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Lawn and Order: The influence of top-down and bottom-up drivers on grass functional traits



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“Green was the colour of the grass...”

-Taylor Swift

This thesis is dedicated to

Lou and Tom “Esh” Eshelman

Without your unconditional love and support throughout my life, this
would not have been possible.

Thesis Abstract

Grasslands cover approximately 40% of the land surface and are central to humanity and its many industries, such as livestock, agriculture, and ecotourism. Their structure and composition are shaped by both top-down (e.g. herbivory and fire) and bottom-up (e.g. temperature, water, light, and nutrient availability) environmental drivers. In particular, grazing is a strong top-down process shaping grassy ecosystems over millions of years. Grassland ecosystems are rapidly changing and increasingly threatened by rising temperatures, increased drought periods, land use change, and altered fire regimes. Furthermore, shifting grazing regimes due to megafaunal extinctions, livestock introductions, or rewilding efforts continue to drive changes in grassland dynamics but in ways that are not well understood. Understanding the diversity of life history strategies within grasses and how species respond to environmental change across a diversity of spatial scales is critical to developing a predictive understanding of ecosystem change. My thesis investigates how grass community composition and structure respond to environmental change, with each research chapter utilising varied data sources and focusing on a different spatial scale and environmental contexts.

Chapter Two addresses the concept of grazing lawns which are short-statured, grazer-dependent vegetation communities, which persist via positive feedback. Through a literature synthesis, I compiled a global database of grazing lawn case studies, incorporating information on climate, dominant vegetation composition and associated grazer communities. By assessing their climate range, vegetation composition, grazers maintaining them, and grazer-vegetation associations, my analysis provides the first standardised framework for identifying grazing lawns offering objective criteria for future research. I found grazing lawns to be globally widespread, arising from diverse grazer-vegetation associations across ecosystems rather than the historic focus on African C₄ grass-centred communities. Grazing lawns occur across wide climate gradients, with climatically-correlated variation in the composition of C₃ grasses, C₄ grasses, sedges, and forbs. Equally, grazers are taxonomically diverse, with body sizes spanning five orders of magnitude rather than the original emphasis on megafauna. The widespread occurrence of grazing lawns indicates that positive feedbacks can emerge from various grazer-vegetation associations,

emphasising the cross-ecosystem relevance of grazing processes and informing global grazing management strategies.

In Chapter Three, I examine how environmental gradients shape grass functional traits and life history strategies across Madagascar. I focused on herbarium specimens as an under-utilised source of plant trait data. Madagascar is an excellent study region, given its rich grass flora (approximately 550 species) and environments that span gradients from warm and wet tropical to Afrotropical. Using herbarium specimens, I measured six grass traits of 260 species related to plant size and the leaf economic spectrum. Linear models revealed strong positive correlations between herbarium and field-collected data supporting herbarium specimens as a reliable data source for trait analyses. Focusing on five hypothesised key drivers of grass differentiation, trait-environment relationships were quantified using phylogenetic linear mixed models (PLMMs) and multi-model inference was used to predict island-wide trait distributions. Model results showed temperature, nutrient availability, and fire occurrence to be strong predictors for most traits, while water availability and grazing had marginal or non-significant relationships. I used Pearson's correlation coefficient and a principal component analysis to examine trait coordination. Trait coordination aligned with well-established leaf economic and size spectra, signifying functional trade-offs between traits related to resource acquisition, retention, and competition shape grass life history strategies. Our findings confirm that grasses, through strong trait trade-offs, exhibit distinct life history strategies that vary along two primary axes of variation, with trait positions along these axes shaped by top-down and bottom-up environmental pressures. My findings contribute to the wider understanding of grass differentiation along environmental gradients at a regional scale and improve predictions of grasses responses to environmental change.

In Chapter Four, I investigated the impacts of 20 years of grazing management on grass species composition and structure in the temperate Scottish Uplands. I asked whether changes in functional composition of grass communities, focused on seven functional traits, resulted from species turnover or intraspecific trait variation. Grass community composition and functional trait data were collected at sites that had experienced one of three intensities of grazing with replicates across three catchments (i.e. location) and two levels of

topographic position (i.e. drainage). Multivariate abundance models were used to assess the effect of grazing, plot drainage, and location on composition. Location explained differences between plots, suggesting that compositional variation was primarily driven by shifts in the relative abundance of widespread species across the landscape. To examine the degree to which intraspecific trait variation is driven by grazing, community trait variation was decomposed into species turnover and intraspecific trait variation. Increased grazing reduced plant height at flowering and leaf size while increasing leaf thickness and specific leaf area, all primarily driven by intraspecific trait variation. High intraspecific trait variations within these grass community responses suggest these ecosystems exhibit resilience to disturbance. Understanding the role of intraspecific variation in shaping community responses will potentially improve predictions of how changes in grazing management impact Scottish grassy ecosystems.

By utilising diverse data sources, my thesis assessed how environmental drivers, like grazing, interact to shape grass functional traits, life history strategies and community composition across environmental contexts. I found that broad climatic gradients primarily shaped large-scale trait patterns, while local factors, such as disturbance and soil conditions, likely drive finer-scale differentiation. Although grazing is a key global driver of grassland dynamics, its detection at broad spatial scales is reliant on high-resolution, locally collected data. Remote-sensing proxies and herbarium-derived trait data can be utilised to detect key trait-environmental relationships; however, the coarse resolution of certain environmental proxies may limit the detection of some relationships. Additionally, incorporating intraspecific trait variation into trait- and community-based analyses clarified how trait trade-offs differentiate grasses across gradients and the mechanisms underpinning grass community change, demonstrating the importance of including intraspecific trait variation in ecological studies. Together, these findings underscore the importance of key top-down and bottom-up drivers in structuring grasslands across scales and provide new insights into the mechanisms underlying grassland resilience to environmental change. This knowledge can improve predictions of how these ecosystems might respond to climate and land-use change, informing policy decisions and guiding effective management strategies.

Layman's Summary

Grasslands are a widespread and globally important ecosystem, covering approximately 40% of the Earth's land surface. Home to over 800 million people globally, grasslands are central to industries such as agriculture, livestock, and ecotourism. The structure and composition of grasslands are shaped by two main types of environmental drivers: top-down drivers, like fire and grazing, which remove plant material and influence how plants grow back, and bottom-up drivers, like temperature, water, light, and nutrient availability, that affect resources available to plants and how well they can grow. Grazing, in particular, is a strong top-down force that has shaped grasslands for millions of years. Today, grasslands are changing rapidly due to rising temperatures, more frequent droughts, conversion to agricultural land, changes in the frequency and intensity of burning, and shifts in grazing – whether due to extinctions, livestock replacements, or efforts to reintroduce wild grazers (i.e. rewilding). To better manage these systems, we must understand how grasslands respond- both their structure and composition- to these changes and whether those responses differ when looking at global, regional, or local patterns. My thesis explores how grass communities respond to environmental change, with each research chapter utilising different data types and focusing on a distinct spatial scale and environmental contexts.

In Chapter Two, I focused on grazing lawns - communities of short-statured plants maintained by grazers that persist through positive grazer-vegetation feedback. I defined a clear set of characteristics to identify grazing lawns. I reviewed the literature to build a global database of grazing lawn case studies that included information about each lawn's climate conditions, dominant vegetation and associated grazers. Despite being historically found in tropical grasslands grazed by large mammalian herbivores, I found grazing lawns occur worldwide in diverse climates and arise from varied grazer-vegetation associations. Grazing lawn vegetation included grasses, sedges, and forbs and grazers included mammals, birds, fish, reptiles, and invertebrates, with body sizes spanning five orders of magnitude. The widespread occurrence of grazing lawns indicates grazer-vegetation feedbacks can emerge from various grazer-vegetation pairings, emphasising the role of grazing as a cross-

ecosystem process. This analysis provides the first standardised framework for identifying grazing lawns offering objective criteria for future research.

In Chapter Three, I examine how grasses differentiate in structure across environmental gradients within Madagascar. Madagascar, which has a grass flora of approximately 550 species and includes a range of environments from warm, wet tropical to Afromontane, was an excellent case study to examine trait-environmental relationships. Using herbarium specimens, I measured six grass traits of 260 species related to plant size and resource use (the leaf economic spectrum). Through linear models, I found a strong positive correlation between herbarium and field-collected trait data supporting herbarium specimens as a reliable source for trait analysis. Through families of trait-environmental models, I found temperature, nutrient availability, and fire occurrence strongly correlated with most measured traits. In contrast, water availability and grazing had weaker or non-detectable relationships. By analysing how traits related to one another, I discovered clear trade-offs where grasses balance growth, resource use and competition in response to environmental drivers. These trade-offs form two major axes of trait variation – the size and leaf economic spectra. Top-down and bottom-up environmental drivers shape trait positions along these axes. My findings contribute to the broader understanding of how grasses adapt to diverse environments at a regional scale, ultimately helping us predict how grasslands might respond to future environmental change.

In Chapter Four, I investigated the impact of different grazing levels, applied over 20 years, on grass species composition and structure in the Scottish Uplands. Focusing on seven traits related to grazing adaptations, I asked whether changes in the structure of these grass communities are due to species turnover (i.e. replacement by species with better-suited trait values), intraspecific trait variation (i.e. trait adjustments within species), or a combination of the two. Grass community composition and functional trait data were collected at sites that had experienced one of three grazing intensities which were replicated across three within-site locations and two hillside positions (i.e. plot drainage). The effects of grazing, plot drainage, and location on composition and structure were assessed using multivariate and mixed linear models. Compositional differences between plots were mainly driven by plot location; however, the effect of grazing on composition

was minimal. Grass community structure did change with more intense grazing, reducing grass height and leaf area. However, these structural changes were primarily due to intraspecific trait variation. High intraspecific trait variations indicate that these grass communities can tolerate grazing disturbances without major shifts in species composition. Recognising how communities respond to increased grazing will improve predictions of how changes in grazing management impact grassy ecosystems, particularly within the Scottish Uplands.

My thesis used different data types to assess how key top-down and bottom-up environmental drivers interact to shape grass structure and community composition across environments. Across my three chapters, I found that climate mainly shapes grass traits at large scales, while local conditions, such as grazing and soil, likely drive small-scale differences. While grazing's effects on grasslands can be seen globally, detecting its influence broadly requires detailed local data. Remote-sensing and herbarium-derived trait data can be useful for detecting important trait-environmental relationships, but the resolution of some remote-sensing data may limit the detection of some relationships across scales. Additionally, incorporating species trait variation into trait- and community-based analyses helped to clarify trait patterns differentiating grass structures across varied environments and grass community changes under grazing. Together, these findings highlight key top-down and bottom-up drivers' important role in structuring grassland systems across spatial scales and provide new insights into how grassland communities respond to environmental change. This knowledge can improve predictions of how grasslands might respond to climate and land-use change, helping to develop effective land management and conservation strategies for these highly important ecosystems.

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Declaration of AI usage

Through the writing of this thesis I used AI softwares such as Grammarly and ChatGPT to help my writing and to fix R code. This has been very helpful given my diagnosed dyslexia and ADHD. In no cases have I used AI-generated text within this thesis.

Chapter 1: General Introduction

Introduction

Ecosystems worldwide are experiencing substantial alterations in plant species dominance and distributions, primary productivity, and nutrient cycles due to shifting anthropogenic management and environmental change (Ellison et al., 2017; Sala & Maestre, 2014). Grasslands and savannas, which cover approximately 40% of the land surface, are undergoing rapid transformations due to climate change and activities such as agriculture expansion, land-use change, and the removal or replacement of large grazing herbivores (Bardgett et al., 2021; Crowley, 2010; Gang et al., 2014; Hoekstra et al., 2005; Johnson, 2009; Jones, 2019; Malhi et al., 2016; Owen-Smith, 1988; Zhu et al., 2024). These alterations influence biodiversity, carbon and nutrient cycling, and ecosystem resilience - an ecosystem's ability to withstand environmental change or disturbance without significantly altering its structure or processes (Byrd et al., 2015; Gossner et al., 2016; Gunderson, 2000; Han et al., 2008; Lamarque et al., 2014). Therefore, a deeper understanding of grassland dynamics- the complex interactions among grassland plants, animals, soils, disturbances, and abiotic conditions (e.g., water, nutrients, climate) that drive changes in community composition, species traits, biotic interactions, and ecosystem functions - is needed for predicting and mitigating the ecological consequences of such changes on a global scale.

Ecosystems are defined by interactions between top-down (e.g. fire or grazing) and bottom-up (e.g. light, nutrient, or water availability) ecological processes that shape their composition and structure across spatial and temporal scales, but the relative influence of these drivers varies across systems (Hunter & Price, 1992; Power, 1992). In grasslands, grazing is a strong top-down process that has shaped grassy ecosystems over millions of years, playing a significant role in their evolution, distribution, composition and function (Niu et al., 2025; Retallack, 2001; Stebbins, 1981). However, shifting grazing regimes- whether through megafaunal extinctions, livestock introductions, or rewilding efforts- continue to drive changes in grassland dynamics but in ways that are not well understood (Malhi et al., 2016; Stebbins, 1981). As grassland distributions are likely to shift with climate change (Jones, 2019; Zhu et al., 2024), a better understanding of how top-down and bottom-up processes interact and shape grassland composition and structure is needed.

Without a clear understanding of these drivers' influence on grasslands, efforts to restore or maintain these systems risk being ineffective or even counterproductive. Therefore, this thesis explores environmental and ecological processes shaping grassland communities, focusing on the role of grazing in structuring grass functional traits, life history strategies and community compositions across spatial scales.

With approximately 11,000 species, grasses are among the most successful and globally widespread plant families, forming the structural and functional foundation of grasslands (Clayton et al., 2014). Although grassland communities also include sedges (Cyperaceae), rushes (Juncaceae), and forbs, grasses dominate due to their high dispersal ability, ecological flexibility, and ability to tolerate disturbances like fire, herbivory, and drought (Linder et al., 2018). Exhibiting substantial functional differentiation, grasses' adaptations enable them to rapidly colonise areas and influence fire and grazing regimes, reinforcing vegetation-disturbance feedbacks that maintain grassland structure (Archibald et al., 2019; Archibald & Hempson, 2016). The deep evolutionary history of grasses, coupled with their functional adaptations to diverse environmental gradients and disturbances, makes them a relevant taxon for assessing functional and community responses, providing important insights into how grasslands may respond to environmental change.

Grassland ecosystems

Grasslands are characterised by a dominant cover of grasses, with woody vegetation present to varying degrees (Blair et al., 2013; Dixon et al., 2014; Gibson, 2008). Despite grasses only accounting for 3% of all plant species on Earth, grasslands cover approximately 40% of the Earth's land surface (approximately 52,544,000 km²), making them the most extensive terrestrial cover type, surpassing forests and agricultural lands (Gibson, 2008; White et al., 2000). These ecosystems encompass a range of habitats, including temperate subhumid grasslands, temperate woodland, hummock savannas, pyric tussock savannas, and trophic savannas, as defined by the IUCN global ecosystem typology (Keith et al., 2020) (Figure 1.1). While the IUCN typology captures most grassy habitats globally, some regions, such as northern Eurasia, remain unclassified, highlighting gaps in our understanding of global grassland dynamics.

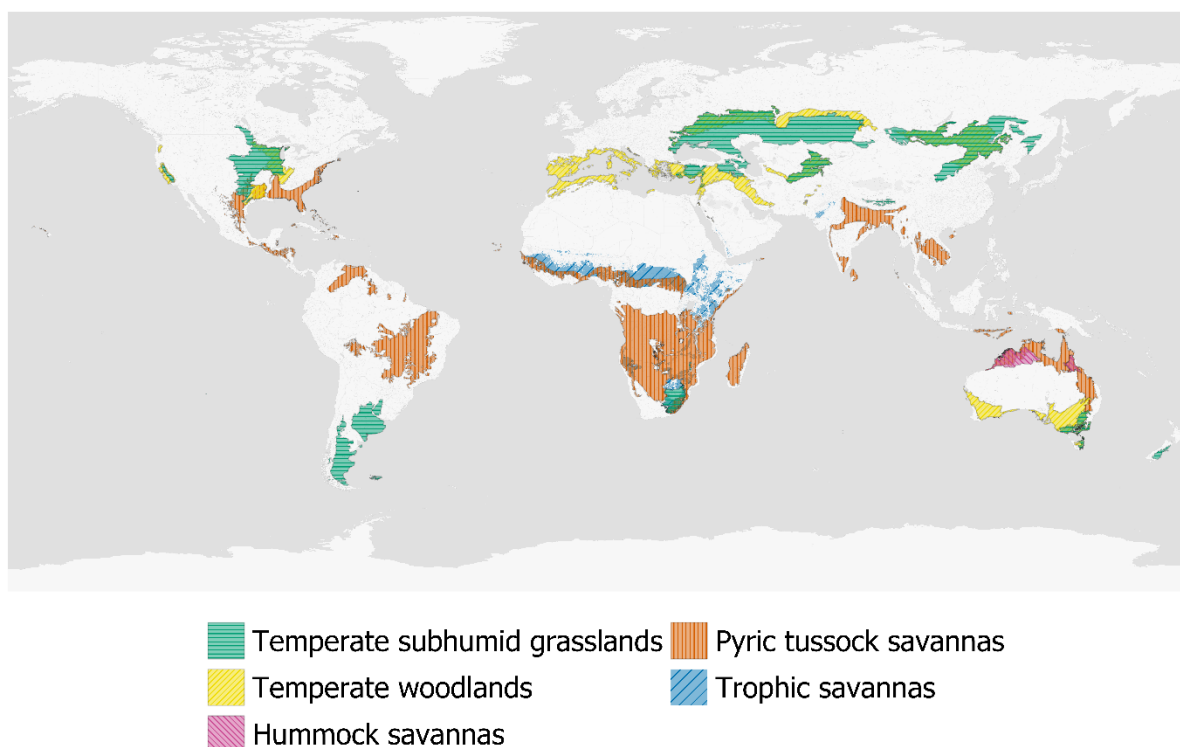


Figure 1.1. **Global distribution of major grassland ecosystems**, based on the IUCN topography classification (Keith et al., 2020).

Origins of grasslands

The history of grasslands is necessarily rooted in the origin of grasses (Poaceae) that first appeared in the Late Cretaceous or Early Tertiary (Paleocene), approx. 70 Million years ago (Ma) (Coughenour, 1985; Jacobs et al., 1999) (Figure 1.2). By the Early to Middle Tertiary (approx. 15 Ma), the opening of Palaeocene and Eocene forested environments facilitated an increase in the abundance of grasses utilising C_3 photosynthesis, the photosynthetic pathway by which the majority of plants fix atmospheric carbon dioxide (CO_2) into a three-carbon compound (Jacobs et al., 1999; Janis et al., 2000; Osmond et al., 1982).

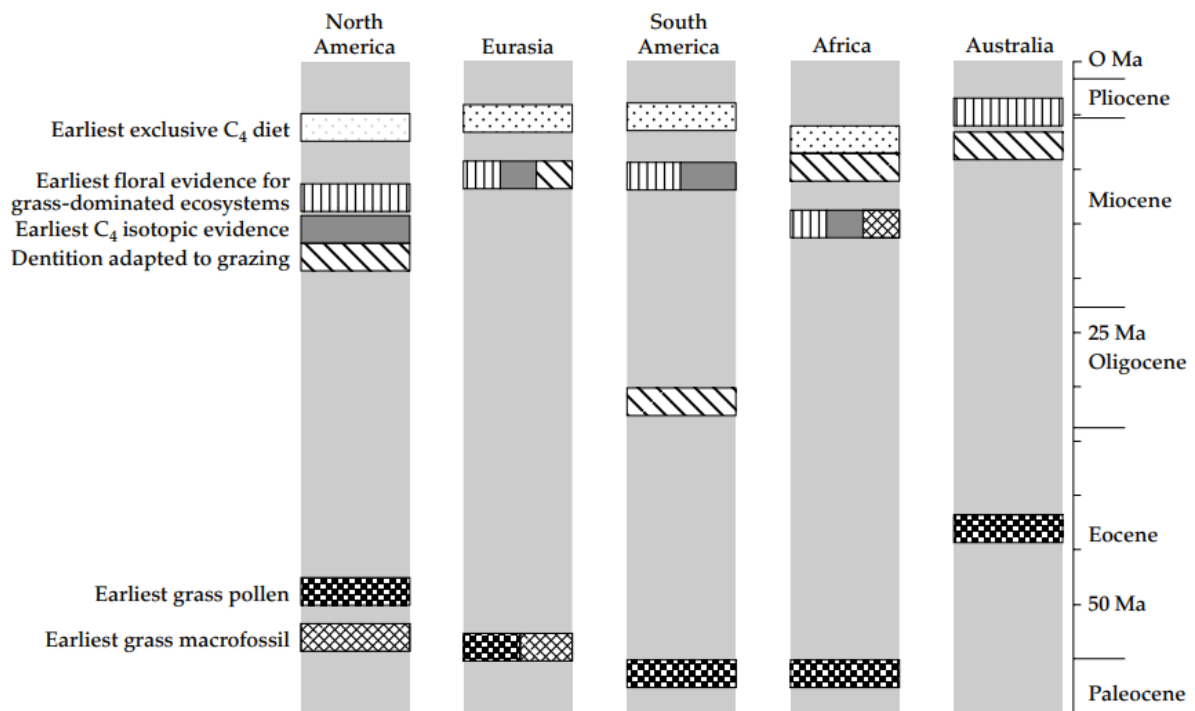


Figure 1.2. **Generalised summary of the establishment of grass-dominated ecosystems worldwide.** Shading within each column corresponds to the events listed on the left, while the timeline on the right denotes geological epochs. Taken from Gibson (2008), which was reproduced with permission of the Missouri Botanical Garden Press from Jacobs et al. (1999)

Grassland expansion has often been attributed to the coevolution of grasses and grazers - animals that consume mostly herbaceous ground forage such as grasses - a process that likely began during the Eocene (55-45 Ma)(Mack & Thompson, 1982; Retallack, 2001; Stebbins, 1981). Around this period, grazers evolved fundamental adaptations such as durable, high-crowned teeth that enable them to withstand wear and efficiently break down the tough fibrous material of grasses (Sanson, 2006). The emergence of such dental adaptations varied across regions, with some fossil records indicating that they appeared as early as 31.5 Ma in South America (Shockey, 1997) (Figure 1.2). Jointly, grasses developed traits, such as basal meristems, deciduous shoots, and belowground nutrient reserves, that enabled them to tolerate, avoid, or resist defoliation (Archibald et al., 2019; Coughenour, 1985; Owen & Wiegert, 1981). Such coevolutionary dynamics facilitated the emergence of grass-grazer positive feedbacks that maintain open ecosystems across wide environmental gradients (Hempson et al., 2015; McNaughton, 1984). In conjunction with these

evolutionary developments, climatic and ecological changes throughout the Miocene likely led to the spread of grasses into open habitats at the expense of woody vegetation (Gibson, 2008; Spriggs et al., 2014).

During the Miocene, grasses evolved the C_4 photosynthetic pathway, a biochemical addition to the ancestral C_3 pathway that allows plants to efficiently concentrate atmospheric CO_2 while minimising photorespiration (Edwards et al., 2010, 2010; Gowik & Westhoff, 2010; Sage, 2004) (Figure 1.2). This adaptation significantly improved water-use efficiency and carbon assimilation, providing a major competitive advantage in hot and dry environments (Hattersley, 1983; Osmond et al., 1982). The C_4 pathway, which has evolved independently 22-24 times in grasses, likely evolved in response to declining atmospheric CO_2 levels and rising global temperatures (Cerling et al., 1997; Christin et al., 2013; Sage, 2004). By the Late Miocene and Pliocene (8-3 Ma), the expansion of C_4 grasses led to the displacement of C_3 grasses in many regions, particularly in the tropics and subtropics (Edwards et al., 2010). As a result, C_4 grasslands became dominant in many regions, establishing their global distribution, which remains largely unchanged today (Cerling et al., 1997; Edwards et al., 2010; Jacobs et al., 1999). Currently, nearly 42% of all grass species use C_4 photosynthesis - a substantial percentage despite its more recent origins (Osborne et al., 2014).

Grassland biogeography

Grasslands are among the most widespread terrestrial ecosystems, found on every continent except Antarctica and occurring across nearly every climatic zone except for the poles, high alpine regions, and extreme arid zones (Squires et al., 2018; Suttie et al., 2005; White et al., 2000). Grasslands span broad temperature and precipitation gradients; mean annual temperatures in grasslands can range from 0 °C - 26 °C, while mean annual precipitation varies from 250 mm/year in arid grasslands to over 1000 mm/year in mesic grasslands (Blair et al., 2013; Whittaker, 1970) (Figure 1.3). These ecosystems frequently experience high intra- and interannual variability in precipitation, leading to fluctuations in net primary productivity (NPP) (Nippert et al., 2006; Shaw et al., 2022). Grasslands occur at elevations ranging from sea level in coastal areas, to over 4500m in montane regions, such as the neotropical páramos (Aparecido et al., 2018; Blair et al., 2013). Their distributions are

not only shaped by climate but also by disturbances such as fire and grazing (Keeley & Rundel, 2005; Lehmann et al., 2011; Staver et al., 2011; Stebbins, 1981). Over the past few centuries, human activities—including burning and livestock grazing—have further modified these ecosystems, altering their extent and composition (Archibald & Hempson, 2016; D’Antonio & Vitousek, 1992; Leys et al., 2018; Li et al., 2019).

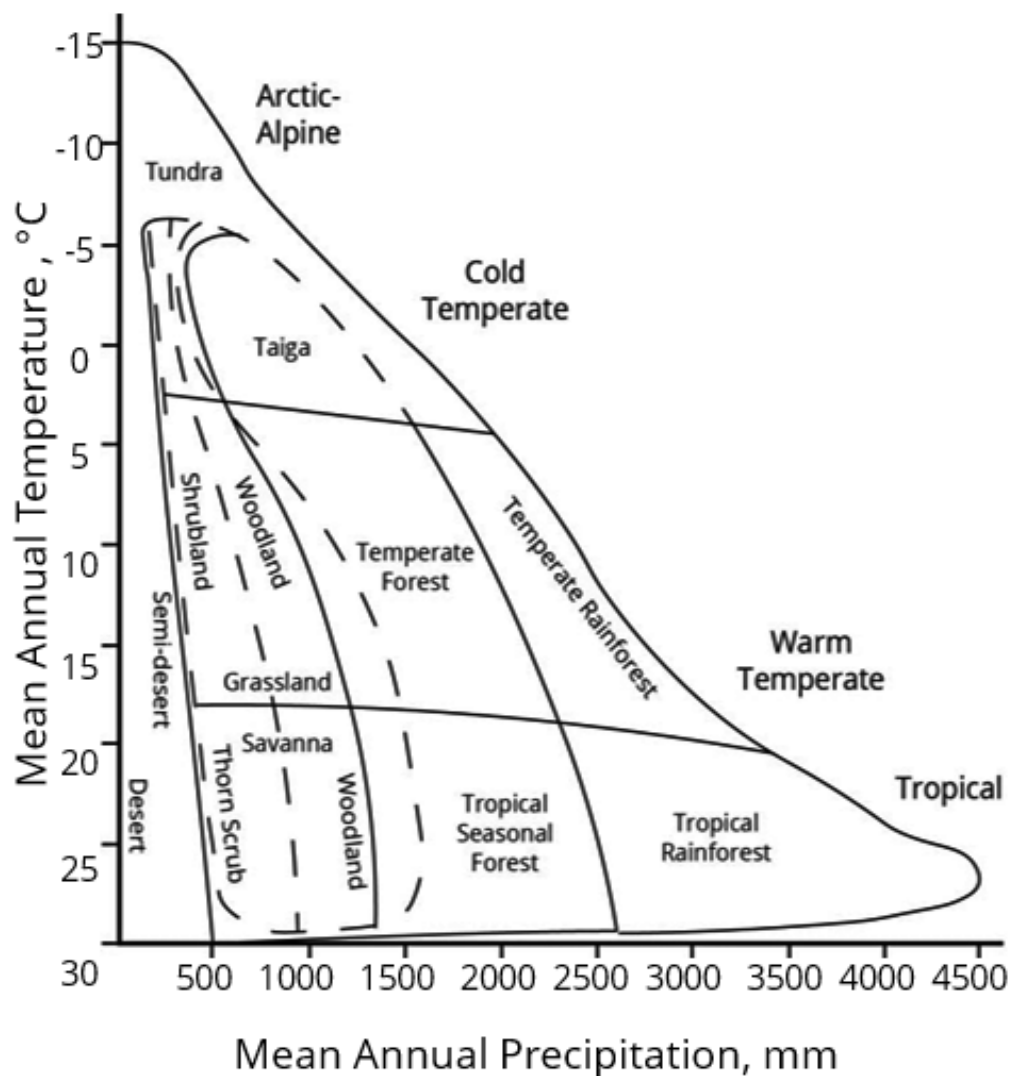
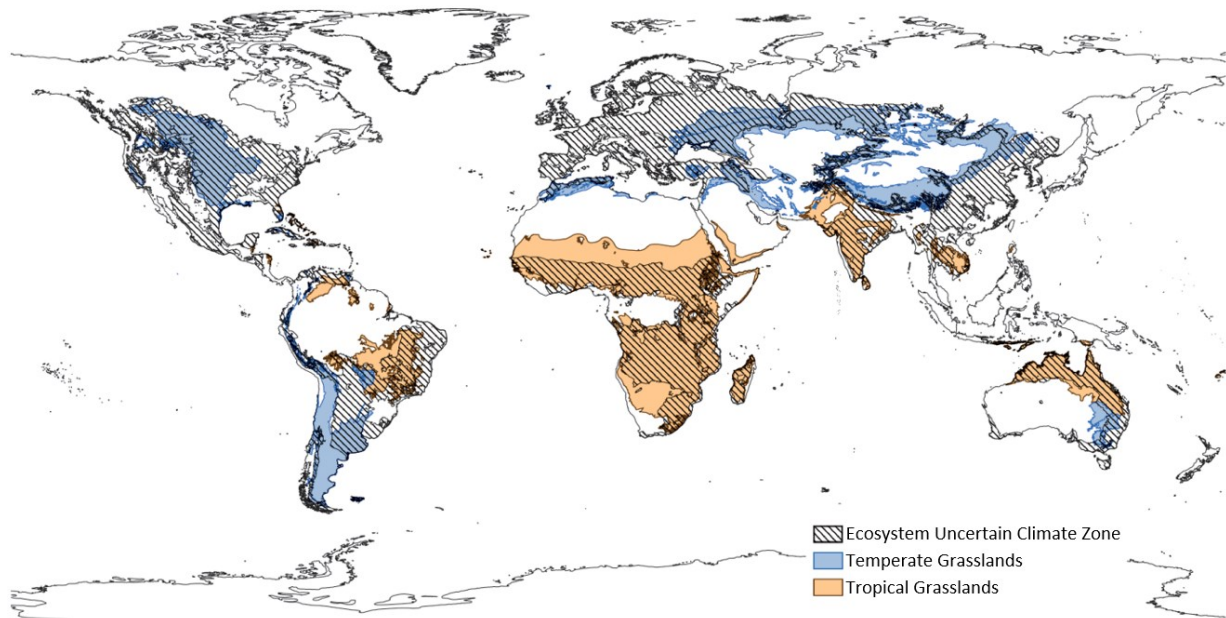


Figure 1.3. **Whittaker's biome distributions are defined by combinations of mean annual temperature and mean annual precipitation.** Overlaid figure follows Whittaker (1970), reproduced with permission from Pearson Higher Education. . Dashed lines represent the Ecosystem Uncertain Climate Zone, areas in parameter space where the resulting biome classification depends on additional factors such as seasonality of fire, drought and grazing.

Despite their global distribution, grasslands exhibit substantial regional variability in composition, structure, and ecological function (e.g. how much carbon they store, how they cycle nutrients), shaped by local (i.e., single site) and regional variations in climate, geology, soil moisture, and disturbance regimes (Gibson, 2008). This variability has led to their broad classification into two major types: tropical and temperate grasslands, which differ in climate, dominate plant functional type, and major ecosystem processes. This distinction has shaped much of grassland research, leading to largely separate fields of tropical and temperate grassland ecology. As a result, much of the scientific understanding of these systems remains divided, with research focusing on the distinct ecological dynamics of each type rather than their shared processes.

Tropical and temperate grasslands

Tropical grasslands, including savannas, dominate 20% of the global land surface, covering significant portions of Africa, Australia, and South America (Pennington et al., 2018; Scholes & Archer, 1997) (Figure 1.4). Found in tropical and subtropical regions, these ecosystems experience wide variations in precipitation, ranging from 800-2500 mm/year in South America, 350-2000 mm/year in Australia, and 300-1500 mm/year in Africa (Pennington et al., 2018). Tropical grasslands are shaped by warm temperatures and highly seasonal precipitation, conditions favouring the dominance of C₄ grasses, primarily from the Andropogoneae and Chloridoideae subfamilies (Edwards & Still, 2008; Griffith et al., 2020; Lehmann et al., 2011; Pennington et al., 2018). Furthermore, fire and grazing strongly regulate their vegetation structure. Both act as competing consumers of above-ground biomass while regulating woody cover, promoting grass persistence, and favouring divergent grass architecture (Archibald & Hempson, 2016). These grasslands, particularly in Africa, support most of the world's remaining mammalian megafauna that remove large amounts of above-ground biomass (Voysey et al., 2023; Waldram et al., 2008). However, these megaherbivore populations face increasing threats from habitat fragmentation, poaching, and the expansion of livestock, which are rapidly altering grazing regimes (Hempson et al., 2017; Ripple et al., 2015).



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Figure 1.4. Global distribution of tropical (orange) and temperate (blue) grasslands. Most grassland falls within the Ecosystem Uncertain Climate Zone (diagonal lines) where their distribution is limited by local factors such as soil properties and disturbances. Taken from Stevens et al. (2022).

In contrast, temperate grasslands are predominantly in the northern hemisphere across North America and Eurasia, receiving precipitation between 150-1200 mm/year (Lieth & Whittaker, 1975) (Figure 1.4). These ecosystems are dominated by C_3 grasses - primarily from the Pooideae subfamily - and support flora and fauna adapted to cooler, less seasonal environments with relatively fertile soils (Blair et al., 2013; Frank et al., 1998). As in tropical grasslands, grazing and fire regulate grassland structures, removing biomass and preventing woody encroachment (Canals et al., 2024; Capozzelli et al., 2020; Kirkpatrick et al., 2020). However, since 50-7k years ago (kya), temperate grasslands have experienced widespread native megafaunal extinctions- particularly in North America and Europe- leading to the replacement of wild herbivores with livestock (Malhi et al., 2016; Owen-Smith, 1988). These extinctions shifted grazing regimes, transformed fire dynamics in areas like North America, and altered the mosaic of open and closed habitats across these continents (Gill et al., 2009; Johnson, 2009; Svenning, 2002). As a result, these shifts have raised key questions about the effects of changing grazing regimes, emphasising the need

for a better understanding of how herbivory interacts with other environmental processes to shape grassland dynamics.

