure 18). Neither functional diversity (Figure 38) nor species diversity (Figure 42) was found to support increased productivity with the strongest negative diversity-productivity relationships found in the GS3 habitat. Diversity also showed either no correlation or negative correlations with soil carbon and nitrogen depending on the habitat in question (Figure 35, Figure 36, Figure 41). Instead, soil pH seemed to be the strongest driver of diversity patterns (Figure 23, Figure 24). Relationships between functional diversity and species diversity also differed depending on the habitat type (Figure 25). Higher NDVI also negatively correlated with soil carbon and nitrogen concentrations (Figure 43), suggesting that the ecosystem services of yield and carbon sequestration cannot be gained simultaneously.

6.1 - Grasslands habitats differed significantly in abiotic conditions

The most distinct difference to be found between the grassland habitats was soil pH (Figure 5). This is unsurprising as two of the three Fossitt habitats are described based on their alkalinity/acidity. This result speaks to the validity of the Fossitt habitat classification system which is often viewed as a classification that lacks distinct boundaries between habitat types (Fossitt, 2000). The GS4 habitat had a high amount of variation in soil pH and one GS4 site (site 7) was the most alkaline of them all. Excluding this site, GS1 was the most alkaline of the three habitats. Since soil pH shows the strongest variation between habitat types, its influence on variation in vegetative traits is likely strong and should be considered. Soil pH has strong effects on the bioavailability of soil nutrients with lower pH soils having higher

water holding capacity which can enhance nutrient uptake (Sujatha, 2016). Also alkaline soils tend to make soil nutrients less bioavailable by binding with them to form inorganic compounds (Bahr et al., 2012). Therefore the variation in soil pH may muddle the relationship between the measured soil nutrients and the fertility of the soil (amount of bioavailable nutrients). Soil pH is also the soil metric that is least likely to be affected by management and grazing intensity and so may provide insight into how the inherent characteristics of each habitat influence the vegetation (Akhzari et al. 2015).

GS1 grasslands had the most fertile soils with significantly more carbon and nitrogen than the highly productive GS4 grassland (Figure 6, Figure 7). GS1 grasslands also had the lowest C:N ratio which is optimal for plant growth as nitrogen is more often the limiting factor. In grasslands, a low C:N ratio is often indicative of a high decomposition which may be due to differences in grazing intensities and litterfall in the different grassland habitats (Chuan et al., 2018). Decomposition rates are also influenced by pH (Curtin et al., 1998) so the significant differences in C:N ratios in the grasslands may be due to differences in soil pH. The high nitrogen content in GS1 grassland soils is surprising considering that only GS4 grasslands were fertilized. It should. However, be noted that the high C and N content in GS1 grasslands is not representative of high soil fertility as minerals in alkaline soils tend to be less bioavailable (Kemmitt et al., 2006).

6.2 - Grassland communities from different habitat types differ in their functional strategy and functional richness

We determined leaf functional traits by field sampling of plants growing in the semi-natural grassland communities at each site. Previous research on grassland functional diversity has mainly relied on database values (Rolo et al., 2016; Anderegg et al., 2024). While database values reflect species composition, they do not represent intraspecific genetic variation or

phenotypic plasticity. The functional strategies of grassland communities presented here are therefore reflective of the plant community composition as well as the response of the individuals in the community to the surrounding environment (Moog et al., 2005; Yu et al., 2022).

The semi-natural grassland habitats monitored in this research differed significantly in their community-weighted functional trait values (Figure 11, Figure 13), their vegetation functional strategy (Figure 16) and their functional richness (Figure 18). GS4 grasslands had the highest competitiveness scores (Figure 16), reflecting high CWM-LA values (Figure 11), which may be expected as it was the most often fertilized of the three grassland habitats (Moog et al. 2005). The GS4 habitat was also the most productive (Figure 8), suggesting a relationship between competition and productivity. The abiotic conditions of GS4 (low soil carbon and nitrogen) however, are not conducive with fast growing, competitive plants. Large leaf areas and high leaf chlorophyll content suggest high nitrogen concentrations in the leaves (Toth, 2002). This is at odds with the infertile soil present in GS4 sites. The amount of plant available water in the soil, which is highest in wet grasslands, may be a stronger explanation for high competitiveness and productivity in GS4 sites. Soil moisture and N concentrations are known to have a combined positive effect on productivity related traits such as CWM-LA (Xu et al., 2018). When analysing GS4 sites on their own, comparisons of leaf area and soil carbon showed significant positive correlations (Figure 32). This, along with significant correlations in figure S1 suggests that, within GS4 grasslands, competitiveness is positively correlated with high C,N and C:N ratios. Communities with a dominant competitive strategy usually indicate optimal growth conditions (Grime, 1977). It may be the case, therefore, that soil fertility is the limiting factor for growth especially in the low fertility soils of wet grasslands. Low soil fertility is generally the limiting factor in growth in semi-natural grasslands (Fay et al., 2015). GS1 and GS3 grasslands showed no variation in