Despite their inherent differences in climate, dominant flora, and faunal assemblages, both tropical and temperate grasslands are shaped by combinations of top-down (e.g. fire, grazing) and bottom-up (e.g. soil moisture, nutrient availability) drivers. Although these ecosystems are often studied separately, this division overlooks shared ecological processes that govern their structure and function. Examining how these drivers influence grassland communities across multiple spatial scales (e.g. local, regional, and global) and ecological contexts (e.g. tropical and temperate) can help bridge this divide, providing a more unified understanding of grassland community assembly and revealing both universal and context-dependent influences and responses.

Ecosystem uncertainty

While climate sets the broad environmental conditions for grasslands, local ecological processes and feedbacks - such as seasonal inundation, edaphic conditions, fire, and grazing - determine whether an area remains open as grassy or transitions to a closed tree- or shrub-dominated state (Bond, 2019). Most grasslands exist within climatic zones where two or more vegetation types can co-exist, termed the Ecosystem Uncertain Climate Zone (Bond, 2005, 2019; Whittaker, 1970) (Figure 1.3; Figure 1.4). Within this climatic envelope, climatic conditions can support either grasslands or woody-dominated ecosystems, but local factors such as soil properties and disturbances, including frost, herbivory, and fire, often prevent tree establishment, maintaining open ecosystems (Archibald & Hempson, 2016; Bond, 2008, 2019; Joshi et al., 2020). The dynamic interactions between climate and local factors contribute to the heterogeneous distributions of grasslands worldwide. However, understanding where and/or why grasslands persist within this Ecosystem Uncertain Climate Zone requires a deeper exploration of how environmental drivers, such as climate and disturbance, interact to shape and maintain grassy ecosystems.

C₃ and C₄ grasses

One of the most defining functional characteristics of grasslands is the dominance of either C₃ or C₄ grasses, with turnover between these two photosynthetic types occurring along both local and global temperature gradients (Edwards & Still, 2008; Sage et al., 1999;

Teeri & Stowe, 1976). C₃ grasses, which thrive in cooler or shaded habitats, tend to dominate higher latitudes and montane regions, whereas C₄ grasses, which are more efficient under high temperatures, intense light, and seasonal drought, are more abundant in tropical and subtropical regions (Gowik & Westhoff, 2010; Osborne et al., 2014; Sage et al., 1999). However, while tropical and temperate grasslands are often distinguished by their dominant grass types, this classification is not absolute. C₃ grasslands can still persist in the high-altitude regions of the tropics, such as the Drakensberg mountain range in South Africa, while C₄ grasslands extend into warm, dry regions of the temperate zone, such as the Great Plains of North America (Edwards & Still, 2008; Griffith et al., 2020). These overlaps highlight how grassland composition can vary substantially, even within regions. Looking across diverse landscapes that span wide environmental gradients can provide valuable insights into the mechanisms driving grassland assembly and differentiation under different conditions. Grassland community structure is shaped by multiple interacting factors, including climate, edaphic properties, and disturbance regimes. Therefore, an integrative approach is needed to understand how these factors interact within and across regions to refine our knowledge of grassland composition and ecosystem dynamics.

Grassland biodiversity and ecosystem services

For millions of years grasslands have supported the evolution of diverse flora and fauna (Bonnefille, 2010; Mack & Thompson, 1982; Owen & Wiegert, 1981). Today, grasslands are globally significant biodiversity hotspots, providing a variety of microhabitats that sustain many specialised microbes, animals (e.g. megafauna, small mammals, birds, insects, and amphibians), and plants (Lemaire et al., 2011). Tropical grasslands, like the African savanna, serve as centres of diversity for grasses, megaherbivores and large carnivores, harbouring most of the world's remaining large mammalian populations (Murphy et al., 2016; Turpie & Crowe, 1994). Temperate grasslands, like the Eurasian steppe, are also highly diverse, with some grasslands exhibiting exceptional levels of plant species richness at small spatial scales (< 100m²) (Wilson et al., 2012). For example, European semi-dry basiphilous grasslands of the Czech Republic are among the most species-rich plant communities globally at a fine spatial scale, with 43 vascular plant species recorded within 0.1m² and 98 species within 10m² (Dengler et al., 2012). Grasslands' role as

biodiversity hotspots makes their conservation critically important for maintaining and preserving their diverse and specialised flora and fauna.

Grasslands provide essential ecosystem services that support both human livelihoods and global environmental processes (Sala & Paruelo, 1997; Zhao et al., 2020)(Figure 1.5). Home to over 800 million people globally, grasslands are central to industries such as agriculture, livestock, and ecotourism (Gibson, 2008; White et al., 2000). A variety of factors - such as environmental drivers and historical legacies - directly or indirectly shape grassland structure and dynamics, which, in turn, impact the ecosystem services they provide (Zhao et al., 2020) (Figure 1.5). The Millennium Ecosystem Assessment (2005) categorises these services into four groups: (1) *Provisioning services*, which are the basic materials that ecosystems provide for maintaining human populations, including food, fresh water, fibres, and habitats for plants and animals. (2) *Cultural services*, which represent the non-material benefits people gain from ecosystems, including cultural heritage, religious or spiritual values, recreation, ecotourism, education, and aesthetic appreciation. (3) *Regulating services*, which are the benefits gained through regulation of ecosystem processes such as climate and water regulation, erosion control, pollination, and carbon sequestration. (4) *Supporting services*, which underpin all other ecosystem services by maintaining fundamental ecological processes, such as soil formation, nutrient cycling, and primary production.

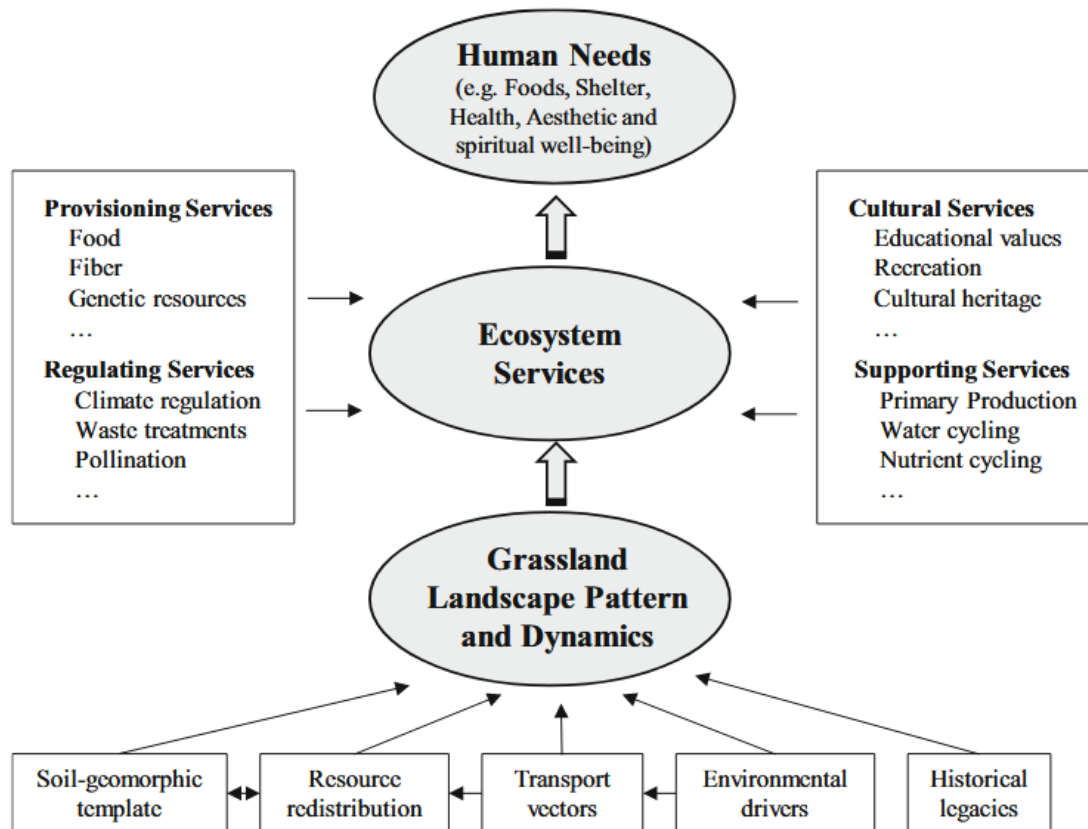


Figure 1.5. **Main categories of ecosystem services of grasslands and their interactions with grassland landscapes and human needs.** Ecosystem services categorised as: provisioning, cultural, regulating, and supporting services. Taken from Zhao et al. (2020), who modified it from Campbell et al. (1996), White et al. (2000), and Havstad et al. (2007).

Provisioning services

For millennia, grasslands have provided essential resources, such as food and fresh water, making them central to global food and water security (Emanuelsson, 2009; O'Mara, 2012; Sala & Paruelo, 1997; Zhao et al., 2020). Covering over 69% of the world's agricultural area, permanent meadows or pastures provide grazing land for numerous domestic animals, including sheep, cattle, horses, and buffalo, which supply meat, milk, wool, and leather products for human consumption and use (Food and Agriculture Organization of the United Nations, 2006; Reid et al., 2008). Furthermore, grasses are important to food security, as many staple crops for direct human consumption and animal forage, including corn, wheat, maize, and millet, are grasses (Gibson, 2008; O'Mara, 2012). In the United States alone,

grasses account for 57% of cattle forage (Barnes & Nelson, 2003). Additionally, grasslands serve as valuable fresh water sources particularly in arid and semi-arid regions, with permanent and seasonal water sources such as rivers, lakes, and marshes supplying drinking water and irrigation for millions (Egoh et al., 2009, 2016).

Cultural services

Grasslands have long been considered cultural landscapes, deeply intertwined with human tradition, livelihoods and heritage. Throughout human history, indigenous communities have influenced grasslands through traditional burning and grazing practices, maintaining open landscapes that support both biodiversity and traditional ways of life (Fischer et al., 2008; Gordon & Prins, 2008; Pyne, 2019). Additionally, many grasslands hold significant cultural and spiritual value, serving as sacred spaces, gathering places, and historical sites (Bullock et al., 2011; Hönigová et al., 2012; Lamarque et al., 2011; Stenseke, 2009; Stevens et al., 2022). In Europe, sacred sites, including burial mounds, have been kept open for centuries through traditional livestock grazing, preserving historical landscapes and cultural heritage (Apostolova et al., 2022; Deák et al., 2021).

Grasslands also provide opportunities for recreational activities, including hiking, fishing, bird watching, safaris, and hunting (Hönigová et al., 2012). As interest in nature-based experiences grows, grasslands are increasingly becoming major ecotourism destinations, attracting visitors to areas like Kruger National Park in South Africa, Yellowstone National Park in the United States, and Hortobágy National Park in Hungary (Gibson, 2008). Such ecotourism generates substantial revenue for local economies, with one study finding that game farms surrounding Kruger generate 15 times more income from tourism than cattle farming (Milton et al., 2003).

Regulating and supporting services

Grasslands provide essential regulating and supporting ecosystem services that contribute to ecosystem stability and resilience (Lemaire et al., 2011; Millennium Ecosystem Assessment, 2005; White et al., 2000; Zhao et al., 2020). These ecosystems regulate local and regional water quality and quantity, and also shape spatial and temporal patterns of runoff, floods, and aquifer recharge (Egoh et al., 2008; Milazzo et al., 2023; Sirimarco et al., 2018). Grasslands also facilitate nutrient cycling through the movement of nutrients

between soil, plants, and animals, with migratory grazing animals contributing to widespread redistribution (Batista-Dubeux et al., 2014; Dubeux & Sollenberger, 2019; Sitters et al., 2020). Furthermore, Grasslands act as a major carbon sink, storing large amounts of carbon in belowground biomass (Bai & Cotrufo, 2022; Sala & Paruelo, 1997). Grasslands account for one-third of global carbon stores while also accounting for approximately 33% of total terrestrial primary productivity, a level comparable to tropical forests (Beer et al., 2010; White et al., 2000). Collectively, these services- along with provisioning and cultural services- underscore the ecological, environmental, and cultural significance of grasslands.

Current status and threats to grasslands

In the last century, up to 49% of grasslands globally have experienced some degree of degradation (Egoh et al., 2016; Gang et al., 2014). This decline has been driven by rising temperatures (Buhrmann et al., 2016; Engelbrecht et al., 2015), increased drought periods (W. Zhang et al., 2019), agricultural conversion (Gibson, 2008; Hoekstra et al., 2005), altered fire regimes (Cunningham et al., 2024), and megafaunal declines (Crowley, 2010; Johnson, 2009). These pressures change grassland communities, leading to biodiversity loss, disrupted ecosystem services, and shifts in vegetation dynamics (Gossner et al., 2016). As climate change and land-use shifts continue to reshape grasslands, understanding how these communities respond to environmental pressures is important for developing conservation and management strategies that promote ecosystem resilience.

Restoring natural disturbance regimes, such as grazing, is increasingly recognised as a strategy for mitigating degradation and enhancing ecosystem resilience (Collins & Barber, 1986; Donlan et al., 2006; Fuhlendorf et al., 2009). In particular, rewilding projects that introduce large grazers are increasingly being used to restore grazing functions in grassland ecosystems that have lost most or all of their megafauna (Cromsigt, Kemp, et al., 2018; Donlan et al., 2005, 2006; Navarro & Pereira, 2012). Grazer rewilding can improve plant species richness, increase pollinator abundance, and limit woody encroachment (Garrido et al., 2019; te Beest et al., 2016; van Klink et al., 2016), while also potentially mitigating environmental change, enhancing ecosystem resilience to climate-driven shifts, and

reducing species extinction risks (Cromsigt, te Beest, et al., 2018; Gillson et al., 2011; Malhi et al., 2016; Olofsson & Post, 2018; te Beest et al., 2016).

As grazer rewilding interventions are expected to expand in the coming century, particularly in Europe (Araújo & Alagador, 2024; Pettorelli et al., 2018), a more unified understanding of how grazing shapes grasslands is needed. In particular, the interaction between grazing and environmental factors - such as temperature, water availability, and nutrient cycles - remains unclear. Therefore, this thesis aims to examine the impact of grazing on grass communities, their composition and structure, and its interactions with other environmental factors across different ecosystems and spatial scales. By clarifying these dynamics, this research aims to contribute to a wider understanding of grazer-grassland interactions, providing insights that can improve the success and effectiveness of rewilding initiatives.

Top-down and bottom-up drivers of grasslands

The widespread distribution, composition, and structural diversity of grasslands are shaped by combinations of top-down and bottom-up environmental processes, referred to hereafter as environmental drivers (Hunter & Price, 1992; Power, 1992). In combination, these drivers determine species composition, ecosystem productivity, and functional differentiation (Archibald et al., 2019; Dalglish & Hartnett, 2009; Pakeman, 2004; Palpurina et al., 2019). Top-down controls, including fire and grazing, are consumer-driven, regulating biomass accumulation, species dominance, and vegetation structure (Archibald & Hempson, 2016; Hunter & Price, 1992; Power, 1992). Conversely, bottom-up controls, driven by abiotic factors such as temperature, water availability, and nutrient availability, control resource availability which determines plant growth and productivity (Hunter & Price, 1992; Power, 1992). The relative influence of these drivers will likely vary spatially and temporally, depending on climate, disturbance regimes, and species interactions (Meserve et al., 2003). However, how these factors interact to shape grassland communities across different environmental contexts remain poorly understood.

Environmental drivers rarely act in isolation but instead interact in complex ways to shape grassland structure and resilience. For example, declining water availability alters nutrient cycling, particularly soil carbon, nitrogen and phosphorus availability for plants

(Dijkstra et al., 2012; Y. Zhou et al., 2025), while also intensifying grazing effects, amplifying the negative impacts on grassland communities (Bonnet et al., 2010; Hempson et al., 2022; Niu et al., 2025; M. Zhang et al., 2023). Despite the clear interactions, many studies examine environmental drivers independently (Bade et al., 1985; Moles et al., 2009), simplifying their influence on ecosystem dynamics. Improving our understanding of these interactions is necessary to link grassland community responses to environmental change (Keddy, 1992; Lavorel & Garnier, 2002; Violle et al., 2007). To address this gap, this thesis investigates how key environmental drivers- temperature, water availability, nutrient availability, fire and, in particular, grazing- jointly shape grassland communities, offering a more integrated perspective on the processes driving grassland composition and function.

Grazing as a key driver

As a defining feature of terrestrial landscapes for at least 300 million years, grazing - the act of consuming predominately herbaceous forage by animals - is an important top-down process shaping grasslands globally (Allen et al., 2010; Behrensmeyer et al., 1992). All grasslands are either currently grazed or have experienced grazing at some point in their evolutionary history (Behrensmeyer et al., 1992; Blair et al., 2013). Grazing influences plant community structure and assembly (Sala et al., 1986; Zainelabdeen et al., 2020), modifies fire regimes (Leonard et al., 2010), regulates nutrients and hydrological cycles (Asner et al., 2004; Augustine, 2003; van der Waal et al., 2011), and increases soil organic carbon storage (Abdalla et al., 2018). In some systems, grazing can also create distinct, productive habitats, known as grazing lawns, of short, palatable vegetation dependent on grazing for their establishment and persistence (Hempson et al., 2015; McNaughton, 1984). However, the effects of grazing are highly context-dependent, varying with climate, herbivore density, and evolutionary grazing history (Cingolani et al., 2003, 2005; Hobbs, 1996; Milchunas et al., 1988; Olff & Ritchie, 1998). This raises the question about the factors that influence grazing effects and whether grazing shapes diverse grassland ecosystems in similar ways despite varying ecological contexts.

Since the late Pleistocene (approx. 50 kya), climate change, habitat loss, and human predation have driven major shifts in grazing dynamics, including the extinction of many large grazers and, in some cases, their replacement by livestock (Cingolani et al., 2014;

Owen-Smith, 1988). These changes in grazing pressure have altered fire regimes (Furquim et al., 2024; Karp et al., 2021), promoted woody encroachment (Hempson et al., 2017; Owen-Smith, 1987) and transformed plant community dynamics (Eby et al., 2014; Koerner et al., 2014), reshaping the structure and function of many grasslands. As global grazing patterns continue to shift, transforming grasslands worldwide, it is important to understand how altered grazing regimes influence grassland community dynamics and the mechanisms by which these changes occur.

Community ecology

Understanding the processes that shape community structure and assembly is a central question in ecology (McGill, 2010). Two major theoretical frameworks in community ecology - niche differentiation theory and neutral theory - offer contrasting explanations for community assembly patterns (Adler et al., 2007; Gravel et al., 2006).

Niche differentiation theory proposes that species sort into communities by occupying different environmental or temporal niches (Silvertown, 2004). This differentiation is governed by their capacity to deal with deterministic processes such as environmental filtering and limiting similarity. Environmental filtering, also referred to as habitat filtering, occurs when abiotic and biotic factors constrain species composition, selecting for morphological attributes that enhance survival and fitness under given conditions (Cadotte & Tucker, 2017; Díaz et al., 1998; Maire et al., 2012). Alternatively, limiting similarity prevents ecologically similar species from coexisting as competition favours species that minimise niche overlaps. (Macarthur & Levins, 1967; Violle et al., 2011).

Neutral theory assumes species are functionally equivalent, suggesting that stochastic processes, such as random death, dispersal, and speciation, determine species distributions and abundances rather than functional differences among species (Caswell, 1976; Hubbell, 2011). Increasingly researchers acknowledge that species diversity and community assembly are likely shaped by a combination of deterministic and stochastic processes (Chase & Myers, 2011; Matthews & Whittaker, 2014; Stokes & Archer, 2010), as species exhibit functional differences that interact with environmental context to shape community structure (McGill et al., 2006). Therefore, examining how species and individuals

differentiate along climatic gradients and in response to disturbance regimes is necessary for understanding species coexistence and community assembly.

Life history strategies and functional trait ecology

Grasses exhibit substantial functional differentiation, driven by diverse life history strategies that allow them to exploit resources and persist across varied environments (da Silveira Pontes et al., 2015; Linder et al., 2018). These strategies are defined by syndromes of functional traits that determine species' ability to survive, grow, and reproduce in response to different environmental drivers (Laughlin, 2014; McGill et al., 2006). Functional traits are measurable morphological, physiological, or phenological attributes that strongly influence an individual's performance or fitness (Violle et al., 2007). Some traits relate to a function directly, such as photosynthetic pathway, while others reflect a function, like specific leaf area representing photosynthetic capacity (McGill et al., 2006; Violle et al., 2007). Functional traits are either shaped by environmental conditions through natural selection and adaptation or actively determine the environment a species inhabits (Lavorel & Garnier, 2002; Westoby et al., 2002). Furthermore, these traits mediate species interactions and resource use, influencing ecosystem processes such as nutrient cycling and primary productivity, thereby linking functional diversity with broader ecosystem processes (Chapin et al., 2000; Díaz et al., 2007).

Trait-based approaches offer a powerful tool to assess and predict community and individual responses along climatic and disturbance (e.g. fire and grazing) gradients (Díaz et al., 2001, 2004, 2007; Garnier et al., 2007; Lavorel et al., 2007; Pakeman, 2004). Because they focus on traits rather than taxonomic identity, trait-based approaches can be used comparatively across species or communities with little to no taxonomic overlap, providing a unified framework for studying ecological processes at multiple scales (Díaz et al., 2004; McGill et al., 2006; Reich et al., 1997; Rusch et al., 2003). However, most trait-based studies focus on woody vegetation (e.g. Cornwell & Ackerly, 2009; Fajardo & Piper, 2011; Koehler et al., 2012; Madani et al., 2018; Messier et al., 2010; Olson et al., 2018; Wigley et al., 2016) with far fewer examining grass traits (e.g. Jardine et al., 2020; Sandel et al., 2016; Simpson et al., 2020; Solofondranohatra et al., 2018). Moreover, when grasses are included in large-scale vegetation analyses, they are often grouped with woody species, which can obscure

distinct patterns of trait variation in grasses (Díaz et al., 2016; Moles et al., 2009; Reich & Oleksyn, 2004). As a result, grass-specific trait-environment relationships are less understood. Therefore, this thesis takes a grass-focused approach to examining trait-environment relationships across scales, identifying patterns of trait variation that underpin grass life history strategies to improve our understanding of community assembly and species adaption to top-down and bottom-up drivers.

Trait coordination

Within life history strategies, traits are functionally linked, often covarying in predictable ways (Armbruster et al., 2014; Díaz et al., 2016; Watson & Szathmáry, 2016; Westoby et al., 2002). However, these covariations are restricted by functional trade-offs, where physiological and morphological constraints limit possible combinations of traits that can be expressed (Chapin et al., 1993; Jardine et al., 2020; Keddy, 1992; Wright et al., 2004). For example, species that allocate resources towards fast growth and high photosynthetic rates often have higher biomass turnover and lower stress tolerance (Grime, 1979; Reich, 2014). These trade-offs shape species' life history strategies and explain their position along resource availability, stress and disturbance gradients (Grime, 1979, 2006; Laughlin, 2014). As a result, coordinated trait syndromes emerge from these trade-offs, defining major axes of variation in grass life history strategies (Díaz et al., 2004; Díaz & Cabido, 1997; Grime et al., 1997; Reich et al., 1997; Wright et al., 2004).

Axes of trait variation

Central to trait-based ecology is the identification of axes of trait variation that define species life history strategies in response to environmental drivers (Díaz et al., 2016; Grime, 1977; Westoby, 1998; Wright et al., 2004). One key axis of variation within grasses is size, reflecting trade-offs in competition, structure, and reproduction (Díaz et al., 2004; Sandel et al., 2016; Westoby, 1998). Along this axis, grass species balance investments in large structures that enhance competitive and dispersal abilities, against smaller, resource-efficient forms that improve stress tolerance and survival in limited resource environments (Grime, 2006; Keddy et al., 2002; Mashau et al., 2021; Westoby, 1998; Zhou et al., 2016). Another major axis of trait variation is the leaf economic spectrum (LES), which captures trade-offs in leaf traits between rapid resource acquisition (e.g. fast growth, high turnover)

and conservation (e.g. slow growth, long-lasting structures) (Díaz et al., 2004; Pierce et al., 2007; Simpson et al., 2020; Wright et al., 2004).

Influence of disturbance on trait variation

Where traits fall along trait variation axes is influenced by disturbances like fire and grazing, two major ‘consumers’ of aboveground biomass that shape grass structure and composition over time (Archibald & Hempson, 2016; Bond & Keeley, 2005). These top-down pressures drive much of the variation in grass communities globally and can be important in differentiating grass species functionally (Belsky, 1992; Koerner & Collins, 2014; Solofondranohatra et al., 2020). In response to these pressures, grasses have evolved distinct traits or plasticity that enable them to persist under these contrasting selective forces (Archibald et al., 2019; Archibald & Hempson, 2016).

Grasses persist under fire and grazing through combinations of avoidance, resistance, and tolerance traits (Archibald et al., 2019; Belsky, 1992; Cingolani et al., 2005). *Avoidance* traits minimise exposure to disturbances, either by reducing palatability to herbivores through tougher, less digestible tissues and sparse architectures or by developing structures with low flammability (Archibald et al., 2019; Cornelissen et al., 1999; Coughenour, 1985; Grime et al., 1996; Simpson et al., 2016). *Resistance* traits limit tissue loss during disturbances, with small, fragile structures minimising biomass removal under grazing or tall, dense growth forms that protect underground buds by keeping fire away from the soil surface (Archibald et al., 2019; Drescher et al., 2006; Gagnon et al., 2010). *Tolerance* traits enhance post-disturbance recovery by promoting rapid regrowth and flexible growth forms to improve competitive ability (Archibald et al., 2019; Díaz et al., 2001; Grime, 1994; Westoby, 1998).

However, fire and grazing select for different, often opposing, traits. For example, traits that reduce herbivory, such as increased leaf carbon and tannins, likely increase flammability, while traits minimizing flammability, like low biomass and high leaf moisture content, increase the likelihood of being grazed (Archibald et al., 2019; Grootemaat et al., 2015). Grasses must balance these fire- and grazing-adapted traits with those required for persistence under specific climatic conditions, yet how these factors interact to shape grass functional differentiation remains unclear. Furthermore, little is known about how

avoidance, resistance, and tolerance traits vary across spatial scales and environmental gradients. For example, are the traits enabling grass to persist under grazing in a tropical grassland the same as in a temperate context? Therefore, research is needed to understand how grasses respond to shifting disturbance regimes in different ecological contexts.

Trait variation's role in community responses

Trait variation can be assessed at two levels: interspecific (differences between species) or intraspecific (differences within species). While most trait-based studies focus on interspecific variation, assuming species-level means capture a majority of the functional differentiation (Bullock et al., 2001; Díaz et al., 2004, 2007; Jardine et al., 2020; Pakeman & Fielding, 2020), intraspecific variation can be substantial and both ecologically and evolutionarily important (Albert, 2015; Bolnick et al., 2011; Violle et al., 2007). Intraspecific variation plays a key role in species coexistence, community assembly, niche differentiation, and ecosystem processes such as nutrient cycling, litter decomposition, and primary productivity (Bolnick et al., 2011; Courbaud et al., 2012; Enquist et al., 2015; Nicotra et al., 2010; Sundqvist et al., 2011; Violle et al., 2012; Wright et al., 2016).

At a community level, trait shifts in response to environmental change can occur through species turnover (i.e. replacement by species with better-suited trait values), intraspecific trait variation (i.e. trait adjustments within species), or a combination of the two (Ackerly & Cornwell, 2007; Kichenin et al., 2013; Lepš et al., 2011). Communities with greater intraspecific variation may be more resilient to environmental change, as within-species trait variation can buffer against shifts in species composition (Hou et al., 2019; Jung et al., 2010). As environmental context and species diversity will alter how species turnover and intraspecific variation mediate community functional responses to environmental change (Albert et al., 2011; Siefert et al., 2015), it is important to capture within-species trait variation as it helps us understand community responses to short-term disturbances, such as shifts in grazing pressure (Volf et al., 2016).

Despite intraspecific variation accounting for approximately 25% of total trait variation within plant communities and 32% among communities globally (Siefert et al., 2015), research on grassland dynamics largely emphasises interspecific trait differences (species turnover), while overlooking or not accounting for intraspecific trait variation's role

in shaping community responses (Violle et al., 2012; Weiher & Keddy, 1995). Large trait databases, such as TRY (Kattge et al., 2011) or Grassbase (Clayton et al., 2014), facilitate the use of species means, as these databases do not always provide data at the individual level. However, incorporating intraspecific variation can strengthen grassland community analysis, improving our understanding of disturbance responses and community assembly processes (Albert et al., 2011; Jung et al., 2010; Siefert, 2012; Volf et al., 2016). Therefore, this thesis utilises herbarium- and field-collected data that incorporate intraspecific variation to better understand trait variation across scales and the role this variation plays in community responses to environmental drivers.

Trait relationships across ecological scales

Trait-environment relationships are inherently scale-dependent, with different patterns emerging at global, regional, and local scales (Messier et al., 2010). Global studies of grass functional differentiation (Jardine et al., 2020; Lehmann et al., 2014) typically reveal broad-scale environmental trends but often fail to capture finer-scale drivers such as soil variation, water availability and disturbance regimes (Grime, 2006). While broad climatic patterns exert strong selective pressures promoting trait convergence, local-scale factors shape competitive or facilitative ecological strategies (Bruehlheide et al., 2018; Díaz & Cabido, 1997; Grime, 2006). As traits vary across both spatial, temporal and organisational scales, from within a single individual (Pigliucci, 2001), within a species (Violle et al., 2012), between species (Westoby et al., 2002; Wright et al., 2001), and communities (Ackerly & Cornwell, 2007), focusing on portions of this variation spectrum results in fragmented understandings of trait variation across scales. Therefore, this thesis aims to identify general patterns and distinguish scale-dependent drivers of variation by assessing the impact of environmental drivers at global, regional, and local scales to develop a more comprehensive understanding of how environmental drivers shape functional traits.

Overall thesis aims and objectives

In my thesis, I aim to address knowledge gaps about top-down and bottom-up pressures shaping grassland ecosystems. I explore how grasses respond to grazing across different spatial scales and environmental contexts, assessing whether these responses follow general patterns, are shaped by local conditions, or result from a combination of

both. Furthermore, I examine how grazing interacts with other top-down and bottom-up drivers, such as temperature, nutrient availability, water availability, and fire, to shape functional traits and community assembly in grasslands.

My thesis investigates the ecological processes shaping grassland ecosystems at multiple spatial scales. My research is structured as three empirical chapters, each of which examine grasslands at a different scale or different environmental context and utilises varying data types (Table 1.1). Chapter 2 compiles case studies from the literature to examine grazing as a global driver in creating grazing lawns- unique habitats defined by positive grazer-vegetation feedbacks- across global environmental gradients. Chapter 3 uses grass functional traits measured from Malagasy herbarium specimens to quantify the relationships among top-down (fire, grazing) and bottom-up (temperature, nutrient availability, water availability) environmental drivers in shaping the functional traits of grasses within a regional flora. Chapter 4 draws on field-collected composition and trait data to examine the long-term effects of grazing on grass community composition and structure in the Scottish Uplands, quantifying the roles of species turnover and intraspecific trait variation in community change.

Table 1.1. **Summary of the analysis spatial scale, ecosystem context, and corresponding data sources**, including the types of data and spatial or temporal scales captured across chapters.

Chapter	Analysis Spatial Scale	Environmental Context	Data Utilised	Data Source	Scales Captured
2	Global	Terrestrial and aquatic ecosystems	Literature-derived vegetation and herbivore data	Species lists	Local
			Herbivore biomass	Trait database	Regional or Global
			Climatic data	Remote sensing	Global
3	Regional	Tropical grasslands	Herbarium-derived trait data	Herbarium trait data	Local or Regional
			Environmental proxies data	Remote Sensing	Regional or Global
			Phylogeny	Molecular analysis	Evolutionary
4	Local	Temperate grasslands	Field-collected trait data	Field surveys	Local
			Field-collect composition data	Field surveys	Local
			Landscape data (Treatment, Block, Drainage)	Field surveys	Local
			Phylogeny	Molecular analysis	Evolutionary

Together these chapters provide a multi-scale perspective on grass community assembly and differentiation under different environmental drivers. I seek for my research to contribute to a more nuanced understanding of grazing as a driver of grassland structure and function, with implications for conservation, restoration, and sustainable land management.

Thesis outline

The three empirical chapters have been written as standalone academic research papers. Chapter 2 has been prepared for submission to *Diversity and Distributions*, Chapter 3 to *Functional Ecology*, and Chapter 4 to the *Journal of Vegetation Science*. As these are intended for publication, there is some overlap in the background information provided in the introduction, particularly regarding trait ecology or the value of grassland ecosystems. At the beginning of each chapter, I acknowledge the authors involved in the research I have led, and where these chapters have multiple authors, 'we' rather than 'I' is used to discuss the research approach.

Chapter 2: Grazing lawns are globally distributed and include a wide range of taxonomic associations

Chapter 2 considers grazing lawns- unique habitats created by concentrated grazing. Based on the work of McNaughton (1984) and Hempson et al. (2015), I developed an attribute-based framework to identify grazing lawn case studies. Through a literature synthesis, I compiled 108 case studies to assess the climatic distribution and taxonomic associations of grazing lawns. This chapter specifically addresses the following questions:

1. What is the breadth of climatic space occupied by grazing lawns?
2. What is the diversity of vegetation functional groups associated with lawns and where do they occur geographically and across climatic space?
3. What is the diversity of grazer taxa and body sizes associated with grazing lawns and what are their geographic and climatic distributions?
4. What are the current vegetation-grazer associations structuring grazing lawns?