competitiveness in relation to soil carbon or nitrogen. In these habitats, leaves were ubiquitously small regardless of soil fertility. This may be due to other limiting factors on growth that were not measured (i.e. sunlight etc.) or may be due to high stress levels, abiotic or management induced, that restricted productivity on these sites. The amount of plant available water may have an impact on the lower competitiveness in these habitats (but more likely in GS1 habitats). There is evidence in other grasslands where soil nutrients only promote a competitive strategy when there is enough plant available water to facilitate nutrient uptake (Yu et al., 2022). Other studies have found similar results where competitiveness did not correlate with stress levels (i.e. low soil nutrients) (Li & Shipley, 2017). One explanation could be that these habitats, even at their most favourable conditions, are still too stressful to promote competitive species.

The CSR stress tolerance strategy was highest in GS3 grasslands (Figure 16). The stress factors in the GS3 environment are likely from grazing or from exposure to heavy winds or frosts as the mean temperature did not differ from the other grassland habitats (Table S1). Precipitation was much higher in the GS3 grasslands and so was also likely not a cause for stress. The CWM-LDMC (Figure 13) does not only indicate lower productivity (as it is a resource conservative strategy) (Wright et al., 2004) but also suggests lower palatability (Dostálek et al., 2020), both of which are not favourable for livestock management (Bumb et al., 2018).

The variation in ruderality (as indicated by CWM-SLA) showed no significant pattern with the habitat types (Figure 16). Specific leaf area is not only indicative of a ruderal strategy but also indicates where a species lies on the leaf economic spectrum between resource acquisition and resource retention. GS3 grasslands showed the highest variation in ruderality ranging from no ruderality to being the dominant strategy present. The absence of variation and low

levels of ruderality in the three grassland habitats may suggest that, though stress conditions were present, the grasslands suffered similarly low levels of disturbance. This was noted by Li and Shipley (2017) who stated that an ecosystem cannot be both high disturbance and high stress as high plant matter destruction and low plant matter production prevents any survival of vegetation.

It is interesting to note that, even though GS3 grasslands are the most stressed habitat (as observed from the LDMC values and from understanding of the ecosystem), there are still communities dominated by a ruderal strategy which is only optimal in ecosystems with high disturbance levels.

The consistently low levels of a ruderal strategy across GS1 and GS4 grasslands (Figure 16) are indicative of good grassland management (Moog et al., 2005). Grasslands that become more degraded (mainly from overgrazing) tend to show a shift in strategy from stress tolerance to ruderality (Zhou et al., 2021). This may be the case for the GS3 grasslands dominated by ruderal species.

Of all the functional diversity metrics only FRic differed significantly between the grassland habitats (Figure 18). This indicates that the total variation in functionality in each community differed significantly between the habitats. The GS4 grasslands showed the highest amount of functional variation within vegetation communities. This is likely indicative of a more favourable environment where no environmental filtering is occurring and so a variety of niche spaces can be occupied. The higher variety of niches seen in GS4 (through a high FRic) may be due to a relaxation of environmental constraints and may benefit the competitiveness and productivity of the GS4 communities. FRic was also significantly higher in GS1 habitats compared to GS3. The spatial heterogeneity in GS1 grasslands, with highly

variable soil depths and its exposed karst landscape, likely had an influence on the high FRic values by increasing the variation in microhabitats (Schippers et al., 2022). The absence of differences in the other functional diversity metrics between habitats indicates that there is no difference in niche partitioning between the grassland habitat types (especially in FDq which is closely related to complementarity effects) (Roscher et al., 2012).