Chapter 3: Functional variation in grasses across Madagascar in response to environment

Chapter 3 uses Madagascar as a case study to investigate how top-down (fire, grazing) and bottom-up (temperature, nutrient availability, water availability) drivers combine to shape grass life history strategies at a regional scale. Utilising herbarium-derived data from Royal Botanic Gardens Kew and Natural History Museum Paris, I analysed over 1,600 individual grass measurements from 260 species- representing over half of the Malagasy grassy flora- measuring traits related to the size and leaf economic spectra. Trait-environment relationships and trait coordination were assessed using families of models to better understand grass life history strategies and differentiations along environmental gradients. This chapter demonstrates the utility of herbarium specimens in assessing trait-environment and trait-trait relationships, advocating for their broader use. This chapter specifically addresses the following questions:

1. How do bottom-up (temperature, nutrient deficiency, water availability) and top-down (fire, grazing) environmental drivers correlate with, and predict, variation in individual functional traits related to plant size (i.e. inflorescence height, culm diameter, leaf length and leaf width) and leaf economic (e.g. leaf nitrogen, leaf thickness) spectra? Do these relationships align with established hypotheses?
2. Are these traits coordinated with one another in their responses to environmental gradients? If so, what are the strengths of these relationships?
3. What is the multivariate nature of these trait relationships, and what do they reveal about grass life history strategies?

Chapter 4: Intraspecific trait variation drives functional shifts in grass communities under grazing in the Scottish uplands

Chapter 4 examines how long-term grazing influences grass community composition and functional traits at a local scale, incorporating landscape-level factors such as topography, catchment, and soil drainage. Using composition and trait data collected from a 20-year grazing experiment in the Scottish uplands - managed by the James Hutton Institute and the Woodland Trust - I investigated the underlying mechanisms driving community responses to grazing. Specifically, I assessed the relative contributions of species turnover

versus intraspecific trait variation (ITV) to community-level trait shifts, applying the decomposition of sums of squares statistical method presented by Lepš et al. (2011). This chapter specifically addresses the following questions:

1. Do trait values shift with grazing intensity? If so, in what direction?
2. Does community composition change with grazing intensity?
3. Are differences in grass community functional composition driven by intraspecific trait variation (ITV)?

Chapter 5: General Discussion

The final chapter synthesises my insights from the preceding chapters, discussing the strengths, weaknesses and limitations of each chapter and placing these findings within the wider context of grassland ecology. Additionally, it outlines potential avenues for future investigations in grassland ecology and trait-based research, emphasising the need for more comparisons across ecosystem types (e.g. tropical *versus* temperate grasslands).

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Chapter 2: Grazing lawns are globally distributed and include a wide range of taxonomic associations

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Abstract

Grazing lawns are short-statured, often biodiverse vegetation communities maintained via positive feedbacks with grazers. However, inconsistent nomenclature and a historical focus on tropical and subtropical C₄ grasslands dominated by large mammalian herbivores have hindered functional synthesis of information on grazing lawns. We aimed to broaden the concept of grazing lawns by assessing four facets of their diversity globally: 1) the climatic space they occupy, 2) vegetation composition, 3) causal grazers, and 4) vegetation-grazer associations.

We used an attribute-based identification framework and literature synthesis to identify grazing lawn studies collecting information on vegetation and grazer composition. We used principal components analysis (PCA) of environmental data to determine the climatic space occupied by grazing lawns globally, and ANOVAs on PCA axes and climatic variables to place grazing lawn vegetation and grazer types in climatic space. We used association grids and a bipartite web to characterise associations between dominant plant functional types and grazer taxonomy and body size.

We identified 108 terrestrial and aquatic grazing lawn case studies spanning six continents. In terrestrial environments, grazing lawns were found in habitats with a wide range of temperature and precipitation regimes, but were absent from extreme climates. The dominant lawn plant components (C₃ grasses, C₄ grasses, sedges or forbs) varied among environments. Grazers came from diverse taxa with body sizes spanning five orders of magnitude, including Mammalia, Aves, Reptilia, Pisces, and Gastropoda. The most frequently identified grazing lawns were dominated by C₄ grasses and grazed by macroherbivores (100-1000 kg).

Grazing lawns are a globally widespread phenomenon maintained by similar positive feedbacks arising from diverse vegetation-grazer interactions. Our attribute-based framework validated well-known examples while uncovering ecologically analogous systems in historically understudied regions, such as Europe and Australia. The widespread occurrence of grazing lawns shows that positive feedbacks can emerge from various vegetation-grazer associations, emphasising the cross-ecosystem relevance of grazing

processes and providing a functional basis for informing global grazing management and conservation strategies.

Keywords: consumer-resource feedback, positive feedback, concentrated grazing, grazer associations, environmental constraints

Introduction

Grazing is the act of consuming predominately herbaceous (i.e. non-woody) vegetation by herbivores and is an important ecological process that shapes ecosystems globally (Allen et al., 2010). Grazers reduce herbaceous biomass and height, maintaining open ecosystems and fostering feedbacks between herbivores and vegetation, driving patterns of plant community structure (Sala et al., 1986; Zainelabdeen et al., 2020), biodiversity (Gao & Carmel, 2020; McNaughton, 1983b; Yuan et al., 2016), nutrient cycling (Augustine et al., 2003; Van Der Waal et al., 2011), and landscape heterogeneity (Hobbs, 1996). These effects apply across varied environments in terrestrial and aquatic systems (Burkepile, 2013; Burkepile et al., 2020). Over evolutionary timescales, feedbacks between grazers and plants has culminated in distinct, productive vegetative communities with unique compositions dependent on grazing for their establishment and persistence (Hempson et al., 2015; McNaughton, 1984). These communities are important components of grazing systems, enhancing biodiversity through the creation of multiple grazing-dependent niches (Hempson et al., 2015; Sankaran et al., 2005; Young et al., 1995) and providing critical nutritional resources for grazers (Fox et al., 2015; McNaughton et al., 1997; Verweij et al., 2006). As such these grazer-dependent communities provide an opportunity to better understand grazing dynamics and its broader ecological impacts.

In terrestrial systems, grazing-dependent plant communities can often be termed “grazing lawns”, reflecting the close and uniform cropping that grazers undertake. First defined by McNaughton (1984), grazing lawns are characterised by a two-dimensional cropped herbaceous surface (termed a sward) of highly productive vegetation created and maintained by frequent grazing and positive feedback mechanisms. Grazing lawn vegetation is small-leaved and typically low-growing, often with horizontal stems and regenerative meristems close to, at or just below the soil surface as a spatial refuge from grazers (Hempson et al., 2015; McNaughton, 1984; Suzuki, 2008). Lawn species typically show high shoot density, deciduous shoots, belowground nutrient reserves, and rapid transpiration (Coughenour, 1985), all of which aid in rapid bottom-up compensatory growth in response to grazing (McNaughton, 1983a; Milchunas et al., 1988; Oesterheld & McNaughton, 1991; Rosenthal & Kotanen, 1994). In tropical grasses, where these plant adaptations have been

predominantly studied, this growth form results in a dense sward dominated by relatively nutrient-rich, digestible and palatable leaf material, offering grazers high biomass per bite and lower foraging costs than surrounding areas, further reinforcing concentrated grazing activity (Fryxell, 1991; McNaughton, 1979; Posse et al., 2000; Stobbs, 1973; Suzuki et al., 2009; Verweij et al., 2006).

Frequent or continuous concentrated grazing is essential for establishing and maintaining grazing lawns (Archibald, 2008; Hempson et al., 2015). This process is maintained by establishing a positive consumer-resource feedback between grazing animals and vegetation. Within this feedback, grazing: (1) promotes the growth of concentrated, palatable vegetation that is resistant or resilient to grazing (du Toit & Olff, 2014; Hempson et al., 2015; Mouissie et al., 2008); and (2) maintains relatively open areas of attractive forage by preventing invasion by taller and less palatable species or growth forms that would otherwise outcompete and overtop short lawn vegetation (Adler et al., 2001; Bond, 2022; du Toit & Olff, 2014; Voysey et al., 2020). This results in forage-rich areas with relatively high net primary productivity compared to surrounding areas, attracting further grazing (Burkepile, 2013; McNaughton, 1984; Milchunas & Lauenroth, 1993). Grazing lawn establishment typically occurs when a landscape feature concentrates grazing pressure (Archibald, 2008). Examples of concentrating agents include areas of higher nutrient concentrations (Arshad, 1982; Knapp et al., 1999; Veblen, 2012), water sources (McNaughton, 1983b), or recently burned areas (Archibald et al., 2005; Fuhlendorf & Engle, 2004). Grazers' social behaviours, such as herding (Augustine & McNaughton, 2006), territoriality (Waldram et al., 2008) or predator avoidance (Cromsigt et al., 2017), can also concentrate grazing for prolonged periods. However, overgrazing (the heavy utilisation of areas through grazers' removal of plant material) can disrupt this feedback, preventing plant regeneration and allowing the establishment of unpalatable vegetation (Hempson et al., 2022; Mysterud, 2006).

While the paradigmatic and best-studied grazing lawns are terrestrial and grass-dominated, such as those grazed by hippopotamus (*Hippopotamus amphibius*), wildebeest (*Connochaetes taurinus*), and white rhinoceros (*Ceratotherium simum*) in African savannas (Cromsigt & Olff, 2008; Hempson et al., 2015, 2022; Leonard et al., 2010; McNaughton,

1984, 1986), similar ecological dynamics have been recognised across a range of biomes, environments and taxa (Gruner & Mooney, 2013). For example, black brant geese (*Branta bernicla nigricans*) maintain sedge-dominated grazing lawns in Alaska, USA (Person et al., 2003), Bluespine unicornfish (*Naso unicornis*) graze on algal turf in the Great Barrier Reef (Hoey & Bellwood, 2009), and Aldabra Giant land tortoise (*Aldabrachelys gigantea*) maintain C₄-dominated “tortoise turf” in the Aldabra Atoll in the Indian Ocean (Walton et al., 2019). Nevertheless, historical associations of grazing lawns with mammalian grazers and grassland ecosystems, along with inconsistent terminology (e.g., “algal turf” and “tortoise turf”), have resulted in habitats that share grazing lawn characteristics but are not identified as such. This limits our ability to understand the true diversity and ecological significance of grazing lawns across climates and taxa. Therefore, here we survey the literature on grazing lawns and similar habitats to synthesise an overview of the climatic breadth and taxonomic characteristics of these habitats.

While all grazing lawns require grazers to exert top-down pressures to maintain the sward, grazer taxa vary enormously in body size. Body size determines grazer energy requirements, forage selectivity, and movement patterns, and hence the spatial scale over which grazers influence plant communities (Bukombe et al., 2019; Hopcraft et al., 2012; Ramesh et al., 2015). For example, large mammalian grazers (e.g. cattle, zebra) have high digestive efficiency and low metabolic demands per unit of body mass, allowing them to survive on lower-quality vegetation and thus exhibit reduced forage selectivity (Belovsky, 1997; Pringle et al., 2023). This broad foraging behaviour suppresses the growth of taller, less-palatable vegetation, making such large grazers well suited to initiation and maintenance of grazing lawns (Bakker et al., 2016; Pringle et al., 2023; Trepel et al., 2024). Conversely, small grazers (e.g. rabbits, geese) are typically selective in their foraging, thus limiting the pressure they can apply to a given ecosystem as individuals, potentially hindering their ability to initiate and maintain grazing lawns. This has led to questions about which taxa and body sizes are associated with grazing lawns, how these associations vary across climates, and whether certain taxa are only capable of creating lawns under specific climatic conditions. Exploring the diversity of vegetation, grazers, and their interactions

offers an opportunity to uncover the ecological and functional drivers of grazing lawn formation and persistence.

Climate exerts strong bottom-up controls on vegetation distribution and productivity, shaping the environmental constraints under which grazing lawns can form and persist (Adams, 2009; O'Sullivan et al., 2020; Wang et al., 2020). Temperature and precipitation directly affect aboveground net primary productivity (ANPP), with higher ANPP supporting vegetation better capable of recovering from defoliation (Hsu et al., 2012; Jung et al., 2022; Sun et al., 2021). Seasonal variations of temperature and precipitation also influence ANPP by defining the length of the growing season, impacting resource availability throughout the year (Jobbágy et al., 2002; Le Houérou et al., 1988; Robinson et al., 2013). These climatic patterns also indirectly influence grazer movement, as the seasonal availability of forage can drive spatial and temporal shifts in grazer presence (Craine, 2013; Staver et al., 2019). While the individual impacts of these variables on vegetation and grazers are well-documented (see examples, Aslam et al., 2022; Bade et al., 1985; Merkle et al., 2016), their combined role in shaping grazing lawn distributions and associated feedback loops remains unclear. Therefore, examining climatic patterns of lawn distribution can help elucidate the climatic limits to grazing lawns and grazing dynamics as a whole.

The grazing lawn concept has made pivotal contributions to the development of grazing ecology, although a historical focus on seasonally dry savannas and large mammalian grazers has potentially limited recognition of grazer-dependent ecosystems more widely. Here, we develop a set of grazing lawn attributes, without preference for environments or plant and animal taxa, that characterise grazing lawns in the broadest sense (Table 2.1), and apply these to identify case studies of potential grazing lawns that can be either author or attribute defined. We quantify the distribution and climatic breadth of grazing lawns worldwide and provide an overview of their taxonomic and functional characteristics. We address four questions: (1) What is the breadth of climatic space occupied by grazing lawns? (2) What is the diversity of vegetation functional groups associated with to lawns and where do they occur geographically and across climatic space? (3) What is the diversity of grazer taxa and body sizes associated with grazing lawns and

what are their geographic and climatic distributions? (4) What are the current vegetation - grazer associations structuring grazing lawns?

Methods

Grazing lawn attributes

McNaughton (1984) and Hempson et al. (2015) are classic research studies defining grazing lawns in African savanna ecosystems. Based on these we compiled 11 attributes typifying grazing lawns in their broadest sense (Table 2.1), representing characteristics of vegetation and grazers, and the feedbacks between the two required to maintain concentrated interactions. We used these attributes to identify case studies for inclusion in our database. Grazing within these case studies was identified as herbivory by any animal of herbaceous ground vegetation, which encompasses sedges, forbs (i.e., non-graminoid, herbaceous angiosperm species), grasses and benthic aquatic algae and macroalgae.

Our definition and analyses excluded woody vegetation. It is worth noting that browsing lawns - communities created through the concentrated browsing of dense, highly branched canopies of woody plants with high foliage density protecting interior foliage - are considered somewhat analogous to grazing lawns, representing a consumption-centred positive feedback between plants and herbivores (Cromsigt & Kuijper, 2011). Browsing lawns have been identified and discussed in previous papers (see Cromsigt & Kuijper, 2011; Du Toit et al., 1990; McNaughton, 1984).

Table 2.1. ***Grazing lawn attributes synthesised from McNaughton (1984) and Hempson et al. (2015).*** Attributes are categorised based on their primary association with (1) ecosystem feedbacks and processes, (2) grazers, or (3) vegetation characteristics.

Grazing Lawn Attributes	
Feedbacks and Processes	Grazing acts as the main disturbance.
	Grazing enhances forage quality and promotes vegetation productivity, making vegetation more attractive to grazers and creating a positive feedback loop.
	Grazing reduces above-ground biomass and maintains an open ground canopy but does not result in permanent bare ground.
Grazers	Animals actively crop herbaceous sward to an even height without damaging important plant parts.
	Grazers concentrate in areas of higher forage quality and productivity, which a concentrating agent could facilitate.
Vegetation	Vegetation must be short in stature relative to the surrounding community.
	Vegetation exhibits traits that tolerate repeated grazing, such as small-leaved, prostrate ecotypes and stoloniferous or rhizomatous growth.
	Biomass is concentrated at the surface typically as a dense, prostrate canopy.
	Grazers attain high biomass per bite to surrounding areas.
	Vegetation is more digestible, nutritious and palatable compared to surrounding.
	Vegetation recovers rapidly after defoliation, producing lots of new growth.

Literature synthesis

We conducted a literature search using the Web of Science to assemble a database of case studies that met the attributes outlined in Table 2.1 regardless of whether the term “grazing lawn” was used in the study. We sought to determine whether examples of grazing lawns that met all criteria could be identified. In so doing, we captured case studies that self-identified sites as grazing lawns which we term author-identified, and explicitly used the term “grazing lawn”. Examples that met all attributes but were not explicitly labelled as such we term attribute-identified. To locate potential studies, searches included the following keywords that could be used in combination: “grazing”, “cropping”, “lawn”, “grazing patch”, “concentrated grazing”, “grazing dynamics”, “grazing turf”, “turf”, “herb fields”, and

“aquatic grazing”. Additionally, we used Google Scholar to search for unpublished studies in government reports, dissertations, and theses. Case study compilation continued until January 2022.

Our literature search resulted in over 500 studies, which we filtered using the attribute list in Table 2.1 to retain only those meeting all 11 attributes. Studies were further required to provide information on location, plant functional type, and grazer species composition. This resulted in a set of 108 case studies, of which 50 were author-identified and 58 were attribute-identified.

From each study we compiled data to enable analyses, including: ecosystem type (terrestrial or aquatic), geographical region (continent), location (site and country), latitude, longitude, lawn terminology, classification as author-identified or attribute-identified, reported lawn plant species, dominant plant functional type(s), lawn-maintaining grazer(s) species, grazer taxa, dominant grazer body size class, article title, authors, and publication year (See Data S2.1). Where necessary, species names were updated in line with the current taxonomy. In cases where two locations were reported in a single publication, separate entries were created for each location. For example, the two locations reported in Arnold et al. (2014) - Serengeti National Park, Tanzania and Kruger National Park, South Africa - are considered separate case studies due to their geographic separation and substantive difference in climates. For each study, latitude and longitude were compiled in decimal degrees with a WGS84 projection.

Extraction of climatic data

Using latitude and longitude for each study, climatic data were extracted from the WorldClim database (Fick & Hijmans, 2017) at a resolution of 5 arc-minutes using the ‘raster’ package (Hijmans, 2022) in R version 4.3.2 (R Core Team, 2023). We defined the global climatic space and the placement of grazing lawns within it using four climatic predictors representing worldwide gradients in temperature and precipitation: (1) Mean Annual Temperature (MAT, °C x 10), (2) Temperature Seasonality (TS, ±°C x 100), (3) Mean Annual Precipitation (MAP, millimetres per year), (4) Precipitation Seasonality (PS, %) (Fick & Hijmans, 2017; O’Donnell & Ignizio, 2012). Temperature seasonality is quantified as the

standard deviation (°C) in monthly temperatures. Precipitation seasonality is quantified as the coefficient of variation of total precipitation (%), with lower percentages representing more evenly distributed precipitation throughout the year and higher percentages representing more variation in precipitation from month to month. For the untransformed case study climatic data, see Data S2.2.

Compilation of vegetation and grazer variables

Grazing lawn vegetation was classified by plant functional type(s): C₃ grasses, C₄ grasses, sedges, forbs, algae, or seagrass. Classifications were based on dominant lawn species or, if no species list was provided, on the functional group(s) identified by the authors. Multiple dominant plant functional types were listed where two or more plant functional types co-dominated. For analysis of associations, individual grazer species and plant functional types were considered separately, allowing a more detailed exploration of relationships between grazers and vegetation.

Grazers were classified by taxon (Mammalia, Aves, Reptilia, Pisces, or Gastropoda). Grazer body size class, referred to as size class hereafter, was determined by first obtaining the body mass (kilograms, kg) for all reported lawn-associated grazer species. Body mass for Mammalia and Aves species was extracted from the EltonTraits database (Wilman et al., 2014), while data for other taxa were sourced from the literature (see Data S2.3). Grazers were assigned to one of five body mass categories: nanoherbivore (0-1 kg), microherbivore (1-10 kg), mesoherbivore (10-100 kg), macroherbivore (100-1000 kg) and megaherbivore (1000 kg +), following Owen-Smith (2013). For analysis of case studies in global climatic space, each case study was assigned a dominant size class, which was determined as the largest size class identified in the study. This classification reflects the dominant role that larger grazers play in maintaining grazing lawns by exerting significant top-down pressure on herbaceous communities (Augustine and Frank, 2001; Waldram et al 2008).

Climatic and taxonomic analyses

Mapping case study locations.

Geographic distribution of grazing lawns were mapped using 'ggplot2', 'raster', 'rworldmap' and 'sf' packages (Hijmans, 2022; Pebesma, 2018; South, 2011; Wickham, 2016). We created contingency tables to identify any regional or taxonomic biases in author *versus* attribute case study identification. While included in the database and mapped geographically, aquatic studies were excluded from climatic and association analyses due to limitations in extracting relevant climatic and body mass data. Although surface-level climatic variables (MAT, MAP, TS and PS) were available for all sites, these variables are less relevant for aquatic ecosystems, where water temperature and hydrodynamics are more important factors shaping ecological processes, vegetation, and herbivory (Freitas et al., 2021). As a result, including both aquatic and terrestrial studies in the same climatic analysis would not provide meaningful comparisons.

Defining the climatic and biome distribution of grazing lawns.

To determine the climatic distribution of grazing lawns, the geolocations of each case study were plotted with associated MAT and MAP values derived from WorldClim and overlain with a Whittaker terrestrial biome plot (Whittaker, 1970).

Using 15000 random geo-locations of the global land surface (excluding Antarctica), at a resolution of 5 arc-minutes, a global climate dataset was generated to place grazing lawns within the global climatic context. For each location, MAT, temperature seasonality, MAP, and precipitation seasonality were compiled. A principal components analysis (PCA) of the global climate and grazing lawn data was undertaken using the 'vegan' R package (Oksanen et al., 2022). Prior to the PCA, values of each climate variable were centred and standardised to a range of 0-1 by dividing by the maximum to ensure comparability of variables with different scales (e.g. MAT vs MAP).

Biplots of the first two PCA axes were generated using 'ggplot2' R package (Wickham, 2016). Within the biplots, groupings of grazing lawns were coloured according to: (1) author-identified *versus* attribute-identified; (2) dominant plant functional type and functional type combinations where there was more than one; (3) dominant grazer size

class. Additionally, 95% confidence ellipses were added to the biplot using the “stat_ellipse” function to specify the area of climatic space occupied by author-identified and attribute-identified case studies.

We used ANOVAs of PC1 and PC2 axis scores to test for differences between the study categories listed above. We restricted ANOVA analyses to those dominated by a single plant functional type of C₃ grass, C₄ grass, forb, or sedge.

Identifying climatic patterns in grazing lawn distribution

We used univariate ANOVA to test for correlations between each climate variable (MAT, temperature seasonality, MAP, and precipitation seasonality) and the following lawn characteristics: (1) author-identified *versus* attribute-identified, (2) single dominant plant functional type, and (3) dominant grazer size class, resulting in a total of 12 ANOVAs. Because conducting multiple statistical tests on the same dataset increases the likelihood of detecting significant differences purely by chance rather than due to true underlying patterns (Benjamini & Hochberg, 1995), we applied a Benjamini & Hochberg, (1995) correction to p-values.

Understanding vegetation (resource) - grazer (consumer) associations.

We generated bipartite association matrices between grazers (separated by taxon and size class category) and dominant plant functional type to visualise plant-animal associations across terrestrial grazing lawn case studies. Association matrices were created in the R package ‘bipartite’ (Dormann et al., 2008) and association networks were generated and visualised using the bipartite functions `visweb()` and `plotweb()`. Since not all studies confirmed grazer consumption of all plant functional types, the resulting networks are of associations rather than trophic interactions. Each instance of plant-grazer co-occurrence within a case study counted as a single association. Multiple associations per case study were possible if two or more plant functional types and grazers were listed within the case study. For example, a case study with forb and sedge dominant vegetation and meso- and macro- grazers would have four associations (forb-mesoherbivore; sedge-mesoherbivore; forb-macroherbivore; sedge-macroherbivore). Number of associations (N_A) per case study ranged from 1 to 13.

Results

Identification and global distribution of grazing lawns

We identified 108 case studies fulfilling all grazing lawn attributes, of which 50 were author-identified and 58 were attribute-identified (Figure 2.1A) (See Data S2.1 for all case studies). Of the attribute-identified lawns, 13 used none of our keyword search terms, while the remainder used alternative terms such as “glades” (Augustine, 2003; Augustine et al., 2003; Veblen, 2012; Young et al., 1995), “turf” (C. W. D. Gibson et al., 1983; Grubb, 1971; Hoey & Bellwood, 2009; Miehe et al., 2009; Van Den Bos & Bakker, 1990; Walton et al., 2019), “herbfield” (N. Gibson & Kirkpatrick, 1985; Kirkpatrick, 1975; Roberts et al., 2011), and “grazing patch” (Christianen et al., 2019; Wilmshurst et al., 1995).

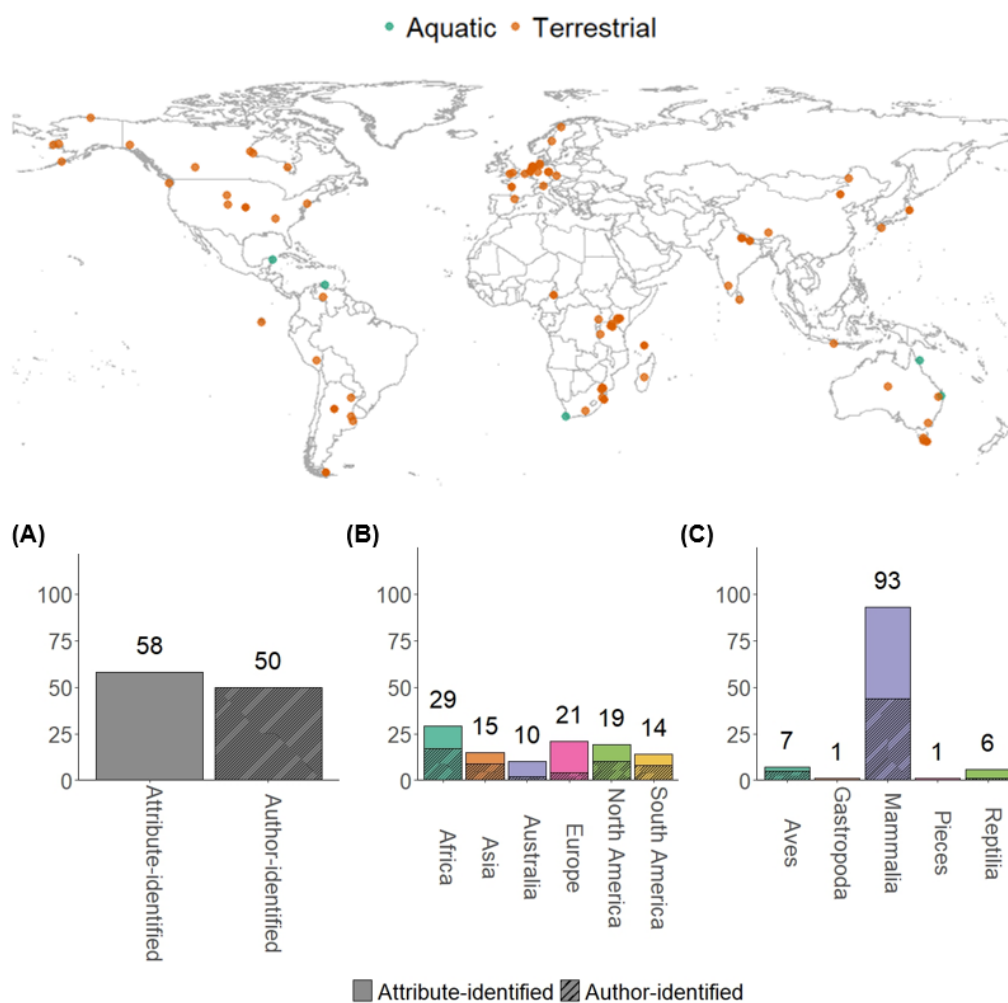


Figure 2.1. **Global distribution of grazing lawn case studies.** Site symbols in the map are coloured by ecosystem type (terrestrial or aquatic). Bar plots show the distribution of studies

by A) case study classification, B) geographical region, and C) grazer taxon. The numbers above bars show the totals in each category, divided between author-identified (black striped) and attribute-identified (plain colour).

Most case studies identified were terrestrial ($N_{study}=103$). Five case studies were aquatic (Christianen et al., 2019; Hernández & van Tussenbroek, 2014; Hoey & Bellwood, 2009; Plagányi & Branch, 2000; Preen, 1995), all of which were attribute-defined (Figure 2.1). Case studies spanned six continents (Figure 2.1B) and involved 77 animal species in 55 genera and 205 plant species in 120 genera (See Data S2.3 and S2.4).

The majority of case studies were recorded in Africa ($N_{study}=29$), most of which were author-identified ($N_{author}=17$) (Figure 2.1B; Table S2.1A; Figure S2.1). In North America ($N_{author}=10$, $N_{attrib}=9$) and South America ($N_{author}=8$, $N_{attrib}=6$), author-identified and attribute-identified were relatively equally abundant. In contrast, Europe ($N_{study}=21$) has a predominance of attribute-identified lawns ($N_{attrib}=17$). More grazing lawns were dominated by C_4 grasses ($N_{study}=48$) than by any other plant functional type, with over half of the C_4 -dominated lawns being author-identified ($N_{author}=28$) (Table S2.1B; Figure S2.2).

All but one of the 108 studies involved vertebrate grazers (Figure 2.1C); the exception was an aquatic study involving the limpet, *Scutellastra (Patella) cochlear* (Plagányi & Branch, 2000). Lawns were most frequently associated with mammalian grazers ($N_{study}=93$), which were the most reported animal taxa for both attribute- ($N_{attrib}=49$) and author-identified ($N_{author}=44$) case studies (Table S2.1C; Figure S2.3). Most associated grazers were either macro- ($N_{study}=50$) or mesoherbivores ($N_{study}=25$) (Table S2.1D). A contingency table of case study classification by region, dominant plant functional type, grazer taxa, and dominant grazer size is available in Table S2.1.

Terrestrial grazing lawns in climatic space

Across all terrestrial case studies, MAT ranged from -13.1 to 27.5 °C, MAP from 122 to 2913 mm per year, temperature seasonality from ± 0.34 to 15.72 °C, and precipitation seasonality from 13% to 127% (See Data S2.2 for case studies' climatic data). The ranges

define the climatic envelope within which grazing lawns were identified in climatic space. Notably, grazing lawns were absent from ecosystems at the extremes of these variables, such as areas with extreme MAT ($< -13^{\circ}\text{C}$) or very low MAP (< 122 mm per year), suggesting that climatic extremes and high seasonality limit their presence. The ranges, means, and standard deviations of our four bioclimatic variables for all case studies are presented in Table S2.2.

Terrestrial case studies were located across 11 of 13 biomes in the Whittaker terrestrial biome environmental space: tundra, taiga, temperate forest, temperate rainforest, woodland, grassland, shrubland, thorn scrub, savanna, semi-desert, and tropical seasonal forest (Whittaker, 1970) (Figure 2.2). The only two terrestrial biomes without grazing lawn studies were tropical rainforests and deserts. One C_3 grass and forb-dominated case study (Schreiner et al., 1996) located in South Fork Hoh River, Olympic National Park, Washington, USA, fell outside the biome boundaries in the simplified Whittaker terrestrial biome plot. However, alternative versions of the biome diagram, such as that presented in Brock et al. (2020), classify this point within the temperate rainforest biome. Both author and attribute-identified lawns were found within each of the eleven biome types (Figure S2.5).

A PCA of the global environmental climate based on four climate variables demonstrated terrestrial grazing lawns occupy a broad climatic envelope (Figure 2.3) with grazing lawns absent from the most seasonal, wettest, driest, and coldest systems. The first two PCA axes captured $< 86\%$ of the variance in the data ($\text{PC1} = 56.38\%$; $\text{PC2} = 29.66\%$). PC1 primarily captured variation in temperature (MAT, PC1 loading = 7.199, PC2 loading = -1.461) and temperature seasonality (TS, PC1 loading = -7.389, PC2 loading = -0.584). PC2 primarily captured variation in precipitation (MAP, PC1 loading = 4.984, PC2 loading = 4.928) and its seasonality (PS, PC1 loading = 2.704, PC2 loading = -6.792).

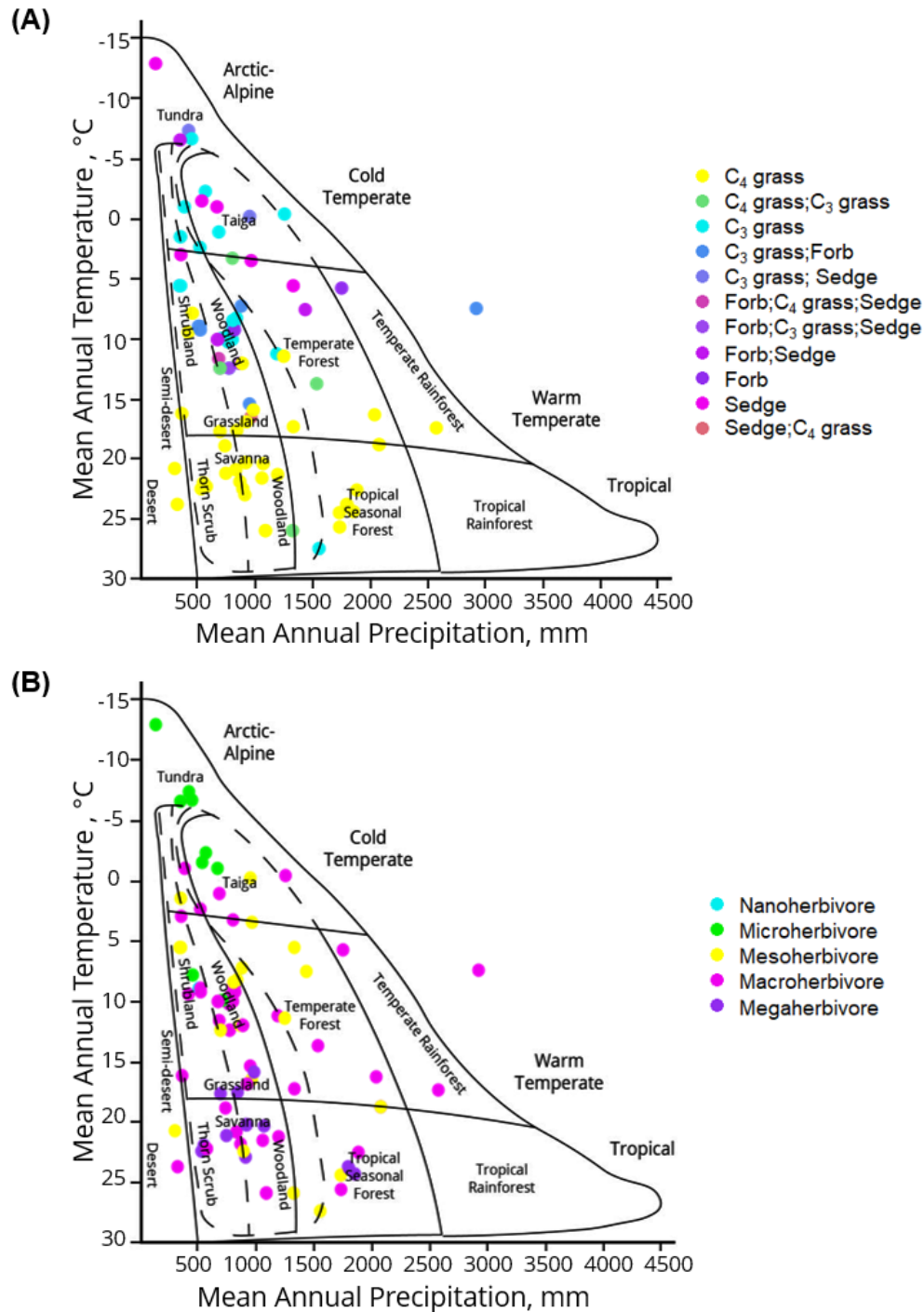


Figure 2.2. **Distribution of case studies across Whittaker's biomes** coloured by (A) the dominant plant functional type and (B) the dominant grazer size class. Overlaid figure follows Whittaker (1970), reproduced with permission from Pearson Higher Education. Distributions are defined by ordination within a space defined by mean annual temperature and. mean annual precipitation. Dashed lines represent areas in parameter space where the

resulting biome classification depends on additional factors such as seasonality of fire, drought and grazing.

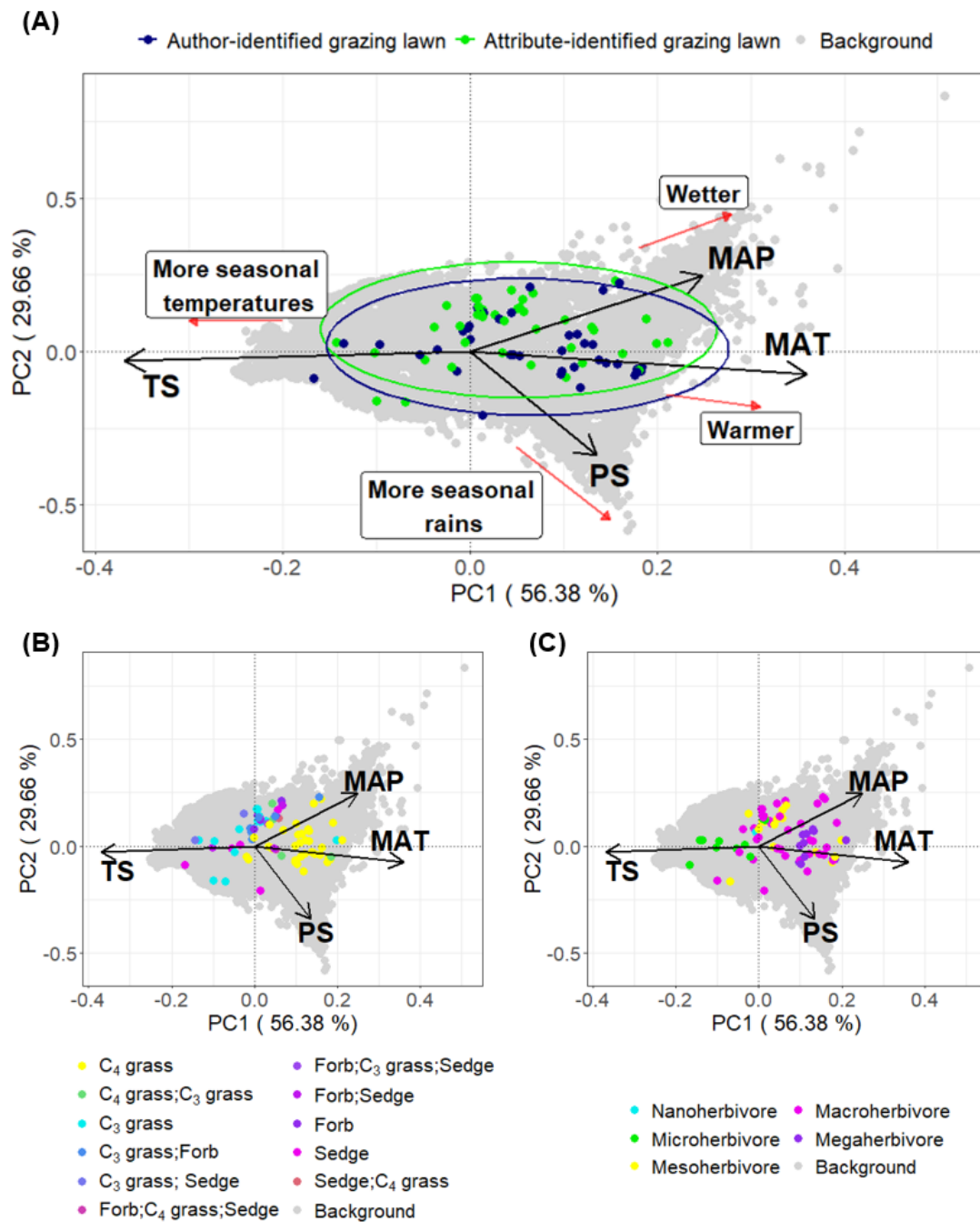


Figure 2.3. **Principal component analysis of grazing lawn climatic data in global climatic space.** Four climatic variables were utilised- mean annual temperature (MAT), mean annual precipitation (MAP), temperature seasonality (TS), and precipitation seasonality (PS)- for all case studies and background data. Biplots are coloured by (A) case study classification with

95% confidence intervals, (B) dominant plant functional type and (C) dominant grazer size class.

Ellipses defining the 95% confidence interval for author-identified ($N=50$) and attribute-identified ($N=58$) terrestrial grazing lawns show substantial overlap (Figure 2.3A). Author-identified and attribute-identified case studies showed no significant difference in PC1 (mean PC1 values were 0.062 and 0.052, respectively; ANOVA, $N=103$, $df=1$, $p=0.549$) (Table 2.2). In contrast, PC2 values were significantly higher in attribute-identified grazing lawns (PC2 mean=0.071) than in author-identified examples (PC2 mean=0.015) (ANOVA $N=103$, $df=1$, $p=0.002$). ANOVAs of raw climatic variables (Table 2.3) showed that precipitation seasonality, which contributed primarily to PC2, was the only single variable to differ significantly between author- and attribute-identified grazing lawns ($df=1$, F -value=6.935, Adjusted $P=0.017$).

*Table 2.2. **Analysis of variance (ANOVA) of principal components axes** (PC1, PC2) for (A) case study classification, (b) singular dominant plant functional type, and (c) dominant grazer size class. Principal components extracted from PCA are presented in Figure 2.3 (see Methods).*

Principal Component	Df	F Value	P Value
(A) Grazing Lawn Classification			
PC1	1	0.362	0.549
PC2	1	10.365	0.002**
(B) Singular Dominant Plant Functional Type			
PC1	3	23.846	<0.001 ***
PC2	3	4.604	0.005**
(C) Dominant Grazer Size Class			
PC1	4	14.724	<0.001 ***
PC2	4	1.603	0.180

Note:

P-value significance: 0-0.001 '***' 0.001-0.01 '**' 0.01-0.05 '*' 0.05-0.1 '.'

Table 2.3. ***Analysis of variance (ANOVA) of climate variables*** for (A) case study classification, (b) singular dominant plant functional type, and (c) dominant grazer size class. Climate variables comprise mean annual temperature (MAT), mean annual precipitation (MAP), temperature seasonality and precipitation seasonality, extracted from the WorldClim database (see Methods).

Climatic Variable	Df	F Value	P Value	Adjusted P Value
(A) Grazing Lawn Classification				
MAT	1	0.741	0.391	0.427
Temp. Seasonality	1	0.049	0.825	0.825
MAP	1	1.157	0.285	0.342
Precip. Seasonality	1	6.935	0.010**	0.017*
(B) Singular Dominant Plant Functional Type				
MAT	3	45.705	<0.001 ***	<0.001 ***
Temp. Seasonality	3	7.908	<0.001 ***	<0.001 ***
MAP	3	4.213	0.008**	0.016*
Precip. Seasonality	3	8.422	<0.001 ***	<0.001 ***
(C) Dominant Grazer Size Class				
MAT	4	16.700	<0.001 ***	<0.001 ***
Temp. Seasonality	4	10.831	<0.001 ***	<0.001 ***
MAP	4	2.697	0.035*	0.053.
Precip. Seasonality	4	2.252	0.069.	0.092.

Note:

P-value significance: 0-0.001 '***' 0.001-0.01 '**' 0.01-0.05 '*' 0.05-0.1 '.'

Grazing lawn vegetation and grazer distributions in climatic space

The distribution of dominant plant functional types in grazing lawns varied with climate. C₄ grasses dominated across a wide range of precipitations (MAP approx. 300-2000 mm per year) in warmer (MAT > 15°C), temperature-stable climates, primarily found in the Whittaker biomes of grassland, thorn scrub, tropical seasonal forests and warm woodland

(Figure 2.2A, Figure 2.3B). Lawns in cooler ($\text{MAT} < 15^{\circ}\text{C}$), more temperature-seasonal climates were commonly dominated (or co-dominated) by sedges, forbs, and C_3 grasses (Figure 2.3B). In multidimensional climatic space, singular dominant plant functional type explained significant variation in values for both PC1 (ANOVA, $N=103$, $\text{df}=3$, $p < 0.001$) and PC2 (ANOVA, $N=103$, $\text{df}=3$, $p = 0.005$) (Table 2.2B). This is in agreement with the univariate climatic ANOVA results, in which the four singular-dominated plant functional types (C_3 grass, C_4 grass, forbs, and sedges) were differentiated by each of the four climatic variables: MAT ($N=103$, $\text{df}=3$, $F\text{-value}=45.705$, Adjusted $P < 0.001$), temperature seasonality ($N=103$, $\text{df}=3$, $F\text{-value}=7.908$, Adjusted $P < 0.001$), MAP ($N=103$, $\text{df}=3$, $F\text{-value}=4.213$, Adjusted $P=0.016$) and precipitation seasonality ($N=103$, $\text{df}=3$, $F\text{-value}=8.422$, Adjusted $P < 0.001$).

Grazer size class distributions also varied with climate. Mega- and macroherbivores (> 100 kg) dominated across a wide range of precipitations (MAP approx. 300-2500 mm per year) in warmer ($\text{MAT} > 15^{\circ}\text{C}$), precipitation-seasonal climates, while microherbivores (< 10 kg) dominated in the cooler ($\text{MAT} < 10^{\circ}\text{C}$), more temperature-seasonal climates (Figure 2.2B, Figure 2.3C). Megaherbivores were largely restricted to savanna, grassland, thorn scrub, and warm woodland biomes, with only two case studies placed in tropical seasonal forests (Figure 2B). Within multidimensional climatic space, grazer size significantly differed for PC1 ($N=103$, $\text{df}=4$, $p < 0.001$) but not for PC2 ($N=103$, $\text{df}=4$, $p = 0.180$) (Table 2.2C). Among individual climatic variables, we found grazer size class was primarily driven by MAT ($N=103$, $\text{df}=4$, $F\text{-value}=16.700$, Adjusted $P < 0.001$) and temperature seasonality ($N=103$, $\text{df}=4$, $F\text{-value}=10.831$, Adjusted $P < 0.001$) (Table 2.3C). This result is consistent with PC1 results as PC1 is driven by MAT and temperature seasonality, both of which significantly differentiate grazer size classes.

Vegetation (resource) - grazer (consumer) associations within lawns

The 103 terrestrial studies yielded 262 interactions between grazers and plant functional types. For grazer taxa and plant functional type, the largest number of associations were recorded between mammals and C_4 grasses ($N=156$) and mammals and C_3 grasses ($N=46$) (Table S2.3A, Figure 4A). Mammalian grazers were associated with all four plant functional types, while Aves were linked to C_3 grasses ($N_A=4$), forbs ($N_A=1$), and sedges ($N_A=4$) but not C_4 grasses. Reptiles were only associated with C_4 grasses ($N_A=4$). The most

frequent associations by grazer size were between macroherbivores and C₄ grasses ($N_A=77$), mesoherbivores and C₄ grasses ($N_A=57$), macroherbivore and C₃ grass ($N_A=24$), mesoherbivore and C₃ grass ($N_A=19$) and mega-herbivores and C₄ grasses ($N_A=21$) (Table S2.3B, Figure 2.4B). Micro-, meso-, and macro-herbivores were associated with all plant functional types. In contrast, mega-herbivores were only associated with C₄ grasses ($N_A=21$), and nanoherbivores were only linked to C₃ grasses ($N_A=1$) and forbs ($N_A=1$).

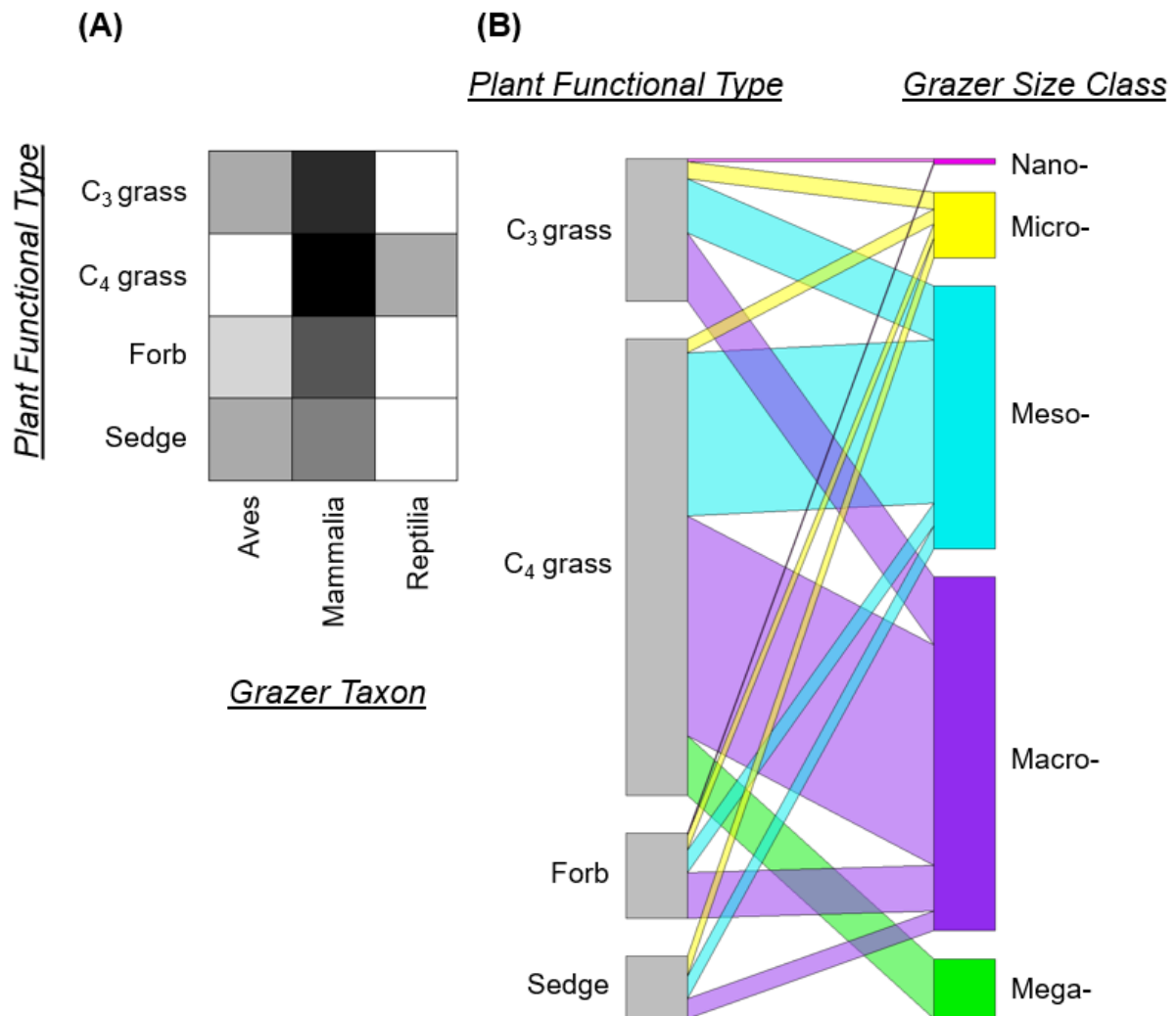


Figure 2.4. **Association matrices and networks between grazers and vegetation.** (A) Matrices showing the number of associations identified between plant functional types and grazer taxa. The darkness of each square represents the number of associations recorded, with darker squares indicating more associations. (B) Network of associations separated by dominant plant functional type and grazer size class. The colour of the line represents the

corresponding grazer size class, and the width of the line represents the number of associations, with a large width indicating more associations.

Discussion

Using an attribute-based definition of grazing lawns, we identified 108 case studies through a literature synthesis. These case studies span continents and biomes with the term “grazing lawn” most frequently applied to African C₄ grass savannas dominated by mammalian mega- or meso-herbivores. Grazing lawn systems exist not only in terrestrial landscapes including temperate biomes and forb-dominated herbaceous ecosystems involving smaller or non-mammal herbivores, but also within aquatic environments (selected examples in Figure 2.5). The diversity of vegetation-grazer interactions highlights the widespread capacity for grazing-mediated feedbacks to shape ecosystems. Grazing lawns are globally widespread, though absent from climatic extremes. Taken together, our results challenge the notion that grazing lawns are prominent only within tropical or sub-tropical grasslands.

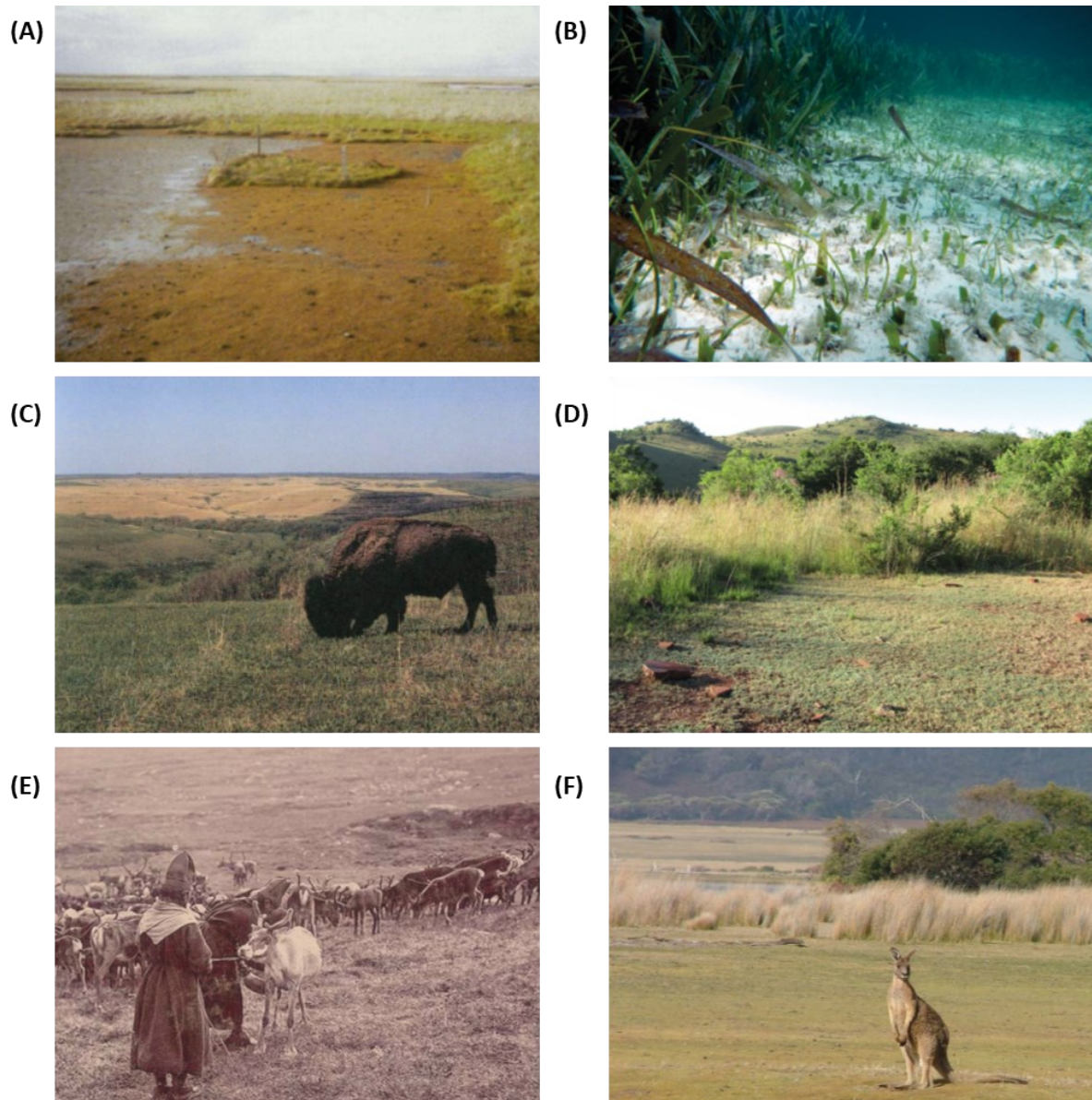


Figure 2.5. Selected grazing lawn examples from compiled case study database. (A) At Tutakoke River, Alaska, USA, black Brant geese (*Branta bernicla nigricans*) create grazing lawns dominated by sedges (*Carex subspathacea* and *Carex ramenskii*) (Person et al., 2003; image reproduced with permission from Springer Nature) (B) In Yucatan Peninsula, Mexican Caribbean Green sea turtle (*Chelonia mydas*) engage in cultivation grazing or rotational grazing of seagrass (*Thalassia testudinum*) (Hernández & van Tussenbroek, 2014; image reproduced under CC BY 4.0). (C) At Konza Prairie, Kansas, USA, American bison (*Bison bison*) maintain grazing lawns or grazing patches dominated by C_4 grasses (*Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, *Schizachyrium scoparium*) (Knapp et al., 1999; image reproduced with permission from Wiley). (D) At Ithala Game Reserve, South Africa,

White rhinoceros (*Ceratotheri umsimum*), plains zebra (*Equus quagga*), and blue wildebeest (*Connochaetes taurinus*) maintain grazing lawns dominated by C₄ grass (*Cynodon dactylon*) (Fox et al., 2015; image reproduced with permission from Springer Nature). (E) In Padjelanta National Park, Sweden, caribou (*Rangifer tarandus*) maintain historical milking grounds dominated by sedges (*Carex* spp.), C₃ grasses (*Festuca* spp., *Deschampsia* spp.), and forbs (*Rumex acetosa lapponicus*) (Egelkraut et al., 2018; image reproduced under CC BY 4.0) (F) In Tasmania, Australia, Bennett's wallaby (*Macropus rufogriseus*), common wombat (*Vombatus ursinus*), and Tasmanian pademelon (*Thylogale billardierii*) maintain marginal herb fields or marsupial lawns dominated by forbs (*Velleia Montana*, *Ranunculus* spp.) and sedges (*Schoenus* spp.) (Roberts, 2009; Roberts et al., 2011; Photo taken by Cynthia Roberts and reproduced with permission).

Identification and global distribution of grazing lawns

Despite only half of identified studies using the term “grazing lawn”, we found substantial overlap in the climatic distribution of author-identified and attribute-identified lawns, validating our attribute-based approach to recognise grazing lawns across ecosystems (Figure 2.3A). As expected, author-identified lawns were most common in African C₄ grass-dominated systems, and mammal-dominated systems, reflecting the historical focus of grazing lawn research. They also occurred more frequently in habitats with more seasonal precipitation (Table 2.3A). With rainfall seasonality an important indicator of savanna presence (Lehmann et al., 2011), this association likely reflects a longstanding bias in the grazing literature toward African savanna ecosystems. Conversely, in less seasonal regions such as Europe, grazing lawns were more likely to be attribute-identified, suggesting that conceptual biases may have hindered recognition of analogous lawns outside savannas.

Five aquatic case studies were identified, broadening the identification of grazing lawns to aquatic ecosystems. One study (Preen, 1995) shows the early application of grazing lawn concepts to seagrass (*Zostera* spp.) beds, though the specific term “grazing lawn” was not used. More recent work (Christianen et al., 2019; Hernández & van Tussenbroek, 2014) revealed similar feedbacks in “grazing patches” of seagrass (*Thalassia testudinum*), where green turtles (*Chelonia mydas*) selectively foraged on the short, nutrient-rich vegetation

(Figure 2.5B). Despite the inherent differences between aquatic and terrestrial grazing systems, grazing-induced changes in plant digestibility, nutrient content, and productivity drive a positive feedback between grazers and vegetation (Bakker et al., 2016; Thayer et al., 1984). These similarities, previously recognised by Burkepile (2013) and Burkepile et al. (2020), underscore the cross-ecosystem relevance of grazing lawn processes and the way in which plant-animal interactions can shape very different ecosystems in analogous ways.

Terrestrial grazing lawns in climatic space

Terrestrial grazing lawns were present within every Whittaker biome except tropical rainforests and deserts (Whittaker, 1970) (Figure 2.2). Extreme temperature, precipitation, and seasonality constrained the distribution of grazing lawns, likely due to the interaction of grazing with vegetation dynamics under such conditions (Figure 2.3) (Eldridge et al., 2022; Maestre et al., 2022). For example, in arid systems like deserts, limited resource uptake and vegetation production reduce available forage for grazers, increasing the risk of overgrazing (Myerud, 2006; Zhang et al., 2023). Conversely, in warmer, wetter systems, tall, fast-growing plants create closed canopies, reducing ground-level light needed by lawn vegetation (Hoffmann et al., 2012; Mestre et al., 2017; Solofondranohatra et al., 2018). Significant interannual fluctuations in precipitation and temperature can trigger boom-bust cycles that further hinder vegetation production and grazing capacity (Asner et al., 2004). However, within the moderate climatic ranges identified, grazing lawns can persist wherever vegetation productivity and grazing pressure remain balanced enough to sustain open, herbaceous swards.

Grazing lawn vegetation and its distributions in climatic space

Grazing lawn vegetation included a variety of herbaceous plant functional types (C_3 grasses, C_4 grasses, forbs, and sedges). While most grazing lawns were grass-dominated, reflecting the evolutionary history of grasses under herbivory (Stebbins, 1981), forb- and sedge-dominated lawns were also globally widespread. All functional types share traits essential for tolerating grazing, such as high photosynthetic capacities and mechanisms enabling rapid regrowth after defoliation (Agrawal, 2000; Hempson et al., 2015; Rosenthal & Kotanen, 1994). For example, grasses and sedges regenerate through basal meristems, while many forbs rely on dormant bud activation following apical meristem damage

(Hawkes & Sullivan, 2001). These tolerance traits underline the resilience of grazing lawn vegetation, allowing it to persist under varying grazing pressures and climatic constraints.

The distributions of lawn vegetation across climatic space were consistent with global vegetation patterns, with C₃ grasses, C₄ grasses, forbs, and sedges occupying distinct climatic envelopes (Figure 2.3B; Table 2.3B). These patterns reflect the well-documented ecological sorting of C₃ and C₄ grasses along climatic gradients (Pau et al., 2013; Sage & Monson, 1998), with lawns dominated by C₄ grasses occurring primarily in warmer, drier systems such as savannas, where water-efficient, heat-tolerant traits confer competitive advantages (Edwards & Still, 2008; Knapp & Medina, 1999). In contrast, C₃ grasses, forbs and sedges were more prevalent in cooler, less seasonal environments where conditions favour their dominance (Figure 2.2A, Figure 2.3B).

Grazers and their distributions in climatic space

Grazers associated with grazing lawns spanned diverse taxa, including mammals (Mammalia), birds (Aves), reptiles (Reptilia), fish (Pisces) and invertebrates (Gastropoda), with body sizes spanning five orders of magnitude. Mammalian grazers were most frequently reported, reflecting their dominance in grazing ecosystems due to co-evolution with grasses (Mack & Thompson, 1982; Stebbins, 1981) (Table S2.1C). Their specialised adaptations for processing and digesting vegetation, such as high-crowned teeth that resist wear (Vaughan, 1986) and both pre-and post-gastric digestive systems (Dehority, 2002; Shipley, 1999) make them highly efficient grazers. However, non-mammalian grazers, including tortoises (*Geochelone elephantopus*) in the Galapagos (Hunter et al., 2021) and Black Brant geese (*Branta bernicla nigricans*) in Alaska, USA (Person et al., 2003) (Figure 2.5A), were also associated with grazing lawns, exhibiting analogous grazing behaviours essential for lawn formation and maintenance. These functional similarities across grazer taxa highlight convergent evolutionary strategies enabling grazing and grazing lawns' persistence globally.

Grazer body size varied widely on a global scale, with most grazing lawns dominated by macro- or meso-herbivores (Figure S2.3). Megaherbivore-dominated grazing lawns were largely restricted to grassland and savanna ecosystems, consistent with Silva's et

al. (2001) larger mean mammal body sizes in savannas than in other biomes. Grazer body size was also strongly associated with temperature and temperature seasonality gradients, with larger herbivores prevalent in warmer, temperature-stable environments and smaller herbivores more common in cooler, seasonally variable environments. Larger herbivores' high energy demands likely explain this pattern, as they require abundant forage, which is more readily available in warmer, productive regions (Clausen et al., 2003; Owen-Smith, 1988). Furthermore, body size distributions have likely been influenced by human-driven extinctions during the late Pleistocene, with North America, northern Eurasia, and South America experiencing significant losses of large herbivores (Brown, 1995; Brown & Lomolino, 1998; Owen-Smith, 1987, 1999). As a result, most extant megaherbivores are restricted to tropical and subtropical regions, particularly African savannas.

We found no case studies of insects acting as the primary maintainers of grazing lawns, despite literature evidence that termites (Arshad, 1982; Cromsigt & Olff, 2008; Davies et al., 2014; Jouquet et al., 2004; Mayengo et al., 2020) and ants (Folgarait, 1998; Purdon et al., 2019) contribute to grazing lawn maintenance by influencing nutrient cycling and soil turnover. Differences in grazer traits, particularly body size which is closely linked to forage selectivity, may determine their ability to initiate, maintain, or simply benefit from grazing lawns. For example, grasshoppers are strongly associated with grazing lawns in temperate grasslands, benefiting from the short, high-quality forage (Ozment et al., 2021). However, their small body size and high forage selectivity likely prevents them from sustaining the uniform, short-statured vegetation characteristic of these ecosystems. The ability to initiate and maintain grazing lawns is also likely influenced by grazer densities and movement patterns in combination with body size, though we were unable to test this in our study (Bukombe et al., 2019; Hopcraft et al., 2012). While our results demonstrated the diversity of grazing lawn-associated grazers, we were unable to distinguish whether specific species primarily function as initiators or maintainers of lawns. Distinguishing between these roles would require standardized data on grazer densities and diet across studies or controlled experimental research.

Vegetation (resource) - grazer (consumer) associations within lawns

Associations between vegetation and grazers were not limited to certain taxonomic or body size combinations (Figure 2.4). Most grazing lawns included mammalian mega-, macro-, and mesoherbivores associated with C₃ and C₄ grass vegetation (see examples Figure 2.5C & D) reflecting co-evolutionary relationships (Stebbins, 1981). However, examples of alternate vegetation-grazer associations (see examples Figure 2.5A, E & F) suggest that grazing lawns demonstrate broader ecological patterns rather than tied to specific taxonomic or size-related relationships. It is important to note that these associations are based on reported species, and other species not explicitly stated, such as hares in savanna systems, may also contribute to lawn dynamics.

The variety of associations and global distribution of grazing lawns identified in this study demonstrates the capacity of grazing to shape diverse ecosystems. Central to grazing lawn persistence are grazers capable of sustaining open ground canopies with ample light through grazing, vegetation that can exploit these high-light conditions while also tolerating grazing, and environmental conditions that facilitate positive feedback between grazers and vegetation. These feedbacks rely on a balance between grazing pressure and vegetation productivity: under-grazing allows taller vegetation to encroach (Archer et al., 2017), while over-grazing degrades plant communities, increases bare ground, and prolongs recovery periods (Teague et al., 2011; van de Koppel et al., 1997). Historically, concentrated grazing has played a central role in maintaining open, herbaceous-dominated landscapes, but these processes have diminished or been lost in many regions due to grazer extinctions and habitat changes (Török et al., 2024). Nevertheless, the diverse plant and grazer associations observed here highlight that grazing lawns remain globally distributed across a variety of climatic contexts, underscoring that grazing processes are analogous across systems.

Data Completeness and future considerations

Our search only considered the English language literature, and is therefore incomplete. Case studies varied in information content and, in some cases, met our attributes for inclusion while obviously lacking complete vegetation and grazer species lists. Some case studies that were excluded due to lack of information on species and dynamics between the grazers and vegetation could be included after further research. This includes

case studies concerning gelada monkeys (*Theropithecus gelada*) in Ethiopia (Fashing et al., 2014), European bison (*Bison bonasus*) in Poland (Kowalczyk et al., 2021) and muskox (*Ovibos moschatus*) in Greenland (Mosbacher et al., 2016), all of which excluded information on vegetation structure and grazer feeding behaviour.

Information such as C: N ratios, density of herbivores, vegetation biomass, grazing lawn size, and presence of a positive vegetation-grazer feedback were inconsistently reported across studies, indicating the need for a reliable framework to identify and report on grazing lawns. These variables would allow for a deeper exploration of lawn dynamics and could aid in our understanding of how grazing lawns are created and maintained.

Conclusions

Here, we developed a clear framework for identifying grazing lawns based on attributes independent of taxonomic and climate specifics. Instead, our attributes focus on universal traits related to feedback and processes, grazer and vegetation characteristics. Our attribute-based framework (Table 2.1) revealed many ‘valid’ but previously unrecognised grazing lawns, likely due to conceptual and regional biases. This approach also validated previously recognised examples while uncovering ecologically analogous systems in regions historically overlooked. We saw that grazing lawns can exist under various environmental conditions, maintained by a diversity of grazers and composed of various herbaceous ground cover. Central to grazing lawn persistence is a balance in grazing intensity, ensuring vegetation recovery while maintaining open canopies with ample light. While grasslands and large herbivores may be the most efficient combinations resulting in grazing lawns, our findings indicate similar positive feedbacks can arise from various vegetation-grazer associations across ecosystems, underscoring the cross-ecosystem relevance of grazing processes.