6.3 - Relationships between functional richness and species diversity are habitat dependent

While functional richness and species diversity metrics are independent of each other, it is logical that a greater diversity of species should come with a greater amount of trait variation (Cadotte et al., 2011). However, relationships between functional diversity and species diversity have been shown to vary along environmental gradients such as disturbance levels and nutrient availability (Cadotte et al., 2011; Mayfield et al., 2010; Biswas and Mallik, 2010).

GS3 and GS4 habitats showed positive correlations between FRic and all species diversity metrics (Figure 25). GS1, however, showed no correlation between FRic and species diversity. This may be due to the consistently high species diversity present in GS1 grasslands. The greater the number of species in a community and the greater the evenness of species abundances (Simpson evenness), the less functionally dissimilar species are as there are only a finite number of functional strategies (Mayfield et al., 2010). So while some communities with high species richness do not amount to high FRic, there are still large amounts of functionally redundant species which is also beneficial for the stability of ecosystem functioning (Mori et al., 2013). In GS3 communities, when species richness is low, higher numbers of species would easily lead to increased functional diversity as more species will lead to greater functional trait variation. FRed was significantly higher in GS1 than GS3 communities which would support this explanation (Figure 19). FRed is just as important as FRic in relation to ecosystem health as higher FRed will minimise the impact

that species diversity collapse will have on ecosystem functions (Fonseca and Ganada, 2001). This difference in FRed between GS1 and GS3 grasslands is of considerable importance as it indicates that the negative effect of species loss on ecosystem functioning may be more significant in different grassland habitats. This high functional redundancy should, in theory, benefit GS1 grasslands as it will have a buffering effect on both shifts in species composition and changes in climatic conditions (Yachi & Loreau, 1999).

Another reason why the functional diversity-species diversity relationship is not apparent in GS1 grasslands could be due to increases in intraspecific functional diversity which allows greater niche overlap (allowing for more species to coexist) without influencing community functional diversity metrics (Mason et al., 2011). This pattern has been observed in other dry limestone grasslands (Le Bagousse-Pinguet et al., 2014).

6.4 - Higher species and functional diversity are associated with lower, not higher productivity

In managed grassland ecosystems, most studies have indicated a unimodal relationship between species diversity and productivity (Brun et al., 2019). Functional diversity metrics and growth related CWM's have also been shown to have positive effects on productivity (Roscher et al., 2012). The results from this study suggest that higher diversity (both taxonomic and functional) does not support greater productivity (Figure 38, Figure 39, Figure 42). The results do not support a positive or unimodal relationship between species diversity and productivity. Instead the relationship is negative with the communities with the lowest species diversity (GS3 communities) showing the strongest negative correlation between diversity and productivity.

The absence of a relationship between CWM-LA and productivity (Figure 37) was unexpected as CWM values of productivity-related leaf traits (leaf area, specific leaf area) tend to be strong predictors of a community's productivity (Xu et al., 2018; Roscher et al., 2012). In this case it appears that measurements of CWM-LA are more likely a reflection on management (frequency of cutting or intensity of grazing) rather than a community functional strategy that would drive productivity. Different relationships between competition and productivity have been suggested in theory however there is little experimental evidence to support any clear relationship between the two (Bennett and Cahill, 2012). In the case of this study there is no support for any relationship between competition and productivity.

High CWM-LA values may also be reflective of vegetation communities that were either abandoned or under-grazed due to selective grazing. This is supported by the observation that sites with the greatest leaf area also had the greatest leaf dry matter content. If large leaf area was an indication of a resource acquisitive strategy then leaf dry matter content would decrease as plants opt for short term growth over preservation of leaf material. Instead the increase in large, tough leaves is more indicative of abandonment (Mori et al., 2013).

The negative correlation between CWM-LDMC and productivity was expected as higher CWM-LDMC is indicative of a stress-tolerant community with a more resource retentive strategy (Figure 37) (Garnier et al., 2001). CWM-LDMC was a better predictor of productivity than CWM-SLA or CWM-LA. Other studies that found similar results have suggested that the stronger predictive quality of CWM-LDMC is due to its lower intraspecific variation (Smart et al., 2017). This makes it a better predictor of productivity in comparison to other traits that are easily influenced by other factors such as light availability (Hodgson et al., 2011). Intraspecific variation in leaf traits was also analysed in this study and LDMC was found to be the least variable within species (Figure 10).