Understanding the relationship between vegetation, grazers, and climate is essential for successful land and rewilding practices. With this knowledge conservationists and land managers will be able to appropriately re-establish or manage grazing and trampling behaviours within grazed ecosystems globally, improving overall ecosystem health and preventing irreversible degradation. While our database is not an exhaustive list

of all potential case studies, it is the first attempt to provide objective criteria for identifying grazing lawns. Moving forward, our outlined attributes will allow for the proper identification of a wider range of grazing lawns and more consistent data collection and analysis.

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Chapter 2 supplemental material

Data (available on request)

Data S2.1- Grazing Lawn case study database including all metadata (condensed case study database table given at end of supplemental)

Data S2.2- Terrestrial case study data for selected BioClimatic variables

Data S2.3- Terrestrial case study individual animal data with body mass

Data S2.4- Case study individual vegetation data

Distribution world maps

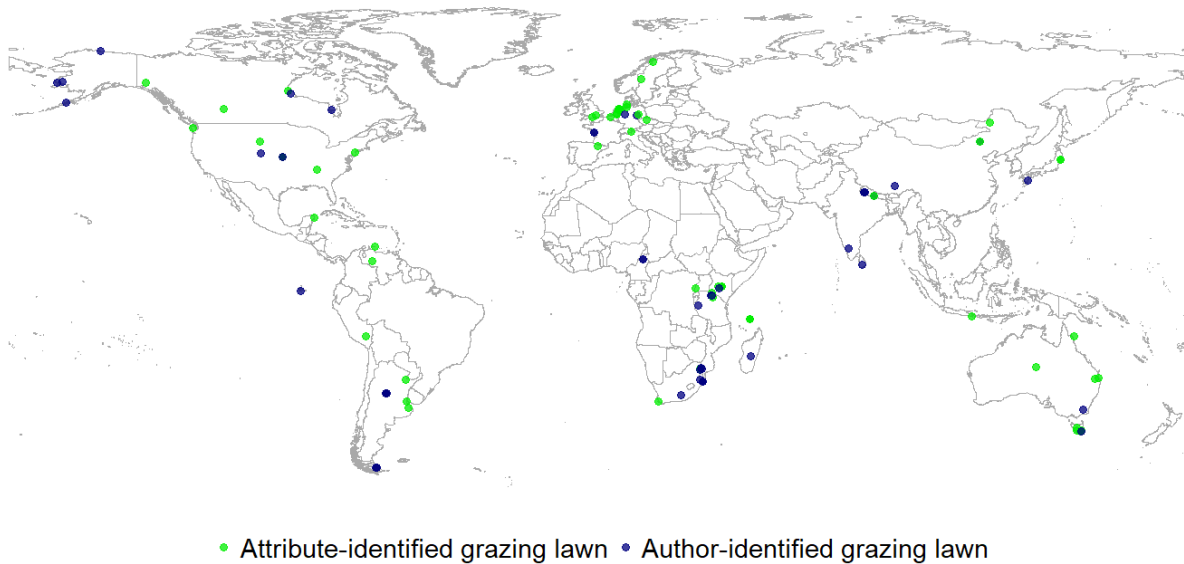


Figure S2.1. **Global distribution of case studies coloured by case study classification.** Case studies were classified as either author-identified, where authors self-identified sites as grazing lawns by explicitly using the term “grazing lawn”, or attribute-identified, where sites met our attribute criteria but were not explicitly labelled as such.

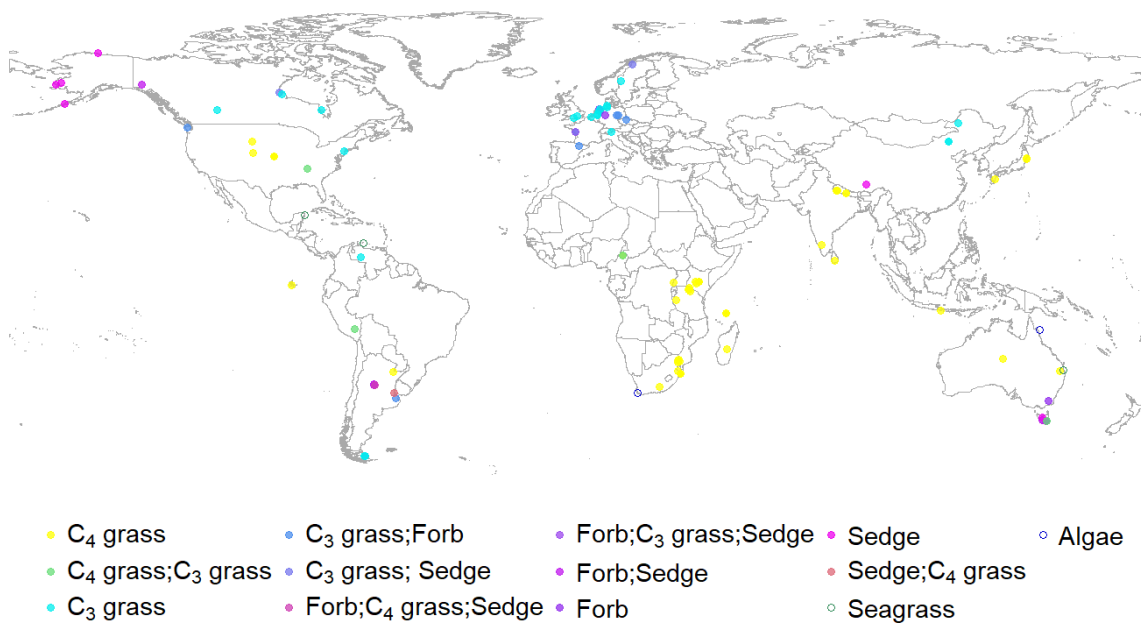


Figure S2.2. **Global distribution of case studies coloured by dominant plant functional type.** Solid circles represent terrestrial vegetation, and open circles represent aquatic vegetation.

Ecosystems were classified into dominant plant functional type(s) based on dominant species found within the lawns (see Methods).

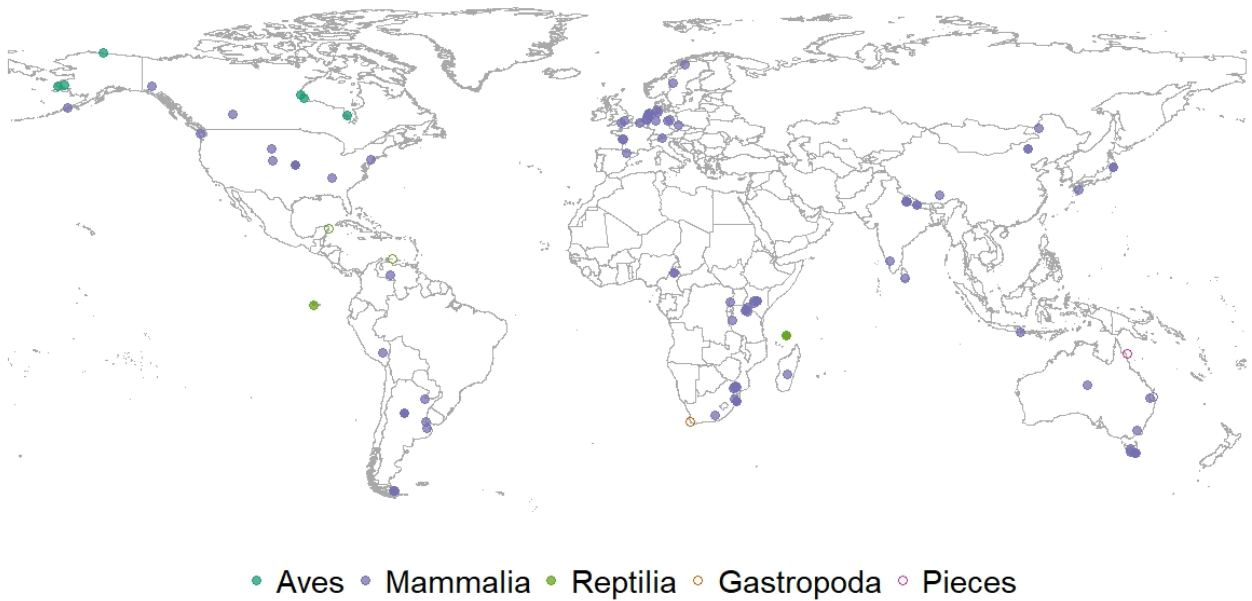


Figure S2.3. **Global distribution of case studies coloured by grazer taxon.** Solid circles represent terrestrial grazers, and open circles represent aquatic grazers.

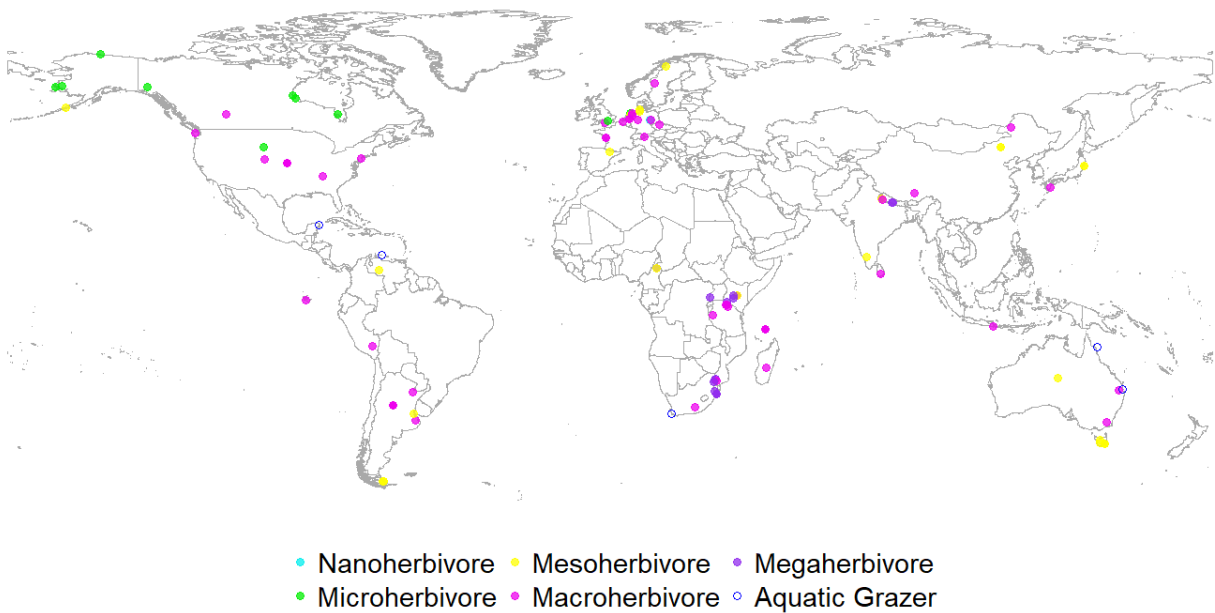


Figure S2.4. **Global distribution of case studies coloured by dominant grazer body class.** Solid circles represent terrestrial vegetation, and open circles represent aquatic vegetation.

Ecosystems were classified into dominant plant functional type(s) based on dominant species found within the lawns (see Methods).

Contingency table

*Table S2.1. **Number of case studies identified** either author-identified, where authors self-identified sites as grazing lawns by explicitly using the term “grazing lawn”, or attribute-identified, where sites met our attribute criteria but were not explicitly labelled as such, per each (A) region, (B) dominant plant functional type, (C) grazer taxa, (D) dominant grazer size class.*

	Attribute-identified grazing lawn	Author-identified grazing lawn	Total
(A) Region			
Africa	12	17	29
Asia	6	9	15
Australia	8	2	10
Europe	17	4	21
North America	9	10	19
South America	6	8	14
(B) Dominant Plant Functional Type			
C ₄ grass	20	28	48
C ₄ grass;C ₃ grass	2	2	4
C ₃ grass	16	6	22
C ₃ grass;Forb	6	1	7
C ₃ grass;Sedge	2	0	2
Forb;C ₄ grass;Sedge	0	2	2
Forb;C ₃ grass;Sedge	0	1	1
Forb;Sedge	3	2	5
Forb	2	3	5
Sedge	1	5	6
Sedge;C ₄ grass	1	0	1
Seagrass	3	0	3
Algae	2	0	2
(C) Grazer Taxa			
Aves	2	5	7
Gastropoda	1	0	1
Mammalia	49	44	93
Pieces	1	0	1
Reptilia	5	1	6
(D) Dominant Grazer Size Class			
Nanoherbivore	0	1	1
Microherbivore	5	5	10
Mesoherbivore	16	9	25
Macroherbivore	26	24	50
Megaherbivore	6	11	17
Aquatic Grazer	5	0	5

Climatic ranges

Table S2.2. Mean, Minimum, maximum, and standard error (SD) values of climate variables calculated for author-identified and attribute-identified grazing lawns, all terrestrial case studies combined, and background environmental dataset. Climate variables comprise Mean annual temperature (MAT), mean annual precipitation (MAP), temperature seasonality and precipitation seasonality, extracted from the WorldClim database (see Methods).

	MAT (°C)				MAP (mm per year)				Temperature Seasonality (±°C)				Precipitation Seasonality (%)			
	Mean	Min	Max	SD	Mean	Min	Max	SD	Mean	Min	Max	SD	Mean	Min	Max	SD
Author-identified grazing lawn	13.5	-13.1	26.0	1.30	881	122	2565	72.81	±5.03	±0.65	±15.17	0.52	61.30	13	127	4.28
Attribute-identified grazing lawn	12.0	-7.5	27.5	1.17	990	288	2913	70.64	±5.19	±0.34	±15.72	0.49	45.60	13	117	4.15
All Case Studies	12.7	-13.1	27.5	0.87	937	122	2913	50.74	±5.11	±0.34	±15.72	0.35	53.22	13	127	3.06
Background	8.3	-26.0	31.3	0.12	695	0	7840	5.44	±8.31	±0.13	±22.61	0.04	60.84	0	240	0.28

Whittaker biomes

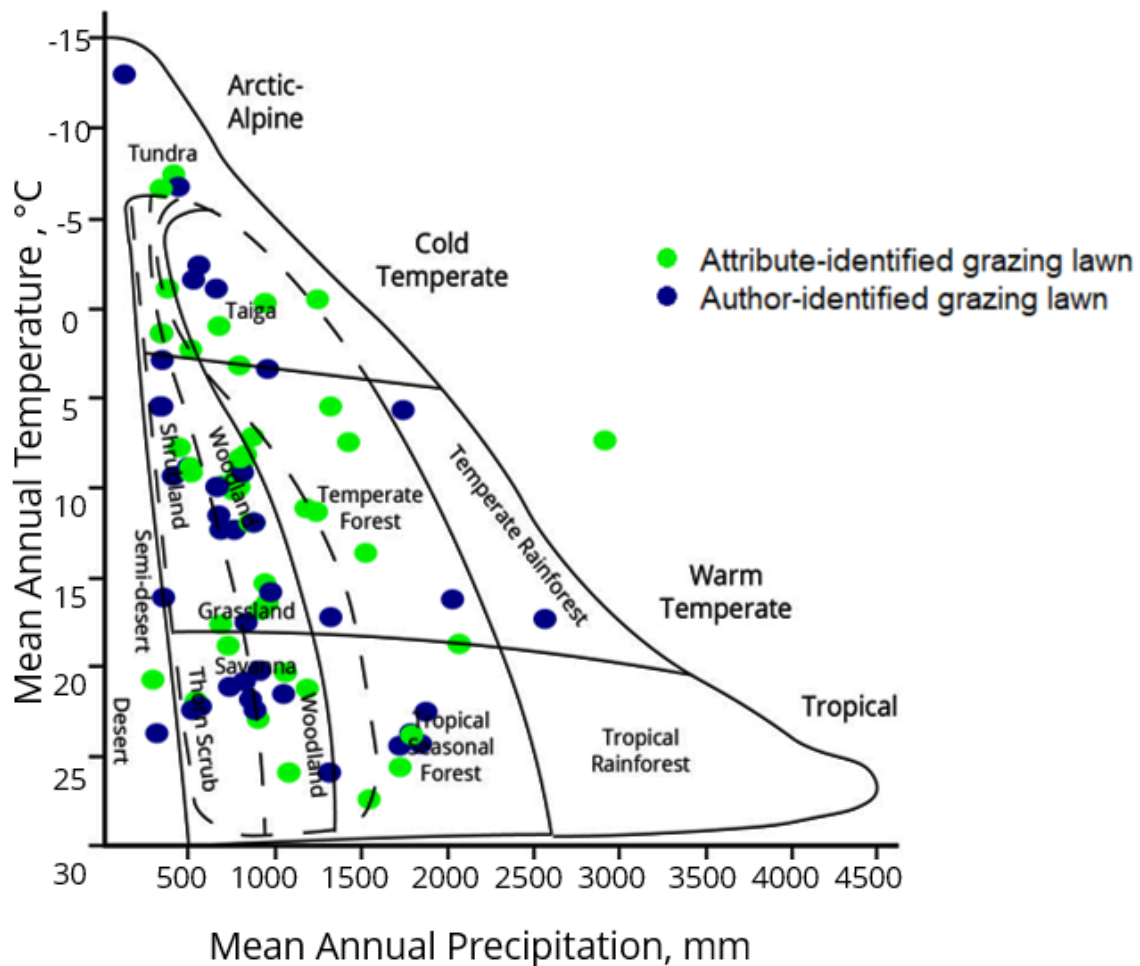


Figure S2.5. **Distribution of case studies across Whittaker's biomes** coloured by case study classification. Overlaid figure follows Whittaker (1970), reproduced with permission from Pearson Higher Education. Distributions are defined by mean annual temperature vs. mean annual precipitation. Dashed lines represent areas in parameter space where the resulting biome classification depends on additional factors such as seasonality of fire, drought and grazing.

Vegetation-grazer association contingency table

Table S2.3. Associations between grazer characteristics and plant functional types. *Grazer characteristics assessed include (A) grazer taxa, and (B) grazer body size classes for terrestrial case studies. Each plant-grazer co-occurrence within a case study counted as a single association. Multiple associations per case study were possible if two or more plant functional types and grazer sizes, taxa, or categories were listed within the case study. The total number of associations for each plant functional type is shown in the bottom row of sections A and B, while the total number of associations for each grazer taxa and size class are presented in the last column.*

	C ₃ grass	C ₄ grass	Forb	Sedge	Total
(A) Grazer Taxa					
Aves	4	0	1	4	9
Mammalia	46	156	29	18	249
Reptilia	0	4	0	0	4
Total	50	160	30	22	262
(B) Grazer Size Class					
Nanoherbivore	1	0	1	0	2
Microherbivore	6	5	5	7	23
Mesoherbivore	19	57	8	8	92
Macroherbivore	24	77	16	7	124
Megaherbivore	0	21	0	0	21
Total	50	160	30	22	262

Data S2.1. Grazing Lawn case study database

CODE	SYSTEM	REGION	LOCATION	LAT	LONG	TERM USED	CLASS- IFICATION	DOMINANT PFT	GRAZER TAXON	DOMINANT GRAZER SIZECLASS
A1	Aquatic	Australia	Moreton Bay, Australia	-27.08	153.05	seagrass meadows	Attribute- identified	Seagrass	Mammalia	NA
A2	Aquatic	Africa	False Bay, Cape Peninsula, South Africa	-34.10	18.47	gardens; gardening interactions	Attribute- identified	Algae	Gastropoda	NA
A3	Aquatic	Australia	Lizard Island, Great Barrier Reef	-14.67	145.47	algal turf	Attribute- identified	Algae	Pieces	NA
A4	Aquatic	North America	Puerto Morelos reef lagoon, Yucatan Peninsula, Mexican Caribbean	20.84	-86.87	cultivation grazing; rotational grazing; grazing plots	Attribute- identified	Seagrass	Reptilia	NA
A5	Aquatic	South America	Eastern Caribbean	12.10	-68.23	grazing patches	Attribute- identified	Seagrass	Reptilia	NA
T1	Terrestrial	Africa	Aldabra Atoll, Seychelles, Indian Ocean	-9.40	46.33	tortoise turf	Attribute- identified	C ₄ grass	Reptilia	Macroherbivore
T2	Terrestrial	Africa	Queen Elizabeth National Park, Uganda	-0.16	29.93	no term given	Attribute- identified	C ₄ grass	Mammalia	Megaherbivore
T3	Terrestrial	Africa	Lamai Guard Post, Serengeti, Tanzania	-1.62	34.89	hippo lawn	Attribute- identified	C ₄ grass	Mammalia	Megaherbivore
T4	Terrestrial	Australia	Saltwater River Scenic Reserve, Tasmania, Australia	-42.95	147.67	closed-herb field	Attribute- identified	Forb; Sedge	Mammalia	Mesoherbivore
T5	Terrestrial	Australia	Alice springs district, Central Australia	-23.69	133.88	marsupial lawn	Attribute- identified	C ₄ grass	Mammalia	Mesoherbivore

CODE	SYSTEM	REGION	LOCATION	LAT	LONG	TERM USED	CLASS- IFICATION	DOMINANT PFT	GRAZER TAXON	DOMINANT GRAZER SIZECLASS
T6	Terrestrial	Europe	Gent, Belgium	51.05	3.72	lawn; nutritive area	Attribute- identified	C ₃ grass	Mammalia	Macroherbivore
T7	Terrestrial	Europe	Schiermonnikoog, NL	53.49	6.17		Attribute- identified	Forb	Aves	Microherbivore
T8	Terrestrial	Europe	New Forest National Park, United Kingdom	50.88	-1.63	non-latrine	Attribute- identified	C ₃ grass	Mammalia	Macroherbivore
T9	Terrestrial	Africa	Aldabra Atoll, Seychelles, Indian Ocean	-9.40	46.33	tortoise turf	Attribute- identified	C ₄ grass	Reptilia	Macroherbivore
T10	Terrestrial	Africa	Serengeti National Park, Tanzania	-2.33	34.57	grazing lawn	Author- identified	C ₄ grass	Mammalia	Macroherbivore
T11	Terrestrial	North America	La Pérouse Bay, Manitoba, Canada	58.84	-94.83		Attribute- identified	C ₃ grass; Sedge	Aves	Microherbivore
T12	Terrestrial	Europe	Drenthe, Netherlands	53.02	6.18	heavily grazed areas	Attribute- identified	C ₃ grass	Mammalia	Mesoherbivore
T13	Terrestrial	Australia	Mount Field West, Tasmania, Australia	-42.68	146.50	short alpine herbfield	Attribute- identified	Forb; Sedge	Mammalia	Mesoherbivore
T14	Terrestrial	South America	Flooding Pampa, Province of Buenos Aires, Argentina	-35.90	-58.05	grazed areas	Attribute- identified	C ₃ grass; Forb	Mammalia	Macroherbivore
T15	Terrestrial	South America	Hato El Frito, Venezuela	7.77	-68.95	bajios	Attribute- identified	C ₃ grass	Mammalia	Mesoherbivore
T16	Terrestrial	North America	Central Plains Experimental Range (CPER), USDA-ARS, Colorado	40.15	- 103.13	grazing-lawn	Author- identified	C ₄ grass	Mammalia	Macroherbivore
T17	Terrestrial	North America	La Perouse Bay, Manitoba, Canada	58.07	-94.05	grazing lawn	Author- identified	C ₃ grass	Aves	Microherbivore

CODE	SYSTEM	REGION	LOCATION	LAT	LONG	TERM USED	CLASS- IFICATION	DOMINANT PFT	GRAZER TAXON	DOMINANT GRAZER SIZECLASS
T18	Terrestrial	Asia	Royal Chitwan National Park, Nepal	27.53	84.45	grazing lawn	Author-identified	C ₄ grass	Mammalia	Megaherbivore
T19	Terrestrial	South America	Peruvian National Research Center for South American Camelids at La Raya, Peru	-14.50	-71.00		Attribute-identified	C ₄ grass; C ₃ grass	Mammalia	Macroherbivore
T20	Terrestrial	Europe	Stroomdallandschap Drentsche Aa, Netherlands	53.08	6.67	short turf	Attribute-identified	C ₃ grass; Forb	Mammalia	Macroherbivore
T21	Terrestrial	Africa	Serengeti National Park, Tanzania	-2.83	35.10	short grass sites	Attribute-identified	C ₄ grass	Mammalia	Macroherbivore
T22	Terrestrial	North America	Wind Cave National Park, South Dakota, USA	43.57	-103.44	no term given	Attribute-identified	C ₄ grass	Mammalia	Microherbivore
T23	Terrestrial	Europe	Karshoek area, Netherlands	53.53	6.53	short patches	Attribute-identified	C ₃ grass	Mammalia	Macroherbivore
T24	Terrestrial	Europe	Renkumse Benedenwaarden, Netherlands	51.97	5.72	short patches	Attribute-identified	C ₃ grass	Mammalia	Macroherbivore
T25	Terrestrial	South America	Parana River Delta region, Argentina	-34.09	-58.59		Attribute-identified	Sedge; C ₄ grass	Mammalia	Mesoherbivore
T26	Terrestrial	Africa	Mpala Research Centre, Laikipia, Kenya	0.28	37.88	glades	Attribute-identified	C ₄ grass	Mammalia	Megaherbivore
T27	Terrestrial	North America	Ministik Field Station, Alberta, Canada	53.30	-114.58	patch	Attribute-identified	C ₃ grass	Mammalia	Macroherbivore

CODE	SYSTEM	REGION	LOCATION	LAT	LONG	TERM USED	CLASS- IFICATION	DOMINANT PFT	GRAZER TAXON	DOMINANT GRAZER SIZECLASS
T28	Terrestrial	North America	Izembek National Wildlife Refuge, Alaska, USA	55.29	-162.68	grazing lawn	Author-identified	Sedge	Mammalia	Mesoherbivore
T29	Terrestrial	North America	Cook College, Rutgers University, New Jersey, USA	40.48	-74.43	lawn; grazing area	Attribute-identified	C ₃ grass	Mammalia	Macroherbivore
T30	Terrestrial	North America	South Fork Hoh River, Olympic National Park, Washington, USA	47.78	-123.93	G patch; Grass-dominated strata	Attribute-identified	C ₃ grass; Forb	Mammalia	Macroherbivore
T31	Terrestrial	Europe	Gimritz Nature Protection Area, Germany	51.58	11.83	grazing lawn; vole lawn	Author-identified	C ₃ grass; Forb	Mammalia	Nanoherbivore
T32	Terrestrial	North America	Konza Prairie, Kansas, USA	39.08	-96.58	grazing lawn; grazing patches	Author-identified	C ₄ grass	Mammalia	Macroherbivore
T33	Terrestrial	Asia	Royal Bardia National Park, Nepal	28.51	81.25	grazing lawn; shortgrass patches	Author-identified	C ₄ grass	Mammalia	Megaherbivore
T34	Terrestrial	Europe	Wolfhezerheide nature reserve, Netherlands	51.78	5.68	lawn	Attribute-identified	C ₃ grass	Mammalia	Macroherbivore
T35	Terrestrial	South America	Magellanic steppe, near Rio Grande, Argentina	-53.78	-67.70	grazing lawn; lawn	Author-identified	Forb	Mammalia	Mesoherbivore
T36	Terrestrial	Europe	Communal des Magnils-Reigniers, France	46.44	-1.22	short grazing lawn	Author-identified	C ₃ grass	Mammalia	Macroherbivore

CODE	SYSTEM	REGION	LOCATION	LAT	LONG	TERM USED	CLASS- IFICATION	DOMINANT PFT	GRAZER TAXON	DOMINANT GRAZER SIZECLASS
T37	Terrestrial	Europe	Commune of Magnils-Reigniers, Vendée, France	46.47	-1.17	grazing lawn	Author-identified	Forb; C ₃ grass; Sedge	Mammalia	Macroherbivore
T38	Terrestrial	North America	Ruby Range Mountains, Yukon Territory, Canada	61.22	-138.27	grazing plots	Attribute-identified	Forb; Sedge	Mammalia	Microherbivore
T39	Terrestrial	North America	Tutakoke River, Southwest Alaska, USA	61.25	-165.50	grazing lawn	Author-identified	Sedge	Aves	Microherbivore
T40	Terrestrial	Africa	Laikipia district, Kenya	0.28	37.88	glades; abandoned-boma	Attribute-identified	C ₄ grass	Mammalia	Macroherbivore
T41	Terrestrial	Africa	Mpala Research Centre, Laikipia, Kenya	0.28	37.88	glades; abandoned-boma	Attribute-identified	C ₄ grass	Mammalia	Mesoherbivore
T42	Terrestrial	Asia	Horton Plains National Park, Sri Lanka	6.80	80.81	grazing lawn	Author-identified	C ₄ grass	Mammalia	Macroherbivore
T43	Terrestrial	South America	Pampa de Achala, Argentina	-31.57	-64.83	grazing lawn	Author-identified	Forb; C ₄ grass; Sedge	Mammalia	Macroherbivore
T44	Terrestrial	North America	Konza Prairie Biological Station, Kansas, USA	39.08	-96.58	grazing lawn	Author-identified	C ₄ grass	Mammalia	Macroherbivore
T45	Terrestrial	South America	María Behety Ranch, Argentina	-53.78	-67.70	grazing lawn; short lawn	Author-identified	C ₃ grass	Mammalia	Mesoherbivore
T46	Terrestrial	Australia	Crows Nest, southeastern Queensland, Australia	-27.27	152.05	lawn	Attribute-identified	C ₄ grass	Mammalia	Macroherbivore

CODE	SYSTEM	REGION	LOCATION	LAT	LONG	TERM USED	CLASS- IFICATION	DOMINANT PFT	GRAZER TAXON	DOMINANT GRAZER SIZECLASS
T47	Terrestrial	Africa	Benue National Park, Cameroon	8.33	13.83	grazing lawn; hippo lawn	Author-identified	C ₄ grass	Mammalia	Megaherbivore
T48	Terrestrial	Africa	Benue National Park, Cameroon	8.33	13.83	grazing lawn; kob lawn	Author-identified	C ₄ grass; C ₃ grass	Mammalia	Mesoherbivore
T49	Terrestrial	Europe	Swiss National Park, Switzerland	46.67	10.25	short-grass type	Attribute-identified	C ₃ grass	Mammalia	Macroherbivore
T50	Terrestrial	North America	Akimiski Island, Nunavut Territory, Canada (Thompson River)	53.19	-81.44	grazing lawn	Author-identified	C ₃ grass	Aves	Microherbivore
T51	Terrestrial	North America	Konza Prairie Biological Station, Kansas, USA	39.08	-96.58		Attribute-identified	C ₄ grass	Mammalia	Macroherbivore
T52	Terrestrial	Africa	Hluhluwe iMfolozi Park (HiP), KwaZulu Natal, South Africa	-28.22	31.95	grazing lawn	Author-identified	C ₄ grass	Mammalia	Megaherbivore
T53	Terrestrial	Africa	KwaZulu Natal (Hluhluwe iMfolozi Park [HiP]), South Africa	-28.22	31.95	grazing lawn	Author-identified	C ₄ grass	Mammalia	Macroherbivore
T54	Terrestrial	Africa	Hluhluwe-iMfolozi Park, KwaZulu-Natal Province, South Africa	-28.21	31.95	grazing lawn	Author-identified	C ₄ grass	Mammalia	Megaherbivore
T55	Terrestrial	Asia	Royal Bardia National Park, Nepal	28.50	81.25	grazing lawn	Author-identified	C ₄ grass	Mammalia	Mesoherbivore
T56	Terrestrial	Europe	Silwood Park, Berkshire, UK	51.41	-0.64	lawn	Attribute-identified	C ₃ grass	Mammalia	Microherbivore
T57	Terrestrial	Asia	Bandipur Tiger Reserve, India	11.67	76.63	grazing lawn	Author-identified	C ₄ grass	Mammalia	Mesoherbivore

CODE	SYSTEM	REGION	LOCATION	LAT	LONG	TERM USED	CLASS- IFICATION	DOMINANT PFT	GRAZER TAXON	DOMINANT GRAZER SIZECLASS
T58	Terrestrial	Asia	Changtang, Tibet	30.38	90.88	grazing lawn; turf; felty turf	Author- identified	Sedge	Mammalia	Macroherbivore
T59	Terrestrial	Asia	Kinkazan Island, Japan	38.30	141.57	lawn grass	Attribute- identified	C ₄ grass	Mammalia	Mesoherbivore
T60	Terrestrial	Asia	Inner Mongolia Grassland Ecosystem Research Station, Mongolia	43.63	116.70	grazing lawn	Author- identified	C ₃ grass	Mammalia	Mesoherbivore
T61	Terrestrial	Asia	Sumiyoshi Livestock Science Station, Kyushu, Japan	31.98	131.47	grazing lawn	Author- identified	C ₄ grass	Mammalia	Macroherbivore
T62	Terrestrial	Australia	'Bangor' Forestier Peninsula, Tasmania, Australia	-42.88	147.92	marginal herb fields; marsupial lawn	Attribute- identified	Forb	Mammalia	Mesoherbivore
T63	Terrestrial	Australia	Central Plateau, Tasmania, Australia	-41.86	146.52	marginal herb fields; marsupial lawn	Attribute- identified	Sedge	Mammalia	Mesoherbivore
T64	Terrestrial	Africa	Associated Private Nature Reserve (APNR), consisting of the Timbavati, Klaserie, and Umbabat Private Nature Reserves and the Balule Nature Reserve, South Africa	-24.26	31.25	nutrient hotspot; abandoned kraal	Attribute- identified	C ₄ grass	Mammalia	Megaherbivore

CODE	SYSTEM	REGION	LOCATION	LAT	LONG	TERM USED	CLASS- IFICATION	DOMINANT PFT	GRAZER TAXON	DOMINANT GRAZER SIZECLASS
T65	Terrestrial	South America	Quebrada del Condorito National Park, Argentina	-31.57	-64.83	moist grazing lawn; dry grazing lawn	Author-identified	Forb; Sedge	Mammalia	Macroherbivore
T66	Terrestrial	Africa	Laikipia District of central Kenya	0.28	36.87	nutrient hotspots; glades	Attribute-identified	C ₄ grass	Mammalia	Megaherbivore
T67	Terrestrial	North America	Beaufort Sea coast, Smith River and Garry Creek, Alaska	70.81	-152.19	grazing lawn	Author-identified	Sedge	Aves	Microherbivore
T68	Terrestrial	Africa	Mountain Zebra National Park, South Africa	-32.14	25.51	grazing lawn	Author-identified	C ₄ grass	Mammalia	Macroherbivore
T69	Terrestrial	South America	Quebrada del Condorito National Park, Argentina	-31.62	-64.80	grazing lawn	Author-identified	Forb; Sedge	Mammalia	Macroherbivore
T70	Terrestrial	Africa	Kruger National Park, South Africa	-23.99	31.55	hotspots; grazing lawn	Author-identified	C ₄ grass	Mammalia	Megaherbivore
T71	Terrestrial	Africa	Serengeti National Park, Tanzania	-2.31	34.85	hotspots; grazing lawn	Author-identified	C ₄ grass	Mammalia	Macroherbivore
T72	Terrestrial	Europe	Lippstadt, Germany	51.67	8.34	ruderal grazing lawn; grazing lawn	Author-identified	Forb	Mammalia	Macroherbivore
T73	Terrestrial	South America	Quebrada del Condorito National Park. Argentina	-31.61	-64.71	grazing lawn	Author-identified	Forb; C ₄ grass; Sedge	Mammalia	Macroherbivore
T74	Terrestrial	Asia	Royal Chitwan National Park, Nepal	27.50	84.33	no term given	Attribute-identified	C ₄ grass	Mammalia	Megaherbivore

CODE	SYSTEM	REGION	LOCATION	LAT	LONG	TERM USED	CLASS- IFICATION	DOMINANT PFT	GRAZER TAXON	DOMINANT GRAZER SIZECLASS
T75	Terrestrial	North America	University of the South, Sewanee, Tennessee, USA	35.20	-85.92	burned patch; forage reserve; grass bank	Attribute-identified	C ₄ grass; C ₃ grass	Mammalia	Macroherbivore
T76	Terrestrial	Europe	Östvallen summer farm, Härjedalen, Sweden	62.36	13.34	grass-dominated pasture	Attribute-identified	C ₃ grass	Mammalia	Macroherbivore
T77	Terrestrial	Africa	Ithala Game Reserve, South Africa	-27.50	31.33	grazing lawn	Author-identified	C ₄ grass	Mammalia	Megaherbivore
T78	Terrestrial	Asia	Xilin River catchment, Inner Mongolia Autonomous Region, P.R. China	43.63	116.70	resource island; patchy grazing patterns	Attribute-identified	C ₃ grass	Mammalia	Mesoherbivore
T79	Terrestrial	South America	Corrientes INTA Research Station, Corrientes Province, Argentina	-27.67	-58.79	High impact grazing (HIG) plots	Attribute-identified	C ₄ grass	Mammalia	Macroherbivore
T80	Terrestrial	Africa	Hluhluwe-iMfolozi Park, KwaZulu-Natal Province, South Africa	-28.21	31.95	grazing lawn	Author-identified	C ₄ grass	Mammalia	Megaherbivore
T81	Terrestrial	Europe	Oranienbaumer Heide, Germany	51.77	12.35		Attribute-identified	C ₃ grass; Forb	Mammalia	Macroherbivore
T82	Terrestrial	Europe	Padjelanta National Park, Sweden	67.37	16.71	Historical milking grounds	Attribute-identified	C ₃ grass; Sedge	Mammalia	Mesoherbivore
T83	Terrestrial	Africa	Kruger National Park, South Africa	-24.39	31.78	grazing lawn	Author-identified	C ₄ grass	Mammalia	Macroherbivore

CODE	SYSTEM	REGION	LOCATION	LAT	LONG	TERM USED	CLASS- IFICATION	DOMINANT PFT	GRAZER TAXON	DOMINANT GRAZER SIZECLASS
T84	Terrestrial	Africa	Laikipia district, Kenya	-0.32	36.90	grazing lawn	Author- identified	C ₄ grass	Mammalia	Megaherbivore
T85	Terrestrial	Australia	Kosciuszko National Park, New South Wales, Australia	-36.50	148.27	grazing lawn	Author- identified	Forb	Mammalia	Macroherbivore
T86	Terrestrial	North America	Konza Prairie Biological Station, Kansas, USA	39.08	-96.58	grazing lawn	Author- identified	C ₄ grass	Mammalia	Macroherbivore
T87	Terrestrial	North America	Yokon-kuskokwim Delta, Alaska, USA	61.59	- 163.68	grazing lawn	Author- identified	Sedge	Aves	Microherbivore
T88	Terrestrial	Australia	Tasmania, Australia	-42.94	147.70	grazing lawn	Author- identified	C ₄ grass; C ₃ grass	Mammalia	Mesoherbivore
T89	Terrestrial	South America	Maria Behety Ranch, Tierra del Fuego, Argentina	-53.78	-67.93	grazing lawn	Author- identified	C ₃ grass	Mammalia	Mesoherbivore
T90	Terrestrial	Africa	Aldabra Atoll, Seychelles, Indian Ocean	-9.40	46.33	tortoise turf	Attribute- identified	C ₄ grass	Reptilia	Macroherbivore
T91	Terrestrial	Africa	Hluhluwe-iMfolozi Park, KwaZulu-Natal Province, South Africa	-28.21	31.95	grazing lawn	Author- identified	C ₄ grass	Mammalia	Megaherbivore
T92	Terrestrial	Africa	Kruger National Park, South Africa;	-24.67	31.12	grazing lawn	Author- identified	C ₄ grass	Mammalia	Megaherbivore
T93	Terrestrial	Europe	high marsh, Schleswig-Holstein, Germany	54.03	8.90	lawn	Attribute- identified	C ₃ grass	Mammalia	Mesoherbivore
T94	Terrestrial	Europe	low marsh, Schleswig-Holstein, Germany	54.63	8.83	lawn	Attribute- identified	C ₃ grass	Mammalia	Mesoherbivore

CODE	SYSTEM	REGION	LOCATION	LAT	LONG	TERM USED	CLASS- IFICATION	DOMINANT PFT	GRAZER TAXON	DOMINANT GRAZER SIZECLASS
T95	Terrestrial	Asia	Hulunbuir Grassland Ecosystem Observation and Research Station, Inner Mongolia, China	49.32	119.93	no term given	Attribute-identified	C ₃ grass	Mammalia	Macroherbivore
T96	Terrestrial	Africa	Central Highlands, Madagascar	-20.59	46.63	grazing lawn	Author-identified	C ₄ grass	Mammalia	Macroherbivore
T97	Terrestrial	Africa	Issa Valley, Tanzania	-5.38	30.58	grazing lawn	Author-identified	C ₄ grass	Mammalia	Macroherbivore
T98	Terrestrial	South America	Galápagos Islands, Ecuador	-0.95	-90.97	grazing lawn	Author-identified	C ₄ grass	Reptilia	Macroherbivore
T99	Terrestrial	Asia	Sadengan Feeding Ground, Alas Purwo National Park, Java, Indonesia	-8.65	114.38	no term given	Attribute-identified	C ₄ grass	Mammalia	Macroherbivore
T100	Terrestrial	Asia	Bardia National Park, Nepal	28.38	81.50	grazing lawn	Author-identified	C ₄ grass	Mammalia	Macroherbivore
T101	Terrestrial	Asia	Kinkazan Island, Japan	38.28	141.57	lawn grass	Attribute-identified	C ₄ grass	Mammalia	Mesoherbivore
T102	Terrestrial	Europe	Milovice, Czech Republic	50.24	14.89	no term given	Attribute-identified	C ₃ grass; Forb	Mammalia	Macroherbivore
T103	Terrestrial	Europe	Parque Natural de Sierra y Cañones de Guara, Spain	42.30	-0.17	no term given	Attribute-identified	C ₃ grass; Forb	Mammalia	Mesoherbivore

Database case studies literature cited

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T42	Padmalal, U. K. G. K., Takatsuki, S., & Jayasekara, P. (2003). Food habits of sambar Cervus unicolor at the Horton Plains National Park, Sri Lanka. <i>Ecological Research</i> , 18(6), 775–782. https://doi.org/10.1111/j.1440-1703.2003.00595.x
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T64	Van Der Waal, C., De Kroon, H., Heitkönig, I. M. A., Skidmore, A. K., Van Langevelde, F., De Boer, W. F., Slotow, R., Grant, R. C., Peel, M. P. S., Kohi, E. M., De Knecht, H. J., & Prins, H. H. T. (2011). Scale of nutrient patchiness mediates resource partitioning between trees and grasses in a semi-arid savanna. <i>Journal of Ecology</i> , 99(5), 1124–1133. https://doi.org/10.1111/j.1365-2745.2011.01832.x
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T84	McCauley, D. J., Graham, S. I., Dawson, T. E., Power, M. E., Ogada, M., Nyingi, W. D., Githaiga, J. M., Nyunja, J., Hughey, L. F., & Brashares, J. S. (2018). Diverse effects of the common hippopotamus on plant communities and soil chemistry. <i>Oecologia</i> , 188(3), 821–835. https://doi.org/10.1007/s00442-018-4243-y
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T97	Mayengo, G., Piel, A. K., & Treydte, A. C. (2020). The importance of nutrient hotspots for grazing ungulates in a Miombo ecosystem, Tanzania. <i>PLoS ONE</i> , 15(3), e0230192. https://doi.org/10.1371/journal.pone.0230192
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Chapter 3: Functional variation in grasses across Madagascar in response to environment

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Abstract

Grasses thrive across diverse environments, from tropical savannas to cold tundra, due to varied life history strategies comprising combinations of co-varying functional traits. Madagascar, with its strong environmental gradients with a relatively well-documented grass flora- including C₃ and C₄ grasses- provides an excellent system to investigate the processes underpinning grass life history strategies. While numerous hypotheses describe trait responses to environmental gradients, studies to date typically exclude phylogenetic covariation, assess drivers in isolation, or condense multiple drivers, potentially misrepresenting trait-environmental relationships.

Using herbarium-derived data for 260 grass species, 47% of Madagascar's grass flora, we quantified correlations between putative bottom-up and top-down drivers and six functional traits related to size and leaf economics that shape life history strategies. We also explored how these traits coordinate (i.e. organise in multivariate space) within these strategies. Herbarium trait data were validated against field-collected data using linear models. We used phylogenetic generalised linear mixed models to assess trait-environment relationships and multi-model inference to predict island-wide trait distributions. Pearson's correlation coefficient was used to assess pairwise trait coordination, while multivariate trait coordination was examined using a Principal Component Analysis.

Herbarium and field-collected data showed strong positive correlations, supporting herbarium specimens as a reliable data source for trait analyses. Trait-environment models showed temperature, nutrient availability, and fire occurrence to be strong predictors for most size and leaf economic traits, while water availability had a marginally significant negative relationship with leaf width and thickness. Global Human Modification Index, used as a proxy for grazing intensity, was not significantly correlated with any trait. All traits co-varied significantly. Size-related traits such as inflorescence height, culm diameter, and leaf length showed the strongest positive correlations, while leaf economic traits such as leaf thickness and leaf nitrogen showed the strongest negative correlations. Within multivariate

space, trait coordination was aligned with well-established leaf economic and size spectra, with varying life history strategies emerging along these axes.

Our findings confirm that grasses, through strong trait trade-offs that balance resource acquisition, environmental tolerance, and growth, exhibit distinct life history strategies that vary along two primary axes of variation, with trait positions along these axes shaped by bottom-up and top-down environmental pressures. By clarifying how traits respond and coordinate at a regional scale, these findings contribute to a broader understanding of grass differentiation along environmental gradients and improve predictions of grass responses to environmental change.

Key Words: trait-based filtering, climate adaptation, predictive models, trait coordination, model averaging

Introduction

Grasses (Poaceae), a family of approximately 11,000 species, are globally widespread and successful (Clayton et al., 2014). Despite accounting for only 3% of plant species on Earth, they dominate approximately 40% of the global land surface and contribute 33% of global primary productivity (Beer et al., 2010; Gibson, 2008). The occupation by grasses of diverse environments, from arid deserts to tropical savannas to cold tundra, is enabled by substantial functional differentiation within the family, reflected in varied growth forms and photosynthetic pathways (da Silveira Pontes et al., 2015; Linder et al., 2018). For example, the evolution of both the C₃ and C₄ photosynthetic pathways allows grasses as a clade to optimise carbon capture and water use efficiency under different climatic conditions, with C₃ grasses - typically smaller and more resource-conservative - prevalent in cooler or shaded habitats, while C₄ grasses - larger, more water-efficient, and better adapted to intense light and heat - generally dominate in warm, open environments (W. Gao et al., 2024; Gowik & Westhoff, 2010; Osborne & Freckleton, 2009; Sage & Monson, 1998). Such functional differences among grasses underpin the diversity of life history strategies that allow grasses to persist across environments shaped by different combinations of biotic (e.g. competition and grazing) and abiotic (e.g. fire, drought, extreme temperatures, nutrient-poor soils) factors. Understanding how grasses differentiate over wide environmental gradients and how biotic and abiotic factors interact to shape grass structure and function is key to linking community responses of grasslands to environmental change (Keddy, 1992; Lavorel & Garnier, 2002; Violle et al., 2007).

Life history strategies are represented by combinations of functional traits - measurable morphological, physiological, or phenological attributes of an individual organism that influence performance or fitness (Laughlin, 2014; McGill et al., 2006; Violle et al., 2007). Functional traits both reflect and mediate how grasses interact with the environment, both being shaped by environmental conditions through natural selection and adaptation and actively determining the environment a species inhabits, often referred to as trait-based filtering or environmental sorting (Lavorel & Garnier, 2002; Westoby et al.,

2002). These environmental conditions include both bottom-up and top-down controls of the environment. Bottom-up controls, including temperature, water, light, and nutrient availability, regulate growth and resource acquisition strategies across environments (Hunter & Price, 1992; Power, 1992). Top-down controls, such as fire and herbivory, influence not only total biomass but enable biotic feedbacks between traits and environment such that divergent strategies are possible within a given environment (Hempson et al., 2019). Bottom-up and top-down controls interact to facilitate the dominance of grasses across a diversity of environments, substantively determining a wide range of plant life history strategies. Taken together, grasses are thus an excellent model taxon to test how functional traits link to and are coordinated in response to environmental gradients.

Numerous studies indicate that temperature (e.g. Baird et al., 2021; Hatfield & Prueger, 2015; Moles et al., 2014), nutrient availability (e.g. Ordoñez et al., 2009; Wright et al., 2004), water availability (e.g. Maire et al., 2015; Moles et al., 2009; Zhang et al., 2019), fire (e.g. Bond & Keeley, 2005; Murray et al., 2013; Simpson et al., 2016) and grazing (e.g. Díaz et al., 2001; McNaughton, 1979) are key drivers of functional differentiation in grasses with environmental drivers interacting in complex ways to shape grass life history strategies. Temperature influences growth, metabolism and resource uptake, with higher temperatures accelerating metabolic processes and increasing nutrient and water uptake efficiency in resource-rich environments, resulting in taller grasses with larger, thinner leaves (Bade et al., 1985; Hatfield & Prueger, 2015; Onwuka, 2018). Nutrient availability can favour either rapid resource capture (e.g. tall stature) or quick turnover (e.g. thin, nutrient-rich leaves), depending on its interactions with other factors such as disturbance. In contrast, nutrient-poor environments favour conservative, resource-retentive traits (i.e. short grasses with small, thick leaves) (Craine et al., 2002; Ordoñez et al., 2009; Tilman & Wedin, 1991). Water availability can constrain growth, with limited water selecting for grasses with smaller, more conservative structures (e.g. short grasses with small, thick, nutrient-poor leaves) (Liu & Osborne, 2015; Oyarzabal et al., 2008). Fire and grazing, as consumers of aboveground biomass, drive positive feedbacks that, over time, select for

distinct trait syndromes- sets of co-evolving traits- with frequent fire favouring tall, dense grasses and heavy grazing favouring shorter, palatable grasses with nutrient-rich tissues (Archibald et al., 2019; Solofondranohatra, 2020). These relationships inform our hypotheses of how traits change along environmental gradients (Table 3.1).

Table 3.1. Hypotheses of the relationships between our six trait variables and our five environmental drivers. Upwards arrows (green) indicate a positive relationship while downwards arrows (red) indicate a negative one.

	Temperature ¹	*Nutrient Deficiency ²	Water Availability ³	Fire ⁴	Grazing ⁵
Inflorescence Height (cm)	↑	↓	↑	↑	↓
Culm Diameter (cm)	↑	↓	↑	↑	↓
Leaf Length (cm)	↑	↓	↑	↑	↓
Leaf Width (cm)	↑	↓	↑	↓	↑
Leaf Thickness (mm)	↓	↑	↓	↑	↓
Leaf Nitrogen (%)	↑	↓	↓	↓	↑

Note:

* Represents overall nutrient availability ,

Relevant literature:

¹ Arthan et al., 2022; Baird et al., 2021; Givnish, 1979; Jardine et al., 2020; Moles et al., 2014; Oyarzabal et al., 2008; Reich & Oleksyn, 2004

² Chapin et al., 1993; Chen et al., 2010; Coughenour, 1985; Fonseca et al., 2000; Pathare et al., 2020; Reich et al., 2001; Tilman & Wedin, 1991; Wright et al., 2004

³ Arthan et al., 2022; Baird et al., 2021; Chen et al., 2010; Givnish, 1979; Jardine et al., 2020; Liu & Osborne, 2015; Maire et al., 2015; Oyarzabal et al., 2008; Pathare et al., 2020; Zhang et al., 2019

⁴ Archibald et al., 2019; Díaz et al., 2001; Maire et al., 2015; Murray et al., 2013; Oyarzabal et al., 2008; Simpson et al., 2016; Solofondranohatra et al., 2020; Wilson et al., 1983

⁵ Anderson et al., 2013; Archibald et al., 2019; Benvenuti et al., 2009; Cayssials & Rodríguez, 2018; Coetsee et al., 2011; Díaz et al., 2007; McNaughton, 1976

While these relationships are well-documented, trait responses to environmental gradients remain highly variable, as few studies account for the interactive effects of multiple drivers (Funk et al., 2017; Garnier et al., 2007). Many studies consider environmental drivers in isolation, simplifying complex environmental gradients (e.g. Bade et al., 1985; Moles et al., 2014) or condense multiple drivers to assess effects simultaneously (e.g. Crowley & Wingler, 2020; Jardine et al., 2020; Maire et al., 2015; Wright et al., 2005). Furthermore, few broad-scale studies account for phylogenetic relationships that can shape trait evolution and community assembly, potentially misattributing trait-environment patterns to environmental filtering rather than shared evolutionary history (de Bello et al., 2017; Xu et al., 2017). One of the aims of this study is to provide robust statistical predictions of the biogeographic distribution of traits which requires an approach that includes important bottom-up and top-down drivers while controlling for phylogenetic and spatial factors. Such models could help disentangle the underlying drivers of trait variation, providing insights into how life history strategies emerge and persist along environmental gradients.

Functional traits, such as leaf size, rarely vary independently but rather co-vary with other traits, such as leaf thickness, along major axes of variation (Armbruster et al., 2014; Díaz et al., 2004; Watson & Szathmáry, 2016; Westoby et al., 2002). In grasses, two major axes are the size spectrum and the leaf economic spectrum (LES) (Jardine et al., 2020; Sandel et al., 2016). The size spectrum reflects trade-offs in competition, reproduction, and structural investment, with large grasses - typically found in wet (Arthan et al., 2022; Oyarzabal et al., 2008) and nutrient-rich (Tilman & Wedin, 1991) environments- exhibiting greater competitive abilities, enhanced seed dispersal and larger range sizes than smaller grasses (Grime, 2006; Keddy et al., 2002; Mashau et al., 2021; Westoby, 1998; Zhou et al., 2016). The LES captures trade-offs in leaf traits related to resource acquisition and conservation with nutrient-rich, thin leaves that enable rapid turnover in high-resource environments, while thicker, more robust leaves that enhance longevity and nutrient retention under stress (Díaz et al., 2004; Pierce et al., 2007; Simpson et al., 2020; Wright et

al., 2004). Disturbances like fire and grazing further shape trait coordination, imposing diverging selection pressures and reinforcing functional trade-offs in resource allocation and structural investment (Bond & Keeley, 2005). Additionally, allometric constraints structure variation along these axes, as taller grasses require wider culms with longer, wider, thicker leaves (Arthan et al., 2022; X. Gao et al., 2024). These coordinated trait trade-offs reflect viable and competitive life history strategies across environments, understanding of which can provide insight into species coexistence, niche differentiation and trait shifts along environmental gradients (Grime, 2006; Laughlin, 2014).

Global studies of grass functional differentiation (Jardine et al., 2020; Lehmann et al., 2014) reveal broad-scale environmental trends but often cannot detect the effects of small-scale drivers such as soil variation, water availability, and disturbance regimes (Grime, 2006). Local-scale factors can drive competitive or facilitative ecological strategies, while broad-scale climatic patterns exert more substantial selective pressures promoting trait convergence (Bruehlheide et al., 2018; Diaz & Cabido, 1997; Grime, 2006). Herbarium specimens offer advantages for bridging these scales as they represent individuals grown under natural conditions across environmental gradients, allowing us to assess fine-scale trait variation within a broader climatic and ecological context (Heberling, 2021; Queenborough, 2017). Despite their potential, few studies have utilised herbarium-derived traits to assess trait-environment and trait-trait relationships (e.g. Jardine et al., 2020; McAllister et al., 2019) and those that do largely focus on global-scale trends, limiting their ability to detect small-scale variations. Therefore, we used herbarium grass specimens from Madagascar to examine regional-scale differentiation to understand how both broad- and fine-scale environmental differences drive variation in grass life history strategies.

Madagascar is home to a diverse and ancient (approximately 20-8 million years ago) grass flora with approximately 550 grass species, nearly half of which are endemic (Hackel et al., 2018; Vorontsova et al., 2016; Vorontsova & Cavaco, 2018). Grasses occupy and dominate a wide range of environments across the island, ranging from the tall fire-driven C₄ grasses of the Central Highlands (e.g. *Loudetia simplex*, *Trachypogon spicatus*,

Schizachirium sanguineum) to the short cold-adapted C₃ grasses of the north east mountains (e.g. *Poa* spp.) and the small, climbing species that occupy forest understories (e.g. *Pseudechinolaena* spp., *Cyphochlaena* spp.) (Lehmann et al., 2022). This diversity reflects a long evolutionary history of grass diversification and adaptation, including both C₃ and C₄ lineages that have evolved in response to fire, grazing, and wide climatic gradients (Solofondranohatra et al., 2018; Vorontsova et al., 2016). Madagascar's strong climatic and ecological gradients, geographic isolation, alongside the expanding understanding of the regional differentiation of grass communities (Lehmann et al., 2022; Solofondranohatra et al., 2018, 2020) and the phylogenetic sampling of grasses (Hackel et al., 2018) make it a suitable study system for quantifying trait-environment relationships and the variation in life histories of grasses.

We use herbarium-derived functional traits representing leaf economics and plant size in grasses to link micro-scale trait responses to larger-scale environmental drivers and assess trait coordination. Specifically, we asked: (1) How do bottom-up (temperature, nutrient deficiency, water availability) and top-down (fire, grazing) environmental drivers correlate with and predict variation in individual functional traits related to plant size (i.e., inflorescence height, culm diameter, leaf length and leaf width) and leaf economic (e.g., leaf nitrogen, leaf thickness) spectra? Do these relationships align with established hypotheses outlined in Table 3.1? (2) Are traits coordinated with each other in their responses to environmental gradients? If so, what are the strengths of these relationships? And (3) What is the multivariate nature of these trait relationships, and what do they reveal about grass life history strategies?

Methods

All analyses were undertaken in R version 4.4 (2023).

Study system

Madagascar is a large (587,000 km²) island located in the Indian Ocean off the east coast of the African continent between 11°57 and 25°29 South and 43°14 and 50°27 East. The island is characterised by wide gradients, from warm wet tropical to Afrotropical, with

mean annual temperatures ranging from 13 to 27 °C and precipitation ranging from 500 to 3200mm per year.

Almost 80% of the island is covered by open, grassy ecosystems (Sarre, 2020), which are diverse and shaped by fire, grazing, and edaphic factors (Lehmann et al., 2022; Solofondranohatra et al., 2018, 2020). These grassy ecosystems can be broadly separated into six ecoregions (descriptions derived from Lehmann et al. 2022): The **Central Highlands** (800-1800m) form a mosaic of open fire-driven C₄ grasslands interspersed with closed gallery forests. Dominant grasses include *Loudetia simplex*, *Trachypogon spicatus*, and *Schizachirium sanguineum*. Above 1800 m, **montane** grasslands are dominated by C₃ species adapted to cold temperatures and endemic to the region, with dominant species including *Andropogon andringitrensis*, *Brachiaria dimorpha*, and *Poa perrieri*. In the **Western** region, grassy ecosystems include fire-adapted and edaphic grasslands, with key species such as *Setaria madecassa*, *Yvesia madagascariensis*, and *Neostapfiella perrieri*. The **Southern** region, characterised by semi-arid or arid conditions (<500 mm rainfall per year), contains many drought- and grazing-adapted species such as *Panicum voeltzkowii*, *Brachiaria humbertiana*, and *Neostapfiella humbertiana*. The **Eastern** and **Sabirano** regions, receiving more than 2000 mm of rainfall per year are dominated by evergreen and littoral forests however some edaphic grasslands or secondary grasslands- often linked to human use- persist, with common species including *Hyparrhenia rufa*, *Aristida similis*, *Aristida rufescens*, and *Imperata cylindrica*.

Data collection

Plant functional traits were measured from herbarium specimens of grasses at the Royal Botanic Gardens, Kew and the Muséum National d'Histoire Naturelle, Paris. Fully intact herbarium specimens were selected with at least one individual measured per species available in the collections. For widely available species, we sampled at least one individual per collection site when possible, to ensure broad environmental representation across the island (Figure 3.1). Longitude and latitude of the collection site were recorded for each herbarium specimen. In total, 1616 individuals from herbarium specimens were measured,

representing 260 species of which 36% are endemic (Table S3.1). Sampling for traits depended on specimen availability and hence the number of replicates and herbarium specimens per species varied from 1 to 36 replicates per species, with an average of six replicates per species. For well collected and widely distributed species, such as *Loudetia simplex*, 17 individuals were sampled from across its range in an effort to capture trait variation related to environment. Conversely, some poorly collected and range restricted species, such as *Dactyloctenium ctenoides* and *Melinis minutiflora*, were limited to a single herbarium specimen as that was all that was available. Species names were cleaned and updated to current taxonomy, and taxonomy checked using the ‘WorldFlora’ R package (Kindt, 2020). Data on photosynthetic pathways were sourced from the checklist of Osborne et al. (2014).

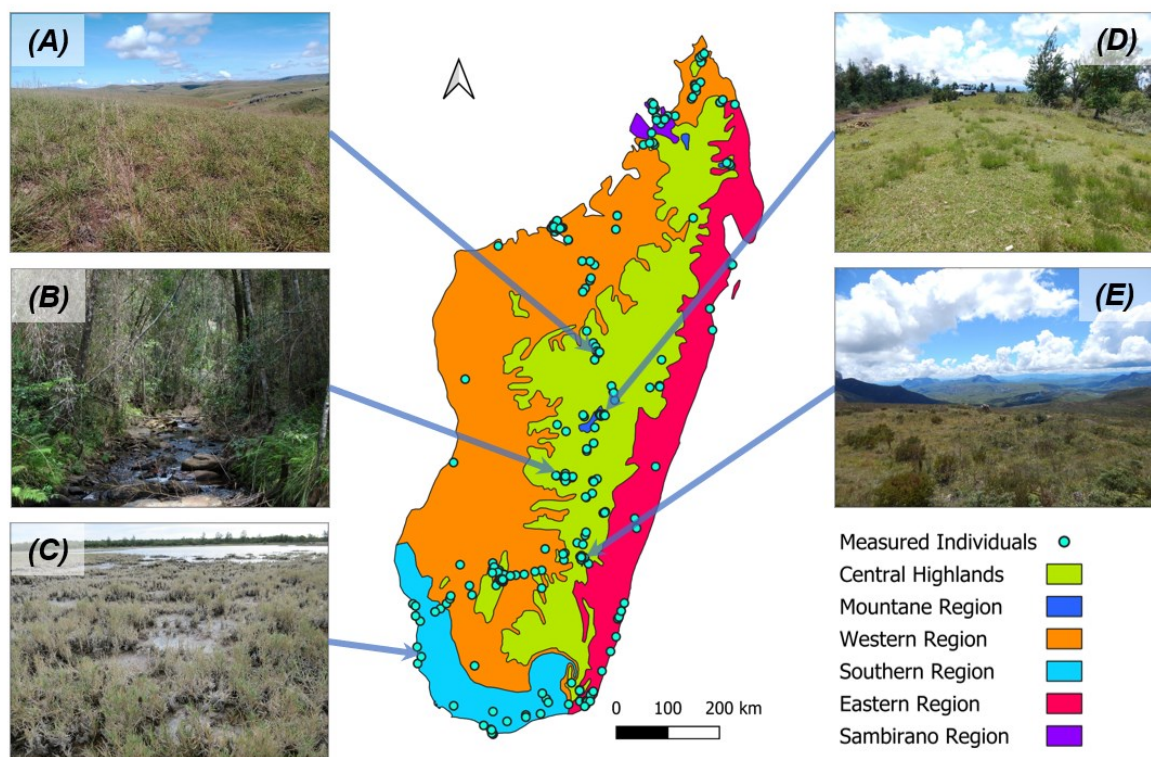


Figure 3.1. Map of Madagascar showing the distribution of measured individuals (N=1616) collected from 422 sites. Map coloured by six ecoregions originally defined by Humbert (1955): Central Highlands, Montane, Western, Southern, Eastern, and Sambirano regions.

Sites represent a wide spectrum of habitats across the island including: (A) Ankafobe burned grassland, (B) Itremo gallery forest understory, (C) Tsimanampetsotse salt flats, (D) Arboretyum Anosiarivo grazing lawn, (E) Andringitra plateau grassland. Photos by Maria Vorontsova.

Trait selection and significance

Six traits related to the leaf economic spectrum (LES) and size-related variation were measured from herbarium specimens. (1) *Inflorescence height* indicates plant size at maturity and canopy position, influencing light acquisition and competition (Lehmann et al., 2019; Linder et al., 2018; Westoby et al., 2002). (2) *Culm diameter* correlating with plant productivity and tensile strength, both of which influence digestibility, herbivory resistance, and fire ignitability (Benvenutti et al., 2009; Drescher et al., 2006; Wigley et al., 2020) (3) *Leaf length* and (4) *leaf width*, which are expected to be correlated and both directly relate to leaf area, determine the photosynthetic area that intercepts light, thereby influencing resource acquisition and competition (Baird et al., 2021; Crowley & Wingler, 2020). Leaf width is also associated with leaf moisture content, with larger widths indicating high moisture availability (Givnish, 1987; McDonald et al., 2003). (5) *Leaf thickness* is linked to stress tolerance and leaf lifespan (Mediavilla et al., 2008; Wright et al., 2004). (6) *Leaf nitrogen*, linked to the LES, is correlated with palatability, plant productivity, and stress tolerance (Archibald et al., 2019; Craine et al., 2002; Grime et al., 1997; Reich et al., 1997; Westoby et al., 2002; Wright et al., 2004),

Several allometric relationships among these traits are expected to support different structural adaptations. We expect there is an allometry of culm diameter with inflorescence height, not unlike tree diameter and height, with taller inflorescence heights having wider culms for structural support (X. Gao et al., 2024). Long, wide leaves are predicted to be associated with taller grasses with wide culms, while longer leaves may also be thicker to provide additional structural reinforcement (Baird et al., 2021; Sandel et al., 2016). Leaf thickness and leaf nitrogen are often positively correlated, as thicker leaves typically have

higher nitrogen per unit area (L. Gao et al., 2020; Pathare et al., 2020), though this relationship is not always consistent across environmental conditions (Craine et al., 2002; Reich et al., 1997).

Trait measurements

Trait measurements followed standard protocols, with adjustments made to accommodate the use of dried material (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013; Wigley et al., 2020). For *inflorescence height* (cm), the tallest flowering culm on an individual was measured from the culm base, at the last rooting node, along the length of the culm to the tip of the inflorescence (Pérez-Harguindeguy et al., 2013). A benefit of grass herbarium specimens is that the entire plant is preserved, allowing for height measurements, even when the culms are bent to fit on a page, by tracing a string or ruler along the inflorescence culm. Inflorescence height is a proxy for plant height as they are generally the tallest part of the plant. In the absence of 3D architectural information about non-flowering culm position, this approach enables comparative height measurements across both tussock and stoloniferous grass species. *Culm diameter* (cm) was measured using digital callipers (± 0.01 mm) at the thickest point of the second internode on the culm measured for inflorescence height, excluding the leaf sheath (Wigley et al., 2020). Leaf traits (e.g. length, width and thickness) were measured on a fully expanded leaf. *Leaf length* (cm) was measured from the base to the tip, while *leaf width* (cm) was measured as the widest portion of the leaf. For some leaves, as it is challenging to measure width without damaging the specimen, the folded width was doubled to estimate leaf width. *Leaf thickness* (mm) was measured at the same portion as leaf width using digital callipers, avoiding the midrib. For *leaf nitrogen*, we sampled one to five undamaged leaves per individual. We pooled leaf samples at the species-site level to ensure ample leafing material for analysis, combining all individuals of the same species from a given collection site into a single sample. This resulted in a subset of 375 samples from the 1616 individuals measured, which was used for all leaf nitrogen models. Leaves were ground to a fine powder using a TissueLyser II (Qiagen) for 10 minutes at 25 beats per second. Approximately 4 mg of ground leaf material was put

into tin capsules and analysed using a Flash SMART 2000 (Thermo Fisher Scientific) elemental analyser. Instrument accuracy was validated by analysing 20 replicates, yielding an R^2 of 0.999.

Herbarium trait validation

Standard protocols for measuring functional traits typically require fresh leaf material, which is impractical for regional scale assessments covering wide environmental gradients. Data collection efforts covering such large regions generally require years of collection effort or incorporate multiple studies with potential variations in trait measurement approaches. Herbarium collections, which are built up over decades, provide an alternative for trait sampling, enabling consistent measurements across broad geographic scales. Further, in grasses, whole plants are collected, and the low relative leaf moisture content of grasses means that trait preservation is not dissimilar to grass leaves and culms collected and explicitly dried for trait collections.

We undertook a calibration of the relationship between herbarium-collected and field-collected functional traits, using the field data and associated herbarium specimens from Solofondranohatra et al. (2020). The dataset of 30 species was represented by trait measurements averaged from three individuals for leaf length, leaf width, leaf thickness and leaf table height. Leaf table height cannot be directly measured from herbarium specimens due to the lack of architectural information, so we used specimen-measured inflorescence height and compared this with the field measure of leaf table height. Culm diameter was not compared due to a lack of field data, but given the robustness of grass culms, we do not expect any significant differences between herbarium and field measurements of culm diameter. Leaf nitrogen was not part of the field study, and we determined that as leaf nitrogen is typically measured from dried leaf material it was not required. Linear models centred at zero were used to quantify the correlation between herbarium and field traits, with the resulting R^2 quantifying the strength of the relationship.