FDq was a significant predictor of productivity (Figure 39). This has been observed in other studies, however most research has found positive correlations between FDq and productivity (Roscher et al., 2012). Low FDq, along with low FEve, indicates a community where the dominant species are functionally similar. This suggests that strong niche partitioning had no beneficial effect on productivity, going against the “diversity hypothesis” (Tillman, 1996).

FRic also showed a negative relationship with productivity (Figure 38). Like FDq and FEve, a low FRic indicates trait convergence with very little differences in functional traits between the most dissimilar species in a community. A low FRic or FEve value indicates unrealised alpha niche space, which should in theory, lead to lower productivity (Petchey, 2003) however the opposite pattern is shown here. GS3 grasslands in particular showed the most stark decrease in productivity at higher FRic. This is unexpected as the benefits of FRic (greater overall variation in functional traits) should be more pronounced in habitats with fewer species as each species’ individual influence is greater and functional redundancy is low. It is likely the case that, in the more stressful GS3 grasslands, vegetation communities are dictated by environmental filtering (where niches are limited) rather than resource partitioning. This would cause the more trait convergent communities to produce more biomass as they are maximizing rather than partitioning resources.

The lack of strong correlations found between diversity metrics and productivity may also be due to an admitted shortfall of this study. The correlation analysis only includes single variables which is not indicative of grassland ecosystems which are influenced by a multitude of factors. Combinations of factors and the inclusion of unrecorded data such as site temperature and precipitation may provide stronger evidence for a relationship between

diversity and productivity. It is suggested, therefore, that further statistical analysis using a mixed effect model approach should be performed on this data to account for the aforementioned multifunctionality of grassland ecosystems.

6.5 - Higher diversity does not predict higher soil carbon and nitrogen

There were no overall patterns between diversity metrics and soil carbon and nitrogen. In GS4 grasslands both CWM-LA and CWM-LDMC showed significant positive correlations with soil carbon (Figure 32). Root length density showed a significant positive relationship with carbon but only at 20 cm soil depth (Figure 34). Functional redundancy showed a significant negative relationship with soil carbon but only in the GS4 grasslands (Figure 36). In the managed GS4 grassland soil carbon was negatively correlated with both Simpson diversity and Simpson evenness but not with species richness (Figure 41).

In theory, Higher levels of competitive CWM leaf traits lead to increased soil carbon (Zou et al., 2016; Yang et al., 2019; Sheng et al., 2022). High levels of functional divergence in communities (as indicated by high FDq and FDiv) should also lead to higher soil carbon through its benefits on niche complementarity (Zou et al., 2016). Species diversity would also be expected to positively affect soil carbon by the same concept. Such diversity should lead to greater variety in rooting patterns, resource use and soil microbial diversity, all of which can benefit soil carbon stocks (Yin et al., 2025). The absence of any such trends in this study suggests that complementarity effects and even niche partitioning have no effect on soil carbon.

Both CWM-LA and CWM-LDMC were positively correlated with soil carbon in GS4 grasslands. If it is presumed that CWM-LA is an influential trait in relation to soil carbon, then

it is likely that a predominantly resource acquisitive vegetation community will both produce more biomass which, through root exudation or by litterfall, leads to increased soil carbon (Poorter & Garnier, 2007; De Deyn et al., 2008). The positive relationship between CWM-LDMC and soil carbon, on the other hand, may be due to the correlation between high LDMC and high litter quality which is less likely to be decomposed and more likely to be stored as soil carbon (Kazakou et al., 2006).

It is also possible that the correlation between CWM-LA, CWM-LDMC and soil carbon may be due to land abandonment. The pattern between these variables was only present in the GS4 grasslands which was the only habitat that included abandoned sites. As mentioned previously, both CWM-LA and CWM-LDMC can increase when grasslands are abandoned (Mori et al., 2013). So too can soil carbon as the decrease in biomass removal leads to more soil inputs.

It should be noted that soil carbon and nitrogen are also likely responsible for influencing functional diversity. Functional diversity metrics and CWM leaf traits are both effect and response traits, meaning they both influence and are influenced by other ecosystem parameters (De Bello et al., 2013; Diaz & Cabido, 2001). In more intensively managed systems such as the GS4 sites, which were fertilised, cut and grazed, the functional traits of vegetation are more likely a response than an influencer on ecosystem functioning.

In the GS4 habitat, higher soil carbon and nitrogen corresponded with a decrease in species diversity but had little effect on functional diversity (Figure 35, Figure 41). FDq and FRed were an exception with FDq showing strong yet insignificant negative correlation with soil carbon (Figure 36). This has been observed in other studies where more favourable soil conditions led to convergence of competition related leaf traits (Helsen et al., 2014; Tillman,

1990). Other studies have suggested that enrichment of soils will have greater influences on functional diversity than species diversity (Flynn et al., 2009); however the opposite was observed here. FRed decreased significantly at higher soil carbon and nitrogen. This is reflective of the loss of species diversity as the number of functionally redundant species decreases with increased soil carbon. It is interesting to note that species richness was uninfluenced by soil carbon and nitrogen. Instead the results suggest that higher soil carbon influences abundances (as can be seen with the negative correlation between both Simpson diversity and evenness with soil carbon). This highlights the importance of assessing functional diversity when considering ecosystem stability as, even though species richness is even throughout the GS4 sites, the loss of species will likely have different effects depending on the site in question (as FRed is suggested to buffer against species loss) (Pillar et al., 2013). This is an important consideration as agricultural improvement often leads to the loss of low abundance species (Goldberg & Miller, 1990).

In comparison to the above-ground traits, the below-ground root traits (root length density) had a more straightforward relationship with soil carbon (Figure 34). At 10 cm soil depth there was no correlation between soil carbon and RLD however at 20 cm the relationship was significantly positive. This correlation was seen across both GS3 and GS4 habitats. This supports other evidence that root length density benefits long term carbon sequestration (Bardgett et al., 2005). The fact that higher RLD supports greater soil carbon than the actual diversity of root systems suggests that species diversity may be less important for soil carbon storage. A study by Yin et al., (2025) found something similar where functionally similar species with large RLD stored more carbon than functionally diverse species that showed greater complementarity in root traits. It is also interesting to note that only at the greater soil depth did RLD correlate with soil carbon. This suggests that the deeper roots are more important for carbon sequestration. It may also indicate that plants with deeper rooting

systems (i.e. have greater RLD in deeper soils) produce the greatest amount of root exudates (Powlson et al., 2011).

While higher RLD at greater soil depths can benefit carbon sequestration, the pattern between RLD and soil carbon in most other studies is usually negative as RLD negatively correlates with soil fertility (Dodd et al., 2011) as higher fertility leads to decreased competition for below-ground resources. This is only true for deeper soils as improvement promotes root growth in the shallow soils where fertiliser is applied (Dodd et al., 2011).

6.6 - Diversity metrics and leaf traits are significantly influenced by soil pH

Soil pH is one of the strongest influencers on plant growth (Adams and Adams, 1983). It has also been observed to strongly impact the diversity and composition of grassland communities (Critchley et al., 2002). This study also found pH to influence species diversity, functional diversity and growth related leaf traits (Figure 21, Figure 23, Figure 24). Strong positive correlations were found between pH and CWM-LA, contradictory to other studies (Dong et al., 2020). This was true both overall and within GS4 habitat types. Considering that CWM-LA showed a positive correlation with soil carbon, this is a somewhat surprising result as application of fertiliser (which would increase soil carbon) usually leads to acidification of soils through nitrification processes (Tuyen et al., 2006).

CWM-LDMC also increased significantly with soil pH in the GS4 sites. The increase in both CWM-LDMC and CWM-LA with increased soil pH may all be confounding variables in relation to management intensity in GS4 grasslands. The sites with lower management intensity that had larger, tougher leaves due to undergrazing may also have higher pH soils due to lower litter input or fertilizer application.

Increases in soil alkalinity in GS4 grassland also coincided with significant decreases in both functional evenness and Simpson diversity/evenness. This suggests that more alkaline relevés contained less even spreads of functionally dissimilar species. While the higher soil pH did not influence functional richness or total species, the decrease in FEve suggests less efficient niche partitioning in the community with decreases in functional redundancy (Figure 23)

Overall the sites with near neutral pH (6-7) supported the greatest functional richness and species diversity (Figure 23, Figure 24). Near neutral grassland habitats are known to be better for plant growth (Marrs, 1993). This in turn can cause a relaxation on environmental filtering, allowing for a greater diversity of species and functional strategies (higher FRic). This is unsurprising as both the upper and lower extremes of soil pH lead to nutrient limitations which in turn limit the available, occupiable alpha niche space (Critchley et al., 2002). This suggests that more neutral soil pH is optimal for grassland diversity and emphasises the importance of monitoring management practices that influence the natural soil pH of semi-natural grasslands. The benefit of soil pH for promoting diversity in grasslands has also been shown to disappear with increased aridity (Pulparina et al., 2016), suggesting that climate change may influence these observed diversity patterns in the future.