Selection and extraction of environmental variables

Using the collection latitude and longitude of each herbarium specimen for which measurements were made, five environmental variables were compiled as proxies for the bottom-up and top-down drivers of interest: (1) *Mean Annual Temperature* (temperature; °C), extracted from the WorldClim database, represented temperature (Fick & Hijmans, 2017) (2) *Soil sand content* (%), measured at a depth of 5–15 cm, represented nutrient deficiency, where higher sand content indicates lower nutrient retention capacity due to the reduced ability of sandy soils to hold nutrients (Hengl et al., 2015; Joswig et al., 2022). (3) The *global aridity index* (water availability index), calculated as the ratio of mean annual precipitation (MAP) to potential evapotranspiration (PET), served as a measure of water availability, with high values indicating more humid environments (Zomer et al., 2022). (4) *Yearly mean burned area* (fire occurrence; km² year⁻¹) quantified fire occurrence on a landscape level with values representing the average area burned per year each 2.5 arc-minute grid cell (approx. 21.4 km²), extracted from Phelps et al. (2022). (5) The *Global Human Modification Index* (grazing index; gHM), which integrates measures of human disturbance such as settlement, agriculture, and roads, acted as a proxy for grazing intensity, as regions with higher human activity typically experience more grazing (Kennedy et al., 2019). Each environmental variable was extracted at a 30 arc-second or 1 km² resolution using the 'raster' package (Hijmans, 2022b). Fire occurrence was only available at 2.5 arc-minute resolution, and so we reprojected this to a 30 arc-second resolution for consistency.

While the environmental variables were chosen because they are considered largely independent and important dimensions of environmental variability, collinearity among variables was calculated using variance inflation factors (VIF) for each environmental variable using the 'HH' package (Heiberger & Robbins, 2014). All variables had VIFs less than 2, suggesting low to no multicollinearity and confirming their suitability as model predictors.

To quantify the breadth of the Malagasy environment gradients captured by our measurements, we generated a dataset of 30,000 random geo-locations across the island.

For each location, we extracted temperature, soil sand content, water availability index, fire occurrence, and grazing index at a resolution of 30 arc-seconds. These data were combined with the environmental data from our trait measurements and analysed using a principal component analysis (PCA). The PCA was conducted on scaled (standardised to unit variance) and centred (mean-subtracted) data using the `prcomp()` function from the 'stats' package (R Core Team, 2023). The PCA demonstrated that the first three principal components combined explained approximately 80% of Madagascar's environmental variation (PC1= 35.96%; PC2=22.19%, PC3=21.46%; Figure S3.2). Based on these results, we concluded that the selected variables effectively encapsulate the primary axes of environmental variation in Madagascar, making them appropriate predictors in our models exploring grass trait-environment relationships.

Statistical analysis

Statistical analyses were conducted at the level of a herbarium specimen without aggregating data to species means. Models of inflorescence height, culm diameter, leaf length, leaf width, and leaf thickness were undertaken on a dataset of 1616 individuals. Measurements of traits were log-transformed to reduce skewness and normalise distributions. Data for our environmental predictors were relatively normally distributed; therefore, we utilised untransformed predictors to enhance interpretability.

Trait-Environment Relationship Models

Phylogenetic linear mixed models (PLMM) using the `pglmm()` function from the 'phyr' package were used to quantify the relationships of each trait with environmental correlates (H. Li et al., 2020). Each PLMM included a single trait as the response, a combination of the five environmental correlates selected a priori, and two random effects of species phylogeny and location. Rather than modelling grasses with C₃ and C₄ photosynthetic pathways separately, we modelled traits across all sampled grasses to capture broader trait-environmental relationships.

Closely related species tend to share similar trait values due to shared evolutionary history, making values in any set of species variably non-independent statistically. Failure to

control for such phylogenetic covariance can potentially bias analyses of trait-environment relationships, leading to misinterpretation (Davies et al., 2013; Freckleton, 2000). To account for phylogenetic non-independence, we constructed a species-level phylogeny for the 260 species analysed here. The time-calibrated molecular phylogeny of Hackel et al. (2020), which includes 73% of Madagascar's known grass species was used, in which 227 of our sampled species could be directly matched with one or more tips (Figure S3.4). Positions of the 33 remaining species were inferred, either by inserting them at the node corresponding to the most recent common ancestor (MRCA) of their genus (when congeners were present in the Hackel et al. (2018) phylogeny) or, when no congeners were available, by inserting them at the midpoint of the branch leading to the MRCA of their most closely allied genus. Tip binding and pruning (i.e., removing all non-sampled species) were performed using the `bind.tip()` and `drop.tip()` functions from the 'ape' and 'phytools' R packages, respectively (Paradis & Schliep, 2019; Revell, 2024). An index of sampled species, their corresponding tip from Hackel et al. (2018), or their inferred placement method, is provided in Supplementary Table S3.1.

Trait data from nearby locations tend to be more statistically correlated than those from distant locations via spatial autocorrelation (Cablak et al., 2002; Dormann et al., 2007). Location was included as a random effect to account for spatial autocorrelation. We generated a spatial distance matrix using the latitude and longitude of measured individuals. Distances between sites were calculated using the `dism()` function from the 'geosphere' package, applying the Haversine method (Hijmans, 2022a) which calculates the shortest distance between points of longitude and latitude accounting for the Earth's curvature (Eason et al., 2019). The distance matrix was converted to a variance-covariance matrix using the 'phyr' package.

For each trait, we fitted a family of 32 models, including a full model containing all five predictors, 30 models representing every possible subset of predictor combinations, and a null model containing only random effects. Model performance was evaluated using both likelihood-based R^2 , which quantifies model fit to observed data, and predicted R^2 ,

which assesses the model's predictive ability, as calculated with the `R2_pred()` function in the 'rr2' package (Ives, 2019). Model fit was assessed using the Akaike information criterion (AIC) values, with lower AIC indicating better fit (Symonds & Moussalli, 2011). AIC weights were calculated to estimate the probability of each model being the best fit within the family. We included all models up to a cumulative AIC weight of 0.9 in our interpretation of trait-environment relationships, which are hereafter referred to as the top models. We only considered predictor significance within the top models. Trait-environmental variable relationships were classified as follows: significant if $p < 0.05$, marginally significant if $0.05 < p < 0.10$, and non-significant if $p > 0.10$ or if the predictor did not appear in any top model.

Predicted Trait Distribution maps

To visualise trait variation across Madagascar, we predicted model-averaged trait values for each of the six traits using our full family of 32 models and a set of Malagasy environmental variables. The dataset included our five environmental variables (temperature, soil sand content, water availability index, fire occurrence and grazing) for each 1 km² pixel across the island, extracted as described in "*Selection and Extraction of Environmental variables*". To ensure predictions were made within the observed and model-fitted environmental space, we filtered the dataset to include only pixels with environmental values within the range of environments associated with the herbarium-collected data, resulting in a 92.34% coverage of the island. Comparisons of herbarium-associated environments to the full range of Malagasy environments for our five environmental variables are presented in Figure S3.3.

Model-averaging was undertaken using all 32 models. Model-averaged predictions incorporated the full variance explained, as AIC weight reflects the relative explanatory power of each model and sum to one across the family. Following Cade (2015), we averaged predicted traits rather than coefficients, as the latter requires predictors to be on the same scale. The environmental variables for each pixel were input to the model equation, combining the coefficients and intercepts to calculate predicted trait values. The results produced 32 predicted trait values per pixel, one for each model. These predictions were

then weighted by their respective AIC weight to account for model-specific uncertainty. The 32 weighted trait values were then summed to produce a single model-averaged predicted trait value for each pixel. The final dataset contained predicted model-average trait values for each 1 km² pixel within the observed environmental range, visualised as a map using the 'ggplot2' package (Wickham, 2016).

Trait Coordination

To quantify relationships among traits, analyses were restricted to data with complete measurements for all six traits (N=375). Pairwise relationships between traits were assessed using Pearson's correlation coefficient (r), calculated with the `cor_phylo()` function from the 'phyr' package which allowed for incorporation of phylogeny to control for phylogenetic non-independence between traits (D. Li et al., 2020). We ran correlations at an iteration of 1000. We visualised a correlation matrix using `corrplot()` from the 'corrplot' package (Wei & Simko, 2024). Pearson's r measures the strength of the linear relationship between two variables with values ranging from -1 to +1, with relationships categorised as no correlation ($r=0$), negligible ($0 < |r| \leq 0.30$), moderate ($0.30 < |r| \leq 0.50$), or high ($0.50 < |r| \leq 1.0$).

To visualise the multivariate relationships among the six traits, we performed a principal component analysis (PCA) with scaled (standardised to unit variance) and centred (mean-subtracted) values, using the 'vegan' R package (Oksanen et al., 2022). Biplots of the first two PCA axes were generated using the 'ggplot2' R package. Given that C₃ and C₄ photosynthetic pathways represent key functional differences influencing environmental tolerance in grasses (Christin et al., 2013; Osborne & Freckleton, 2009), we used the `stat_ellipse()` function to add 95% confidence ellipses for C₃ and C₄ grasses, delineating the trait space occupied by each pathway to determine if there is broad differentiation in grasses between these pathways (Wickham, 2016). To further compare PC distributions between pathways, we used the `ggMarginal()` function from the 'ggExtra' package to display histograms of PC value distributions on the PC1 and PC2 axes for both groups (Attali & Baker, 2023).

Results

We measured 1616 individuals from 738 herbarium specimens found at 422 locations across the island (Figure 3.1). Trait data sampled represents 260 species of 96 genera and nine subfamilies, representing 47% of the Malagasy grassy flora (Table S3.1). Of the 260 species, 195 have a C₄ photosynthetic pathway, and 65 have a C₃ photosynthetic pathway. 94 species of the 260 are endemic to Madagascar.

Locations spanned a temperature range of 11.7 to 27.5 °C, soil sand content from 31.6 to 76.8%, water availability index from 0.21 to 1.68, fire occurrence from 0 to 0.9 km² year⁻¹, and human modification values (grazing index) from 0.1 to 0.91. Trait values varied widely with inflorescence height ranging from 4.3 to 244.0 cm, culm diameter from 0.011 to 0.667 cm, leaf length from 0.15 to 65.70 cm, leaf width from 0.03 to 1.14 cm, leaf thickness from 0.01 to 1.14 mm, and leaf nitrogen content from 0.324 to 3.793%.

Herbarium trait validation

Herbarium and field measurements in 30 grass species showed strongly positive correlations for all four traits: leaf length ($R^2=0.845$), leaf width ($R^2=0.886$), leaf thickness ($R^2=0.938$), and leaf table height ($R^2=0.776$) (Figure 3.2).

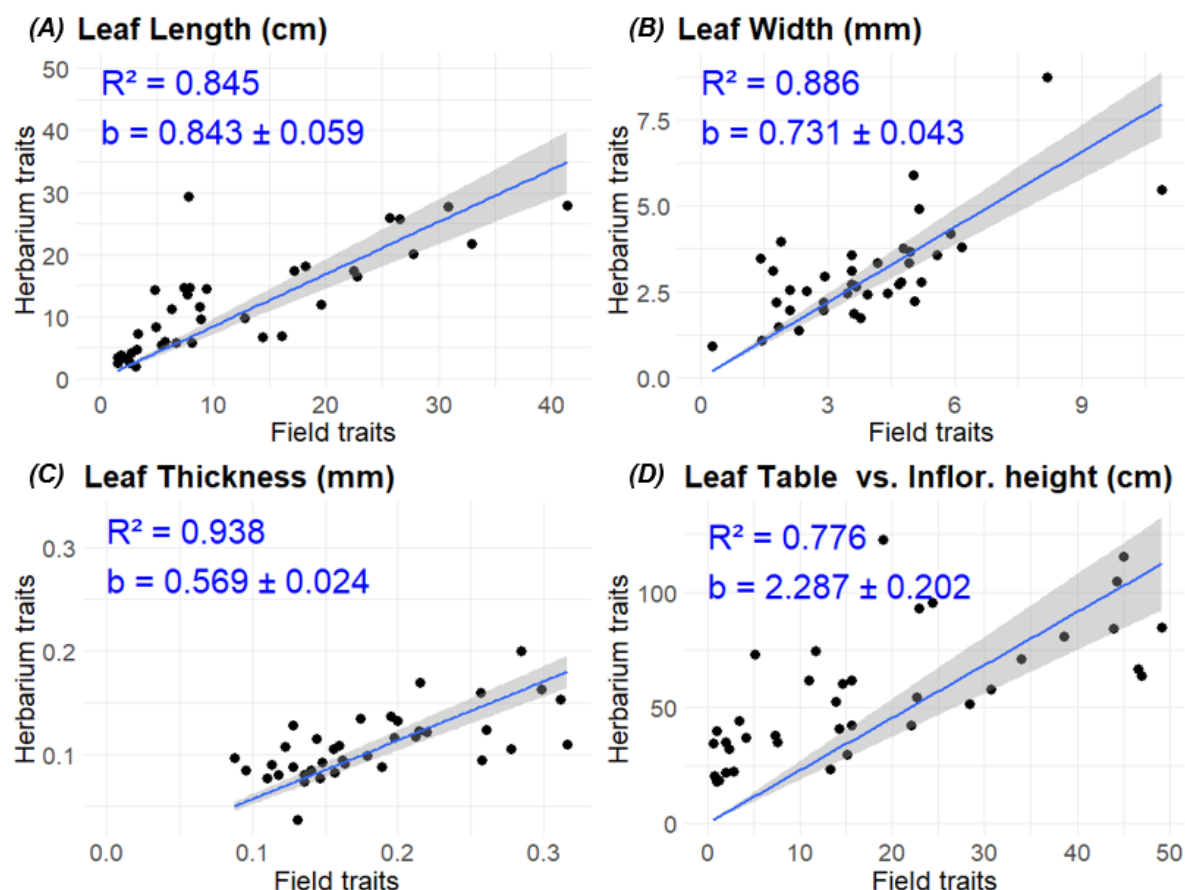


Figure 3.2. **The relationship between herbarium and field measurements collected by Solofondranohatra et al., (2020) for four traits:** (A) leaf length, (B) leaf width, (C) leaf thickness, and (D) leaf table, represented by inflorescence height in the herbarium data. R^2 and linear model equations are presented in the top left corner. Errors (grey) represent 95% confidence limits.

Trait-environment relationship models

For all six traits, we derived general patterns of trait-environment relationships by evaluating the direction of the relationship in the top models (cumulative AIC weights ≤ 0.9). Table 3.2 summarises these results. Complete model outputs, including all tested models, can be found in the supplemental material (Tables S2.3-S2.8).

Table 3.2. **Consensus results of top PGLMM models analysing the relationships between our six trait variables and our five environmental drivers with proxies listed directly below.**

Upwards arrows (green) indicate a significant positive relationship, downwards arrows (red) indicate a significant negative relationship, and 'ns' indicates a non-significant relationship ($p > 0.1$) between the trait and environmental variable.

Proxy	Temperature	*Nutrient Deficiency	Water Availability	Fire	Grazing
	Mean Annual Temperature (°C)	Soil Sand Content (5-15cm depth) (%)	Global Aridity Index	Yearly Mean Burned Area (km ² year ⁻¹)	Global Human Modification Index
Effect of Proxy Increase	Higher temperatures	Lower nutrient availability	Higher water availability	More fire disturbance in area	More human disturbance in area
Inflorescence Height (cm)	↑ *	↓ *	ns	↑ *	ns
Culm Diameter (cm)	↑ *	ns	ns	↑ *	ns
Leaf Length (cm)	ns	↓ *	ns	ns	ns
Leaf Width (cm)	↑ ***	↓ **	↓ .	↑ *	ns
Leaf Thickness (mm)	↓ *	↑ .	↓ .	ns	ns
Leaf Nitrogen (%)	ns	ns	ns	ns	ns

Note:

* Represents overall nutrient availability

P-value significance: 0-0.001 = *** 0.001-0.01 = ** 0.01-0.05 = * 0.05-0.1 = .

Inflorescence height

Inflorescence height of measured individuals ranged from 4.3 to 244 cm (M = 48.65; SD = 31.45) across the island, with C₃ grasses ranging from 4.7 to 144.7 cm (M = 42.47; SD = 25.46) and C₄ grasses ranging from 4.3 to 244 cm (M = 50.41; SD = 32.75).

From our model family, we selected nine models for interpretation with an accumulative AIC weight of 0.898 and predicted R² values ranging from 0.777 to 0.781 (Table S3.2). Overall, temperature, nutrient deficiency and fire were key drivers of variation

in inflorescence height across the island (Table 3.2). Inflorescence height showed significant positive relationships with temperature in six of the nine models, with a coefficient range of 0.020 to 0.0275 and p-values between 0.014 to 0.039. Inflorescence height had negative relationships with soil sand content in five of the nine models. However, only two of these models showed significant negative relationships, with coefficients of -0.007 and p-values of 0.043. Inflorescence height showed significant positive relationships with fire occurrence in the eight models it occurred in, with coefficients ranging from 0.238 to 0.306 and p-values between 0.043 to 0.013. No significant ($p > 0.10$) relationships were found between inflorescence height and water availability index or grazing.

Predicted inflorescence height ranged from 25.61 to 56.05 cm ($M = 36.38$, $SD = 3.38$) (Figure 3.3A). Taller grasses were predicted in areas with warmer temperatures, lower soil sand content, and higher fire occurrence. The tallest inflorescence heights were predicted to be in western and northwest Madagascar. While the region is defined by variable fire occurrence ($0.8\text{--}1.5 \text{ km}^2 \text{ year}^{-1}$), areas with the tallest inflorescences had the highest fire occurrence in our dataset (around $0.9 \text{ km}^2 \text{ year}^{-1}$). The region is also defined by high temperatures ($25\text{--}28^\circ\text{C}$) and areas of low sand content ($<40\%$). Lower heights were predicted within regions of the Central Highlands where temperature ($<17^\circ\text{C}$) and fire occurrence were lower than other portions of the island ($<0.5 \text{ km}^2 \text{ year}^{-1}$).

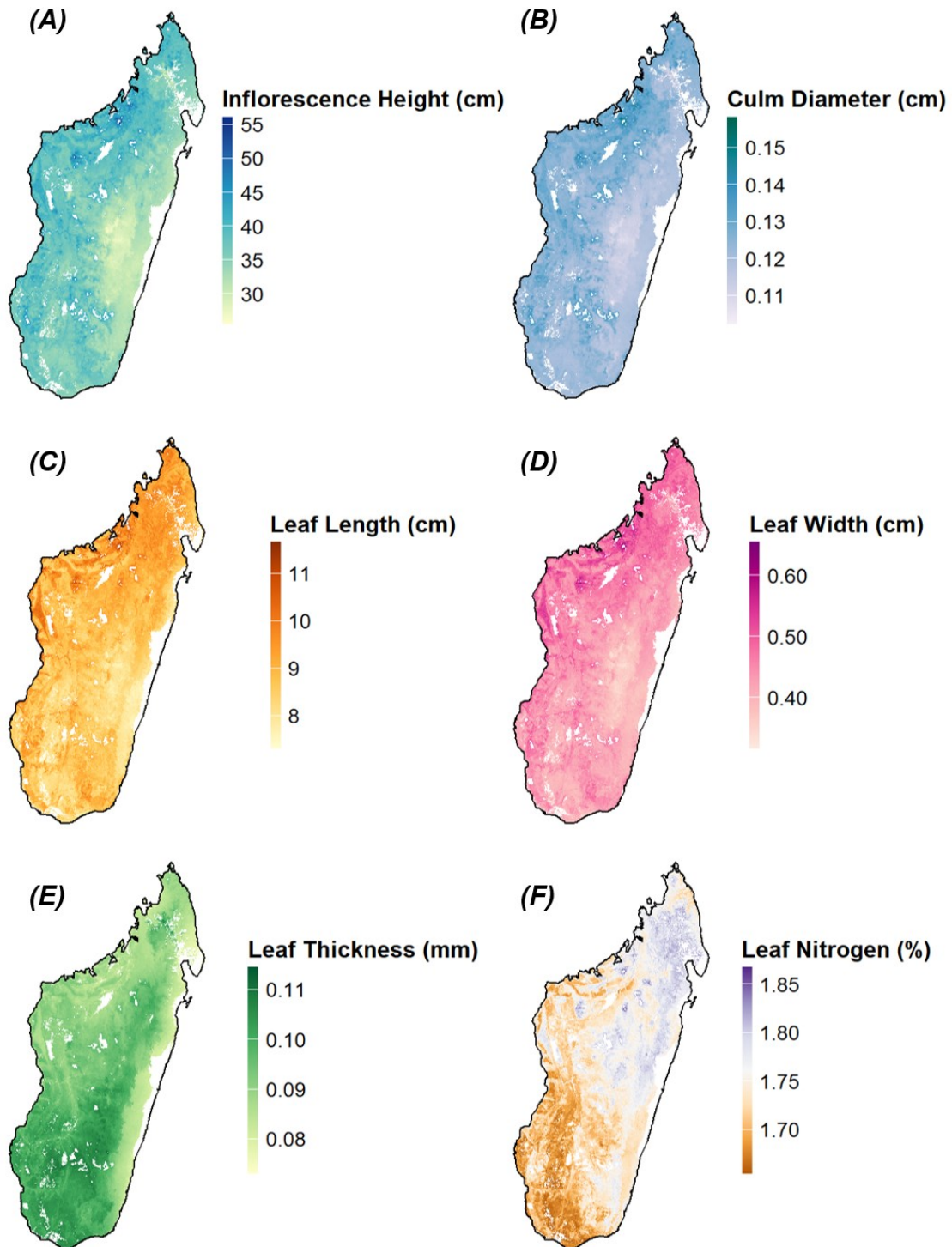


Figure 3.3. **Maps of predicted trait values** for: (A) inflorescence height, (B) culm diameter, (C) leaf length, (D) leaf width, (E) leaf thickness and (F) leaf nitrogen. Predicted trait values were calculated using model averaging of response variables restricted to environments

captured by our herbarium data. The maps are displayed at a resolution of 1 km². Each pixel represents the averaged predicted value for that trait at that location.

Culm diameter

Culm diameter of measured individuals ranged from 0.011 to 0.667 cm (M=0.13; SD=0.09) across the island, with C₃ grasses ranging from 0.011 to 0.654 cm (M = 0.11; SD = 0.07) and C₄ grasses ranging from 0.015 to 0.667 cm (M = 0.14; SD = 0.09).

We selected 19 models for interpretation with an accumulative AIC weight of 0.892 and predicted R² values ranging from 0.793 to 0.798 (Table S3.3). Overall, temperature and fire were key drivers of variation in culm diameter across the island (Table 3.2). Culm diameter showed positive relationships with temperature in 13 of the top models, but these relationships were significant in only three models, with coefficients ranging from 0.018 to 0.019 with p-values between 0.035 to 0.047. Culm diameter also had positive relationships with fire occurrence in 14 top models. Significant relationships were observed in five of these models with coefficients ranging from 0.182 to 0.216 and p-values of 0.036 to 0.046. No significant relationships were found between culm diameter and soil sand content, water availability, or grazing.

Predicted culm diameter ranged from 0.102 to 0.158 cm (M = 0.12; SD = 0.01), with consistently higher values in the western and central areas of the island (Figure 3.3B). As with inflorescence height, the largest culm diameters were predicted in the northwestern region, which is characterised by high temperatures (25-28°C) and variable fire occurrence (0.8-1.5 km² year⁻¹). Smaller diameters were predicted within the central plateau and far north, where temperature (<15°C) and fire occurrence (0-0.4 km² year⁻¹) are lower.

Leaf length

Leaf length of measured individuals ranged from 0.15 to 65.7 cm (M=9.8; SD=9.19) across the island, with C₃ grasses ranging from 0.15 to 46.2 cm (M = 7.78; SD = 7.31) and C₄ grasses ranging from 0.8 to 65.7 cm (M = 10.37; SD = 9.58).

We selected 17 models for interpretation with an accumulative AIC weight of 0.8996 and predicted R² values ranging from 0.816 to 0.819 (Table S3.4). Overall, nutrient

deficiency was the key driver of variation in leaf length across the island (Table 3.2). In the 14 top models where soil sand content appeared, leaf length consistently showed negative relationships. Statistically significant relationships were observed in six of these models, with coefficients ranging from -0.009 to -0.008 and p-values between 0.027 to 0.045. Leaf length showed no significant relationships with temperature, water availability, fire occurrence, or grazing.

Predicted leaf length ranged from 7.31 to 11.66 cm ($M = 8.81$; $SD = 0.57$) across the island (Figure 3.3C). Longest leaves were predicted along the west region and northern coasts in areas characterised by low soil sand content ($>40\%$). Shortest leaf lengths were predicted for the southwestern region in areas with high soil sand content ($<70\%$).

Leaf width

Leaf width of measured individuals ranged from 0.03 to 3.306 cm ($M=0.43$; $SD=0.36$) across the island, with C_3 grasses ranging from 0.03 to 2.486 cm ($M = 0.57$; $SD = 0.43$) and C_4 grasses ranging from 0.042 to 3.306 cm ($M = 0.39$; $SD = 0.32$).

For leaf width, we selected four top models for interpretation with an accumulative AIC weight of 0.8360 and predicted R^2 values ranging from 0.865 to 0.866 (Table S3.5). Overall, temperature, nutrient deficiency, water availability, and fire were key drivers of variation in leaf width across the island (Table 3.2). Leaf width had significant positive relationships with temperature, with coefficients ranging from 0.020 to 0.028 and p-values between 0.0003 to 0.001, and fire occurrences, with coefficients ranging from 0.195 to 0.215 and p-values between 0.026 to 0.039, in all top models. Percent sand had significant negative relationships in all top models, with coefficients ranging from -0.009 to -0.008 and p-values between 0.001 to 0.003. In the two top models where water availability appeared, leaf width had marginally ($0.05 < p < 0.1$) significant negative relationships, with coefficients ranging from -0.135 to -0.132 and p-values between 0.075 to 0.078. No significant relationships were found between leaf width and grazing.

Predicted leaf widths ranged from 0.316-0.654 cm ($M = 0.44$; $SD = 0.04$), with larger widths predicted in the north western region, characterised by high temperatures ($>24^\circ\text{C}$)

(Figure 3.3D). The largest widths were associated with areas containing less than 50% soil sand content. In contrast, the smallest widths were predicted in the central plateau and northern portion. The central plateau experiences relatively lower temperatures ($<18^{\circ}\text{C}$) and has sandier soils in portions (40-70%), while the northern region has some of the island's lowest temperatures ($<16^{\circ}\text{C}$).

Leaf thickness

Leaf thickness of measured individuals ranged from 0.01 to 1.14 mm ($M=0.09$; $SD=0.06$) across the island, with C_3 grasses ranging from 0.01 to 0.25 mm ($M = 0.07$; $SD = 0.04$) and C_4 grasses ranging from 0.01 to 1.14 mm ($M = 0.1$; $SD = 0.06$).

From our family of models, we selected 14 models for interpretation with an accumulative AIC weight of 0.897 and predicted R^2 values ranging from 0.739 to 0.740 (Table S3.6). Overall, temperature, nutrient deficiency, and water availability were key drivers of variation in leaf thickness across the island (Table 3.2). Leaf thickness had significant negative relationships with temperature in eight of the 12 top models it appeared in, with coefficients ranging from -0.025 to -0.023 and p-values between 0.026 to 0.046. Soil sand content appeared in 10 of the top models but had marginally significant positive relationships in only two, with coefficients of 0.006 and p-values of 0.089. Water availability also appeared in 10 top models and showed marginally significant negative relationships in four, with coefficients ranging from -0.237 to -0.225 and p-values between 0.053 to 0.070. No significant relationships were found between leaf thickness and soil sand content, water availability, fire occurrence, or grazing.

Predicted leaf thickness ranged from approximately 0.073-0.114 mm ($M = 0.09$; $SD=0.01$) (Figure 3.3E). The thickest leaves were predicted in the central plateau and southwestern region. The central plateau experiences variable temperatures, ranging from moderate to cooler temperatures ($\sim 12\text{-}20^{\circ}\text{C}$). The southwestern region has higher temperatures ($20\text{-}24^{\circ}\text{C}$), but experiences higher aridity (water availability index <0.5) and sandy soils ($>70\%$). The thinnest leaves were predicted along the eastern and northwestern regions of the island in areas with lower soil sand content ($<50\%$) and higher temperature

(>24 °C). Notably, the eastern coast experiences much wetter conditions (water availability index>1.5) compared to the rest of the island, contributing to thinner leaves in this region.

Leaf nitrogen

Leaf nitrogen of measured individuals ranged from 0.32 to 3.79 % (M=1.65; SD=0.76) across the island, with C₃ grasses ranging from 0.58 to 3.79 % (M = 2.18; SD = 0.71) and C₄ grasses ranging from 0.32 to 3.63 % (M = 1.47; SD = 0.68).

From our model family, we selected 24 models for interpretation with an accumulative AIC weight of 0.8918 and predicted R² values ranging from 0.4329 to 0.4398 (Table S3.7). We found no significant relationships between leaf nitrogen and any of our environmental variables (temperature, soil sand content, water availability index, fire occurrence and grazing) (Table 3.2).

Predicted leaf nitrogen ranged from 1.66-1.87% (M = 1.74; SD = 0.04) (Figure 3.3F). The highest leaf nitrogen values (>1.8%) were predicted to occur in the northwest, while the lowest values (<1.7%) were predicted along the south- and central-east portions of the island.

Trait coordination

All pairwise comparisons of traits were highly significant ($p < 0.001$), with all traits showing low phylogenetic signals ($d < 0.1$) (Figure 3.4; Table S3.8). Positive correlations were observed for inflorescence height-culm diameter ($r=0.749$), leaf length-culm diameter ($r=0.701$), leaf length-inflorescence height ($r=0.600$), leaf width-culm diameter ($r=0.376$), leaf thickness-inflorescence height ($r=0.450$), and leaf nitrogen-leaf width ($r=0.307$). A moderate negative correlation was found for leaf nitrogen-leaf thickness ($r=-0.315$).

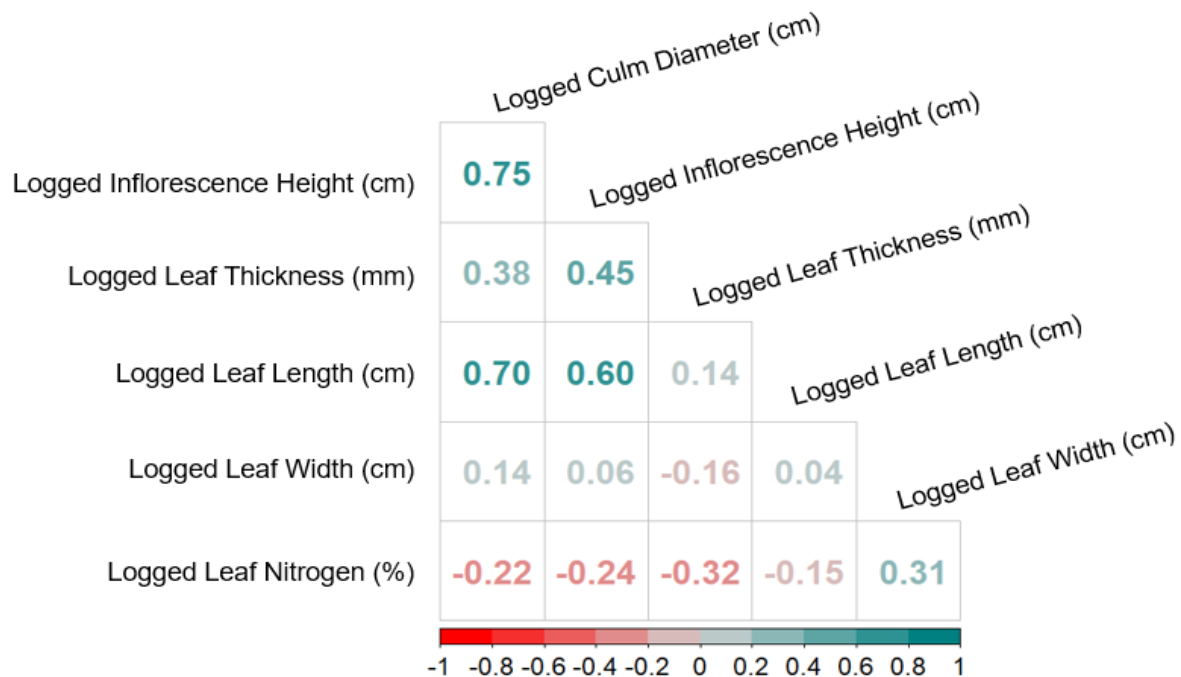


Figure 3.4. **Phylogenetic Pearson's coefficient (r) correlation plot for all six logged functional traits.** Positive correlations are coloured teal while negative correlations are coloured red. Strength of the colouration indicates the strength of the relationship and the r value with relationships being either no correlation ($r=0$), negligible ($0<|r|\leq 0.30$), moderate ($0.30<|r|\leq 0.50$), or high ($0.50<|r|\leq 1.0$).

A PCA ordination of the six traits showed that 71.8% of the total variance was captured within the first two principal components (PC) (Figure 3.5). PC1, primarily driven by size-related traits (i.e. inflorescence height, leaf length, and culm diameter), explained approximately 45% of the variance, while PC2, associated with resource acquisition traits (i.e. leaf nitrogen, leaf thickness and leaf width), accounted for a further 27% of the variance. Individual specimens were broadly dispersed across trait space, indicating substantial variation among samples. Consistent with our pairwise trait analysis, traits with vectors in similar directions, such as inflorescence height, leaf length, and culm diameter, suggested strong positive correlations between these traits. Conversely, traits with vectors

pointing in opposite directions, such as leaf thickness and leaf nitrogen, indicated a stronger negative correlation.