6.7 - Diversity-productivity relationships are habitat dependent

There were overall negative relationships found between diversity and productivity in this study. Both functional and species diversity varied in their relationship with productivity in the different grassland habitat types (Figure 38, Figure 39, Figure 42). Though no control was exerted over management or abiotic factors, there are evident differences among the grassland habitats in relation to management, soil conditions and environmental conditions. Other studies that have analysed manipulated grassland ecosystems have found the

diversity-productivity relationships to shift along gradients of management intensity (Nie et al., 2024) and soil nutrients (Guo et al., 2023).

The dry-humid acid grassland (GS3) showed the strongest negative relationship between diversity and productivity. These grasslands were species poor and, based on their significantly higher CWM-LDMC (Figure 13), were more stressful environments. This goes against previous studies that suggest that, in lower resource environments, diversity has a stronger positive effect on productivity (Wang et al., 2022). The observed differences between habitats in the diversity-productivity relationship may also be due to differences in the most limiting resource in each habitat type.

The GS3 grasslands also had a wide range of management intensities ranging from heavy grazing to near abandonment. So while the heavily grazed GS3 grasslands may have increased in diversity (Hallett et al., 2017) they could have simultaneously suffered in their productivity. This change in the biodiversity-productivity relationship from unimodal to negative due to high management intensity has been observed elsewhere (Brun et al., 2019).

6.8 - Productivity and soil carbon are better predicted by inherent habitat characteristics than either functional or species diversity

It was hypothesised, based on previous observations, that grassland productivity could be predicted by measurements of functional diversity and species diversity (Roscher et al., 2012, Tillman, 1996). Previous research that found strong correlations between functional diversity and productivity have been performed in manipulated grassland systems where efforts are exerted to control for all variations in management and abiotic conditions (Roscher et al., 2012). Such experiments may thus exacerbate the effect that diversity may have on natural ecosystems where other variables differ considerably. The results of this study,

therefore, do not disregard the importance of functional and species diversity but rather indicate how such relationships are less apparent when the ecosystems in question vary significantly in both their inherent characteristics and their management practices.

While the functional diversity shows little predictive power for productivity it may be the case that the functional traits presented by the most dominant species, which are uninfluenced by functional or species diversity, may better illustrate grassland productivity. CWM-LDMC showed strong negative correlations with productivity across all grassland habitats, which agrees with most theoretical predictions (Lavorel and Garnier, 2002). Once again this pattern may be due to variations in management intensity and abiotic stresses with CWM-LDMC being more of a response trait (Mori et al., 2013; Zou et al., 2018).

Like productivity, soil carbon and nitrogen were not well predicted by either functional or species diversity, contrary to the significant correlations found in other studies (Zou et al., 2016; Yang et al., 2019). CWM values related to resource acquisitive traits have elsewhere been hypothesized to positively correlate with soil carbon (Zou et al., 2016; Yang et al., 2019; Sheng et al., 2022). This study found positive correlations between CWM-LA and soil carbon and nitrogen, potentially supporting the theory that a predominant resource acquisitive strategy leads to greater soil fertility. The fact that this pattern was only observed in the extensively managed and fertilized grassland GS4 habitat may suggest that such variables are likely confounding and are both responses to nutrient input or, alternatively, land abandonment. The significant negative correlation between Simpson diversity and evenness with soil carbon in GS4 grasslands also suggests the former as both under and over management can lead to diversity loss (Uchida et al., 2018).

Chapter 7 - Conclusions

Semi-natural grasslands are an important source of biodiversity, productivity and carbon sequestration. It was hypothesized that high biodiversity and functional diversity would have positive impacts on productivity and soil carbon and nitrogen through better resource partitioning leading to complementarity effects. Instead the observed relationships between productivity and both species diversity and functional diversity were either negative or absent, suggesting that farmers will be forced into a trade-off between monetary and ecological gains. Differences between habitats in their functional diversity and CSR strategy were predicted due to observed differences in management and abiotic conditions. The grassland habitats not only differed significantly in functional diversity and functional strategy but also in their productivity-diversity relationships. Therefore management practices that maximise productivity while maintaining biodiversity should take into consideration the habitat and abiotic conditions in question. Higher productivity was negatively correlated with soil carbon and nitrogen, suggesting that the ecosystem services of climate change mitigation and agricultural production do not co-occur in the studied semi-natural grasslands. The benefit of increased species diversity for increased functional diversity is also habitat dependent. Relationships between diversity and soil carbon and nitrogen concentrations were either absent or negative, becoming more negative in intensively managed grasslands. Overall the results do not suggest any benefits of increased functional or species diversity for productivity or soil carbon in semi-natural grasslands. Any future analysis with aims of finding functional diversity-productivity relationships should aim to minimise other influencing variables as it appears that, if functional diversity does in fact positively impact ecosystem processes, its influence is dwarfed by stronger forces such as management and inherent habitat conditions. It is also important to note that productivity and soil carbon concentrations alone do not indicate the current or future health of a grassland ecosystem. Therefore a multifunctional

approach (considering yield stability, drought resistance, disturbance recovery/resilience)
must be taken when assessing how diversity may benefit grassland ecosystems.

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Appendix

Site	Relevé	Mean NDVI	Max NDVI	Min NDVI	StDev NDVI	Survey date	Spatial resolution (cm)
215	215_1	0.83	0.92	0.19	0.03	17/07/2024	5.32
215	215_2	0.82	0.93	0.33	0.04	17/07/2025	5.32
215	215_3	0.79	0.90	0.17	0.06	17/07/2026	5.32
215	215_4	0.84	0.93	0.29	0.03	17/07/2027	5.32
227	227_1	0.695	0.89	0.10	0.13	16/07/2024	5.4
227	227_4	0.761	0.92	0.12	0.09	16/07/2025	5.4
227	227_5	0.731	0.89	0.12	0.10	16/07/2026	5.4
227	227_3	0.827	0.92	0.35	0.05	16/07/2027	5.4
463	463_2	0.75	0.92	0.31	0.04	19/06/2024	6.11
463	463_3	0.70	0.85	0.33	0.05	19/06/2025	6.11
642	642_4	0.84	0.95	0.5	0.04	11/07/2024	5.59
642	642_2	0.85	0.94	0.3	0.05	11/08/2024	5.59
642	642_1	0.87	0.95	0.3	0.05	11/09/2024	5.59
825	825_11	0.75	0.87	0.12	0.09	17/07/2024	5.42
825	825_10	0.80	0.90	0.37	0.04	17/07/2025	5.42
825	825_9	0.75	0.89	0.17	0.07	17/07/2026	5.42

1624	1624_1	0.72	0.93	0.13	0.12	18/07/2024	6.13
1854	1854_1	0.82	0.93	0.24	0.86	18/07/2024	6.07
1854	1854_3	0.83	0.90	0.51	0.86	18/07/2025	6.07
1854	1854_4	0.85	0.94	0.30	0.88	18/07/2026	6.07
1854	1854_5	0.75	0.93	0.04	0.85	18/07/2027	6.07
2702	2702_1	0.82	0.92	0.68	0.02	05/07/2024	5.47
2702	2702_2	0.81	0.91	0.57	0.03	05/08/2024	5.47
2702	2702_3	0.80	0.89	0.20	0.03	05/09/2024	5.47
2719	2719_1	0.85	0.92	0.64	0.023292	08/07/2024	5.76
2719	2719_3	0.86	0.93	0.67	0.021875	08/08/2024	5.76
2719	2719_7	0.88	0.94	0.62	0.024234	08/09/2024	5.76
2719	2719_8	0.86	0.93	0.64	0.02818	08/10/2024	5.76
2722	2722_3	0.87	0.95	0.57	0.02	12/07/2024	5.36
2722	2722_4	0.87	0.94	0.57	0.02	12/08/2024	5.36
2722	2722_6	0.73	0.88	0.42	0.04	12/09/2024	5.36
2722	2722_7	0.76	0.90	0.28	0.06	12/10/2024	5.36
2722	2722_8	0.85	0.94	0.54	0.03	12/11/2024	5.36
2722	2722_9	0.86	0.94	0.54	0.02	12/12/2024	5.36

Table S1. NDVI data for each relev  from the 2024 season

The table includes NDVI values for each relev  along with the surveyed dates as well as the overall ground resolution.

Table S2. Link with information on all Settings and filters used in generating the orthomosaics for NDVI analysis.

<https://docs.google.com/spreadsheets/d/12v6h9EHe4w2RGq1TFOPqdQiSNWGfNSyq/edit?usp=sharing&ouid=115442016640992531937&rtpof=true&sd=true>

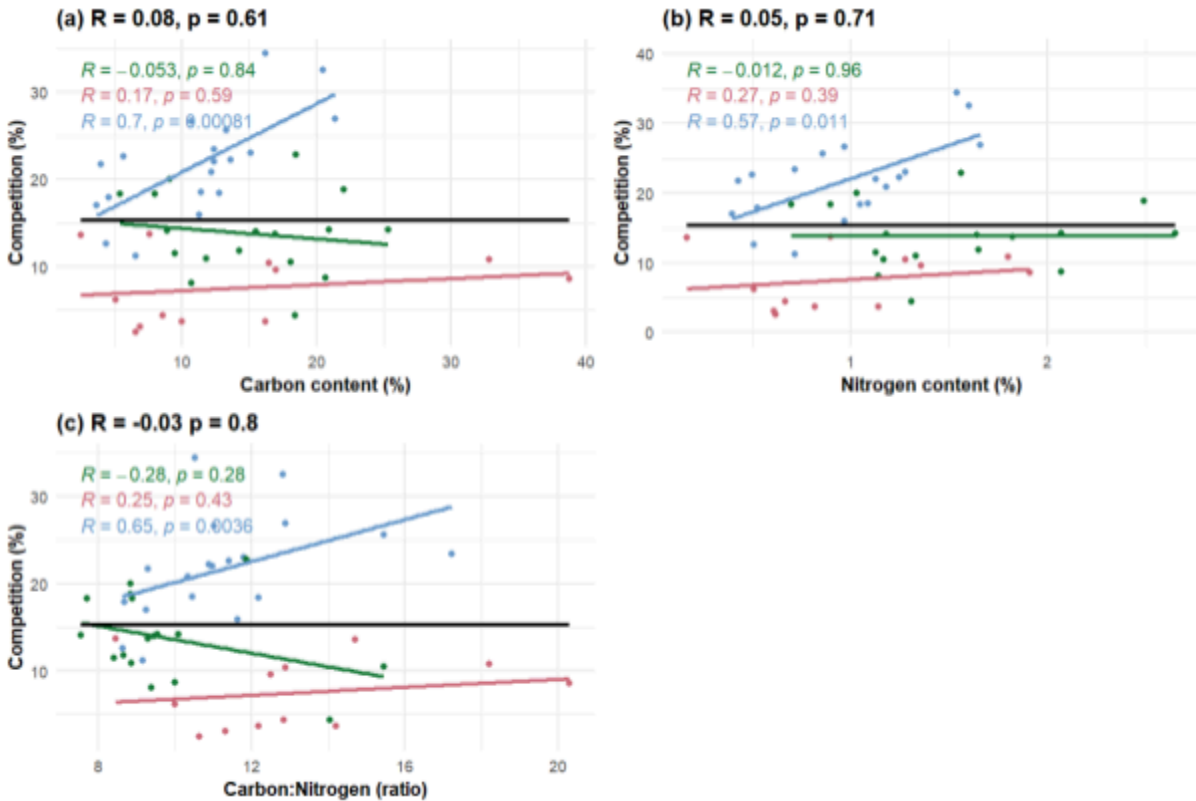


Figure S1: Relationship between Competition and soil parameters.

Relationship between Competition (derived from CSR) with soil carbon content (a), soil nitrogen content (b) and carbon:nitrogen ratio (c). The overall linear regression between the two variables is indicated by the black line and the regression based on habitat type is indicated by coloured lines (green for GS1, red for GS3 and blue for GS4). The statistics are derived from Spearman-Rank tests. Data points, representing individual relevés, are also coloured based on habitat.