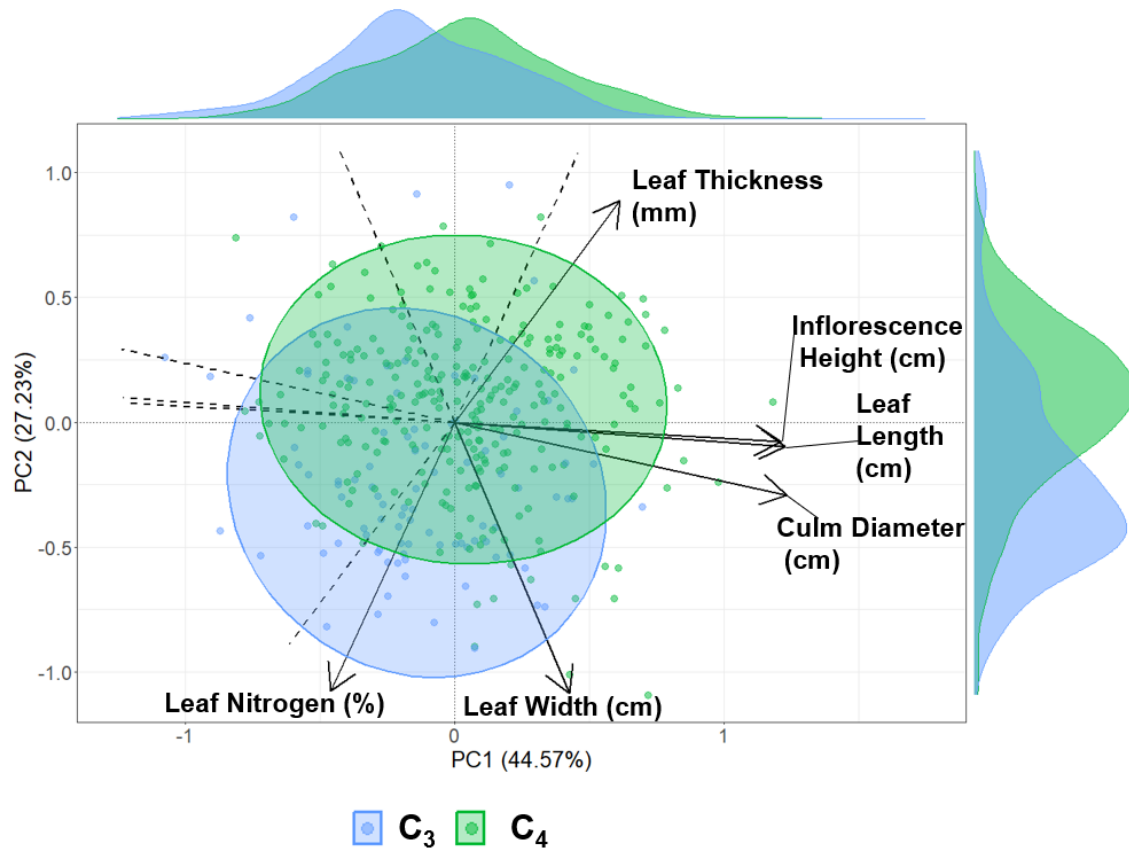


Figure 3.5. Principal component analysis (PCA) of functional traits from herbarium grass specimens. Each dot represents an individual specimen, coloured by photosynthetic pathway: C₃ (blue) or C₄ (green). 95% confidence ellipses indicate the area of trait space occupied by each pathway. Solid arrows indicate the direction and magnitude of the loadings for six traits: inflorescence height, culm diameter, leaf length, leaf width, leaf thickness and leaf nitrogen. Dashed extensions of the arrows denote the full vector direction. Density diagrams along the axes show the distribution of PC values for C₃ and C₄ grasses on the respective axes.

C₃ and C₄ grasses overlap substantially in multivariate trait space, as indicated by the overlap of the 95% confidence ellipses (Figure 3.5). However, C₄ grasses tended to have more positive values along both PC1 ($M = 0.046$; $SD = 0.352$) and PC2 ($M = 0.077$; $SD =$

0.317), and broader range along PC1, extending toward larger plant size traits (i.e. inflorescence height, culm diameter, and leaf length). In contrast, C₃ grasses tended to have more negative PC1 (M = -0.139; SD = 0.334) and PC2 (M = -0.231; SD = 0.369) values and a broader range on PC2, associated with higher leaf nitrogen and smaller, thinner leaves.

Discussion

Our use of herbarium data enabled a regional scale study of grass functional trait variation to test trait-environment relationships. Herbarium-derived and field-collected traits showed strong positive correlations ($R^2 > 0.77$) for inflorescence height, leaf length, leaf width and leaf thickness (Figure 3.2), supporting the reliability of herbarium-collected trait measurements. The use of herbarium traits allowed for a more extensive examination of trait-environment relationships and trait coordination at a regional scale, offering insights that would be difficult to achieve through field-collected trait measurements alone.

Our trait-environmental models revealed significant positive relationships between inflorescence height, culm diameter and leaf width with temperature and fire (Table 3.2). In contrast, leaf thickness has a significant negative relationship with temperature, while inflorescence height, leaf length, and leaf width showed significant negative relationships with nutrient deficiency. Additionally, leaf thickness showed a marginally positive relationship with nutrient deficiency, whereas leaf width and leaf thickness had marginal negative relationships with water availability. Our models also indicated that leaf width responded opposite to expectations in relation to water availability and fire (Table 3.1; Table 3.2). Furthermore, we detected no discernible effect of any environmental predictor on leaf nitrogen, suggesting that key environmental influences on this trait may not have been fully captured by our selected environmental proxies. Lastly, our grazing proxy (Global Human Modification Index) had no detectable relationship with any grass traits, likely due to the scale of the variable and reflecting the persistent problem in quantifying grazing pressures in regional-scale studies.

Mirroring life history variation, traits demonstrated coordination, with strong correlations between size-related traits such as inflorescence height, culm diameter, and

leaf length (Figure 3.4). In contrast, leaf economic traits, such as leaf thickness and nitrogen, had a moderate negative correlation. In multidimensional space, these patterns are aligned with the size-spectrum and the leaf economic spectrum, two major axes of trait-coordination, with C_3 and C_4 grasses differing in their trait distributions along these axes, indicating differences in life history strategies (Figure 3.5).

Trait-environment relationship models

Both bottom-up (e.g. temperature, nutrient availability and water availability) and top-down (e.g. fire) controls interacted to shape grass trait values across Madagascar. Size-related traits - inflorescence height, culm diameter, leaf length, and leaf width - increased with temperature and nutrient availability, supporting existing evidence that warmer, nutrient-rich environments favour larger structures that enable rapid resource capture, growth, and competition (Table 3.2; Figure 3.3A, B, C) (Baird et al., 2021; Moles et al., 2009, 2014; Reich & Oleksyn, 2004). Furthermore, these results align with strategies along the size spectrum, which suggests that taller grasses with larger leaves are better competitors in high-resource environments (Arthan et al., 2022; Keddy et al., 2002; Tilman & Wedin, 1991; Zhou et al., 2016). In contrast, leaf thickness decreased with temperature, nutrient availability and water availability, aligning with the leaf economic spectrum (LES), where resource-rich environments favour thinner leaves that enable fast turnover (Díaz et al., 2004; Pierce et al., 2007; Simpson et al., 2020; Wright et al., 2004).

Leaf width decreased with water availability, showing a marginally significant negative relationship, challenging the prediction that water availability should promote broader leaves with higher leaf moisture content (Givnish, 1987; McDonald et al., 2003). Sampling limitations likely contributed to this pattern as herbarium collections underrepresented the wettest parts of Madagascar, particularly the eastern coast (Figure 3.1), where broad-leaf grasses are likely more prevalent. Furthermore, the direction of this relationship could be an artifact of broader issues around leaf morphology and the collection of data on it. Working with herbarium specimens constrains the traits measured as leaf area or specific leaf area are difficult to measure from dried specimens. Instead, we

used leaf width as a singular measurement, which may not fully capture variations in leaf size in relationship to water availability when considered on its own.

Fire also emerged as a strong driver of trait variation, with inflorescence height, culm diameter, and leaf width increasing with fire occurrence (Figure 3.3A, B, D), suggesting that fire selects for traits that enhance fire resistance, such as tall structures, and post-fire regeneration, such as wide leaves that increase photosynthetic capacity (Archibald et al., 2019; Murray et al., 2013; Simpson et al., 2016). Fire-vegetation feedbacks typically drive the selection of fire-adaptive traits, such as increased flammability, which promotes hot, fast-spreading fires that reduce competition, stimulate new growth, and sustain fire regimes through positive feedback loops over time (Archibald et al., 2019; Archibald & Hempson, 2016; Bond & Midgley, 1995; Pausas et al., 2017). However, the positive relationship between leaf width and fire occurrence contrasts with this expectation, as wider leaves are expected to decrease flammability due to their higher leaf moisture content (Archibald et al., 2019; Givnish, 1987; McDonald et al., 2003; Simpson et al., 2016). Instead, a prolonged history of fire may select for wider leaves due to allometric constraints, as taller, thicker culms - also positively associated with fire - require wider leaf sheaths to wrap around the culms (Baird et al., 2021; Sandel et al., 2016). Thus, fire-driven increases in plant size will necessitate broader leaves, reflecting a structural adaptation rather than a direct response to fire.

Despite models explaining over 40% of the data variance, leaf nitrogen showed no significant relationship with any environmental predictors. The substantial explanatory power of the null model suggests that evolutionary history and location-specific effects (potentially capturing fine-scale soil variations not captured by remote sensing data) strongly influence this trait. Previous studies found strong associations between leaf nitrogen and soil fertility but weaker links to climate (Jardine et al., 2020; Ordoñez et al., 2009), suggesting that soil properties may be an important predictor of nutrient availability. However, the resolution of our soil data cannot capture the small-scale spatial and temporal variations in nutrients and moisture that are known to strongly influence nitrogen

availability for plants (Bruehlheide et al., 2018; Fridley et al., 2011). Additionally, using soil sand content as a proxy for nutrient availability may not adequately reflect nitrogen availability, as Jardine et al. (2020) also found no relationship between soil sand content and leaf nitrogen. Finally, our reduced leaf nitrogen dataset may have limited statistical power, constraining the effect size we are able to detect.

Temperature, soil sand content, and fire occurrence were consistently good predictors for most of our traits, while water availability and grazing had weaker or no detectable effect (Table 3.2). Detecting trait-environmental relationships can depend heavily on the temporal and spatial scales of sampling, with different patterns of variation emerging at different levels (Messier et al., 2010). Trait differentiation driven by temperature, nutrient availability and fire may be more pronounced at broader spatial scales, while water availability and grazing can substantially vary across landscapes. Specifically, the water availability index may not fully capture water availability at finer spatial scales, where soil moisture more directly influences plant growth (Tardella et al., 2016). Similarly, grazing effects are inherently spatially and temporally variable (Bruehlheide et al., 2018), making them difficult to detect using remote sensing data. Our grazing variable, which incorporated 13 anthropogenic stressors, may have confounded the effects of grazing with other anthropogenic disturbances, potentially obscuring any significant relationships (Kennedy et al., 2019). As a coarse proxy for grazing intensity, it lacks the resolution to capture both localised and seasonal variation in grazers densities. Instead, understanding grazing-driven trait variation would require finer-scale field studies, ideally incorporating experimental treatments.

We used a carefully structured analysis to identify quantitative patterns and inter-relationships between multiple environmental drivers and key size and leaf economic traits. While previous studies that focused on individual drivers (Bade et al., 1985; Moles et al., 2014) risked misrepresenting trait-environmental relationships, our results show that the predictive ability of multiple environmental drivers remains largely consistent with their individual effects. Furthermore, the agreement between our model predictions and

hypothesised relationships indicated that the collective ability of multiple environmental drivers to predict trait variability does not differ greatly from their contributions when considered separately. This suggests that trait responses to environmental factors remain largely predictable at regional scales, even when considering multiple drivers simultaneously.

Trait coordination and the multivariate nature of grass life history strategies

Grasses show strong signs of trait coordination, with all pairwise correlations being significant ($p < 0.001$). However, traits showed weak phylogenetic signal ($d < 1$), suggesting that shared evolutionary history among species played a limited role in shaping trait variation (Figure 3.4; Table S3.8). The strongest ($r > 0.6$) correlations occurred among size-related traits such as culm diameter, inflorescence height, and leaf length, while leaf thickness and leaf nitrogen had a moderate negative correlation, with thicker leaves having lower leaf nitrogen. These relationships were reflected in the trait principal component analysis (PCA), where traits varied along orthogonal axes corresponding with the size spectrum and the leaf economic spectrum (LES), consistent with patterns observed at global scales (Díaz et al., 2016; Grime, 1977; Jardine et al., 2020; Sandel et al., 2016) (Figure 3.5).

The size spectrum, which aligned with PC1, was primarily associated with the strongly correlated size-related traits: inflorescence height, leaf length, and culm diameter. These correlations reflect allometric relationships, where taller grasses require thicker culms for structural support, while longer leaves similarly need taller, sturdier culm structures (Baird et al., 2021; X. Gao et al., 2024; Wigley et al., 2020). Furthermore, high trait values along this axis suggest increased competitive abilities, as larger grasses with longer leaves improve access to light, while taller inflorescence enhances seed dispersal potential (Keddy et al., 2002; Mashau et al., 2021; Westoby, 1998; Zhou et al., 2016). In contrast, PC2 was closely aligned with the LES, capturing trade-offs in resource acquisition and allocation to growth, particularly in leaf nitrogen, leaf thickness and leaf width (Pierce et al., 2007; Reich, 2014; Wright et al., 2004). At one end of this axis, thicker and nitrogen-poor leaves indicate resource conservation and longer lifespans, whereas at the other end, thinner, nitrogen-rich

leaves facilitate rapid growth and biomass turnover (Pierce et al., 2007; Reich et al., 1997; Wright et al., 2004). The persistence of these two axes at regional scales provides strong evidence that these trade-offs are fundamental mechanisms underlying plant life history strategies while suggesting that grasses optimise different aspects of their life history strategies across environments, reinforcing well-documented ecological trade-offs.

The distributions of C_3 and C_4 grasses within multidimensional trait space overlapped but differed in their positioning along the size spectrum (PC1) and LES (PC2) axes (Figure 3.5). C_3 grasses, typically found in cooler or well-shaded environments such as high altitudes or forest understories, were shorter, with smaller, thinner leaves, and higher leaf nitrogen than C_4 grasses (W. Gao et al., 2024; Havrilla et al., 2023; Pau et al., 2013). These traits align with conservative growth strategies along the size spectrum and resource acquisitive strategies on the LES, both of which enhance survival under low-light or cold conditions (Gommers et al., 2013; Pierce et al., 2007; Westoby, 1998). Conversely, C_4 grasses, which typically dominate warmer, open environments, occupied the larger end of the size spectrum, with taller statures and longer, thicker leaves, that support the idea C_4 grasses optimise structural traits for competitive success in high-light, high-temperature and arid conditions, where rapid growth and efficient water use are key advantages (Edwards & Still, 2008; Keddy et al., 2002; Osborne & Freckleton, 2009; Zhou et al., 2016). Furthermore, differences in the spread of trait values along each principal component suggest differences in functional diversity between the two photosynthetic types. C_4 grasses had greater trait variation along PC1, indicating these grasses occupy a wider functional niche within the size spectrum, while C_3 grasses exhibited more variation along PC2, suggesting broader differentiations along the LES (Liu et al., 2019).

C_3 and C_4 photosynthesis represent fundamental differences that influence where grasses persist, shaping species distributions and life history strategies across environmental gradients (W. Gao et al., 2024; Pau et al., 2013). While the primary goal of this study was to examine overall trait-environment and trait coordination relationships regardless of species or photosynthetic pathway, comparing how C_3 and C_4 separate in trait space provides

insights into how trait coordination supports different life history strategies while operating along the same fundamental trait axes. Despite trait differences between C₃ and C₄ grasses, the overall patterns of trait coordination remained largely consistent, with both groups following similar allometric and physiological trade-offs. Although these patterns indicate potential differentiation in functional strategies between photosynthetic pathways, further statistical testing would be needed to confirm if these differences are significant.

The coordination of traits along size and economic axes is consistent with grasses exhibiting distinct trait syndromes shaped by bottom-up and top-down environmental pressures (Archibald et al., 2019; Chapin et al., 1993; Reich et al., 2003). These syndromes, in conjunction with the trait-environment relationships we detected, reveal trade-offs and adaptations that balance resource acquisition, environmental tolerance, and growth, providing support for long-standing hypotheses about grass life history strategies. For instance, the positive relationships of inflorescence height, culm diameter, and leaf width with temperature suggest a coordinated strategy that maximises above-ground growth, competition, and reproduction investment in warm environments (Reich, 2014). In contrast, the negative associations between inflorescence height, leaf length, and leaf width with nutrient availability indicate a coordinated shift towards more conservative resource-retention strategies in nutrient-poor environments (Colesie et al., 2020). These patterns underscore how functionally related traits co-vary in response to environmental constraints.

Environments are inherently complex, with numerous feedbacks between community composition and environmental factors, like drought, fire, and grazing, shaping traits over time. For example, frequent fire can select for flammable grasses that reinforce fire cycles, while heavy grazing may favour short, palatable species that attract grazers and perpetuate grazing regimes (Archibald et al., 2019; Archibald & Hempson, 2016; Bond & Keeley, 2005; Simpson et al., 2016). Our results are correlative, meaning we can only interpret trait-environment and trait-trait correlation rather than infer causal mechanisms or assess feedbacks. However, understanding how these feedbacks shape trait variation may provide further insights into grass life history strategies across environmental

gradients. Capturing these feedbacks or testing their underlying mechanisms would require an experimental approach- similar to those used by Archibald et al. (2005) and Simpson et al. (2016, 2021)- which was beyond the scope of this study.

Conclusion

Disentangling the direct and indirect effects of environmental drivers on traits is challenging, as multiple factors interact, confound one another, and produce different biological responses (Crowley & Wingler, 2020). Here, our model-based approach incorporated five important environmental drivers, realistically capturing some of the complexity of trait-environmental relationships. Using herbarium-derived trait data, we modelled trait-environment relationships, finding that temperature, soil sand content, and fire occurrence are consistently good predictors for most size and LES traits measured. Our results confirmed many expectations from previous literature examining individual drivers, reinforcing the idea that at a regional scale, the combined influence of multiple environmental drivers shape traits in similar ways to their individual effects.

Grass traits were highly correlated along two major axes of trait variation- the size spectrum and the leaf economic spectrum- with life history strategies emerging through trade-offs between growth, competition, reproduction and stress tolerance. The divergence of C₃ and C₄ grasses along these axes highlights how fundamental physiological differences structure functional diversity across environmental gradients.

Broadening our understanding of trait coordination and environmental responses is essential for assessing grassland resilience and predicting community responses to environmental change. Using herbarium specimens, we demonstrate the utility of a widely recognised set of environmental predictors of plant traits to explore trait variation, offering a framework that could be extended to other traits, regions, and taxa. While herbarium specimens provided a powerful tool for this, enabling broad geographical coverage while preserving individual-level trait variation, the extent to which herbarium material is useful in other regions and taxa remains an open question. Furthermore, while our findings contribute to the broader understanding of how grasses differentiate over environmental

gradients at a regional scale, multi-scale analyses are needed to fully capture the complexities of trait-environment relationships and trait coordination across spatial scales.

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Chapter 3 supplemental material

Data that supports this study's findings is fully available upon request.

Environmental variables

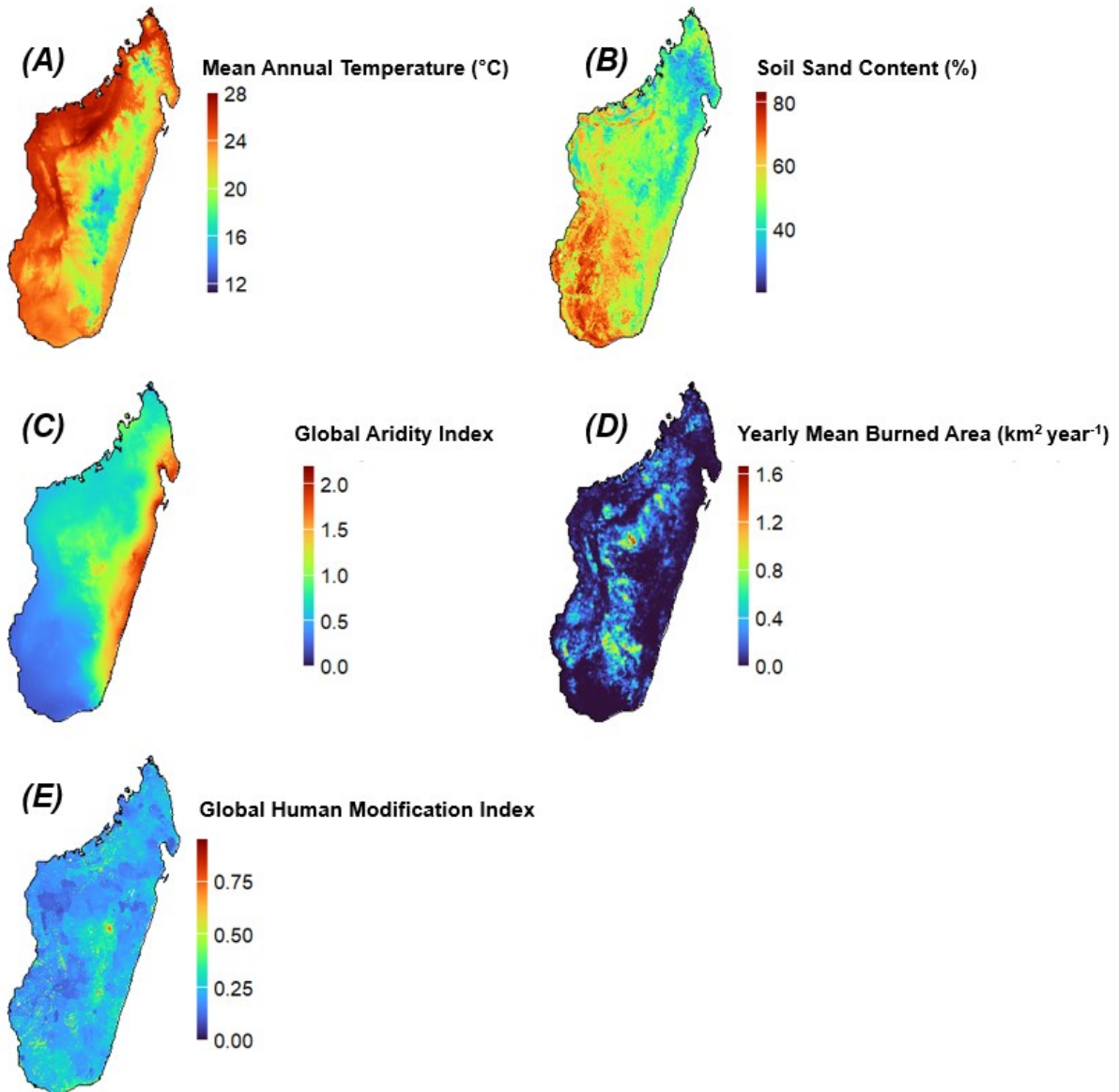


Figure S3.1. **Maps of five environmental variables:** (A) mean annual temperature, (B) soil sand content at 5-15cm depth, (C) global aridity index (D) yearly mean burned area, and (E) global human modification index. The maps are displayed at a resolution of 1 km².

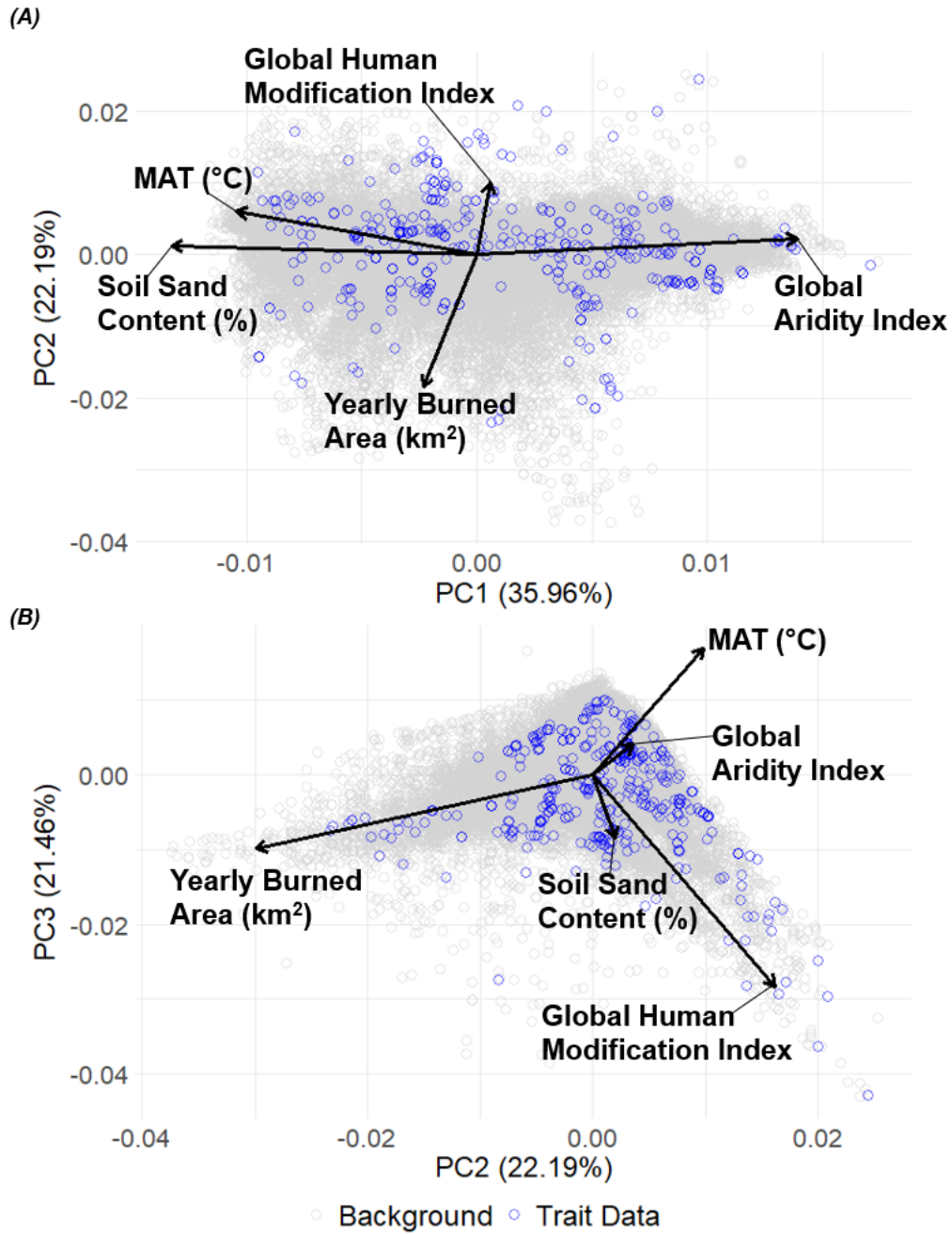


Figure S3.2. **PCA of environmental data**: mean annual temperature (MAT), soil sand content, global aridity index, yearly burned area, and the global human modification index- for all herbarium specimen collection sites and background environmental data representing Malagasy environmental space with A) PC1 vs. PC2 and B) PC2 vs. PC3.

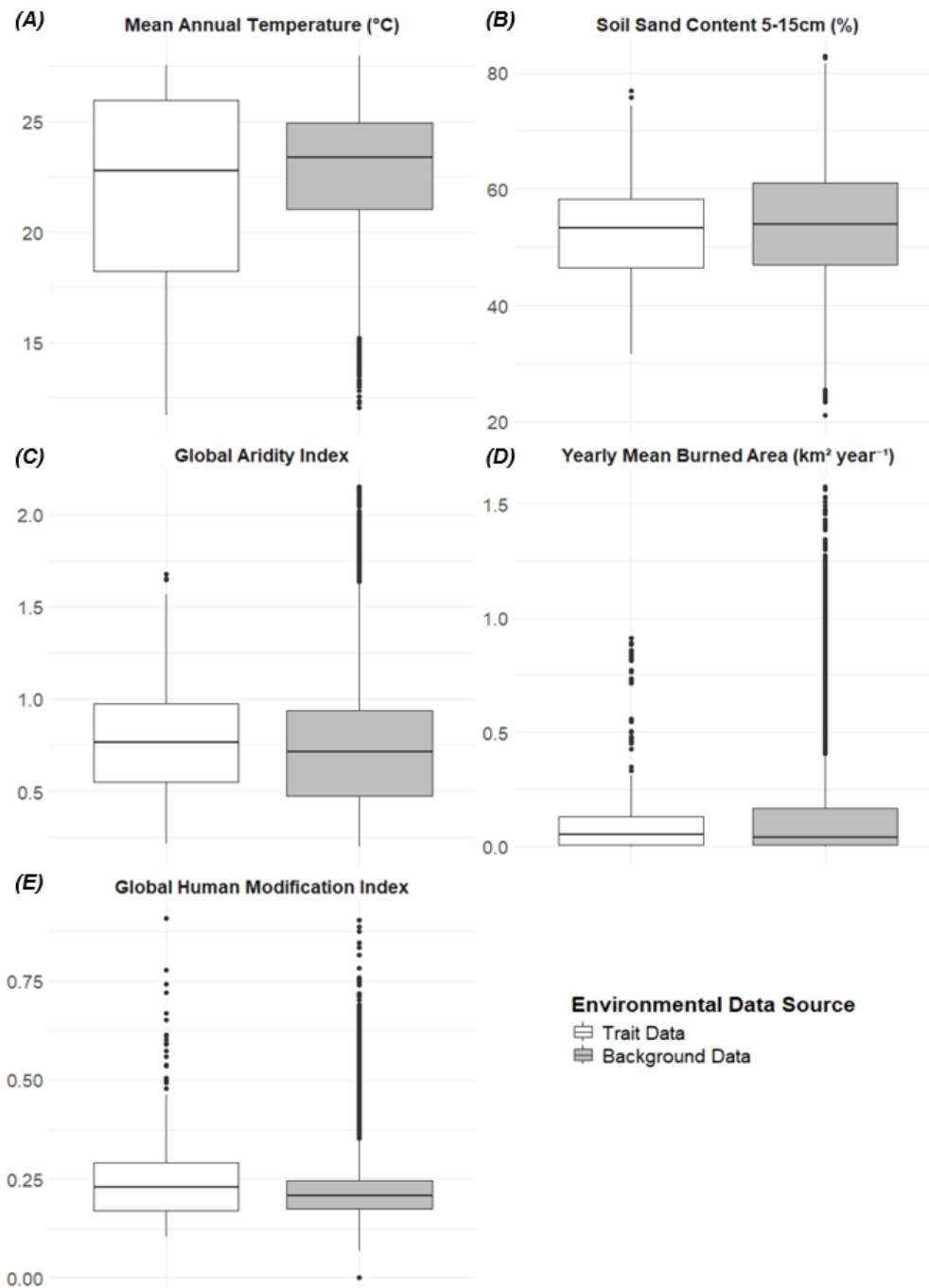


Figure S3.3. **Boxplots comparing environmental variable distributions between trait data (white) and background data (gray).** Environmental variables include (A) mean annual temperature, (B) soil sand content, (C) global aridity index, (D) yearly mean burned area, and (E) the global human modification index. Trait data represents the environmental conditions

of sampled herbarium specimens, while background data represents environmental conditions across all of Madagascar.

Species list

Table S3.1. **List of 260 grass species measured for traits.** The first column provides the species name as recorded in the dataset, the second column presents the accepted species name, and the third column lists the species authorship. The fourth column lists the corresponding tip labels from the phylogeny of Hackel et al. (2018), or the method used to infer the tip position for those taxa not represented in the Hackel et al tree.

Data Species Name	Accepted Species Name	Authorship	Corresponding tip
<i>Acroceras boivinii</i>	<i>Acroceras boivinii</i>	(Mez) A.Camus	LRK2014_Acroceras_cf._boivinii
<i>Acroceras calcicola</i>	<i>Acroceras calcicola</i>	A.Camus	NOP215_Acroceras_calcicola
<i>Acroceras tenuicaule</i>	<i>Acroceras tenuicaule</i>	A.Camus	RCH61_Acroceras_tenuicaule
<i>Adenochloa hymeniochila</i>	<i>Adenochloa hymeniochila</i>	(Nees) Zuloaga	MSV602_Panicum_hymeniochilum
<i>Agrostis elliotii</i>	<i>Agrostis elliotii</i>	Hack.	LRK2033_Agrostis_elliotii
<i>Agrostis emirensis</i>	<i>Agrostis emirnensis</i>	(Baker) Bosser	MSV600_Calamagrostis_emirnen sis
<i>Alloteropsis cimicina</i>	<i>Alloteropsis cimicina</i>	(L.) Stapf	Alloteropsis_cimicina
<i>Alloteropsis paniculata</i>	<i>Alloteropsis paniculata</i>	(Benth.) Stapf	Alloteropsis_paniculata
<i>Alloteropsis semialata</i>	<i>Alloteropsis semialata</i>	(R.Br.) Hitchc.	MSV919_Alloteropsis_semialata
<i>Andropogon andringitrensis</i>	<i>Andropogon andringitrensis</i>	(A.Camus) Voronts.	MSV1260_Andropogon_andringitrensis
<i>Andropogon eucomus</i>	<i>Andropogon eucomus</i>	Nees	MSV576_Andropogon_eucomus

<i>Andropogon ibityensis</i>	<i>Andropogon ibityensis</i>	A.Camus	MSV754_Andropogon_ibityensis
<i>Andropogon itremoensis</i>	<i>Andropogon itremoensis</i>	Voronts.	MSV753_Andropogon_itremoensis
<i>Andropogon ivohibensis</i>	<i>Andropogon ivohibensis</i>	A.Camus	Added as a sister taxon to the MRCA of the 13 tips belonging to the genus <i>Andropogon</i> in the Hackel et al tree.
<i>Andropogon trichozygus</i>	<i>Andropogon trichozygus</i>	Baker	
<i>Anthoxanthum madagascariense</i>	<i>Anthoxanthum madagascariense</i>	Stapf	MSV613_Anthoxanthum_madagascariense
<i>Aristida adscensionis</i>	<i>Aristida adscensionis</i>	Sw.	Aristida_adscensionis
<i>Aristida barbicollis</i>	<i>Aristida barbicollis</i>	Trin. & Rupr.	Added as a sister taxon to the MRCA of the 60 tips belonging to the genus <i>Aristida</i> in the in the Hackel <i>et al</i> tree.
<i>Aristida congesta</i>	<i>Aristida congesta</i>	Roem. & Schult.	MSV1334_Aristida_congesta
<i>Aristida cumingiana</i>	<i>Aristida cumingiana</i>	Trin. & Rupr.	0103_Aristida_cumingiana
<i>Aristida junciformis</i>	<i>Aristida junciformis</i>	Trin. & Rupr.	Aristida_junciformis
<i>Aristida rufescens</i>	<i>Aristida rufescens</i>	Steud.	MSV337_Aristida_rufescens
<i>Aristida similis</i>	<i>Aristida similis</i>	Steud.	0258_Aristida_similis
<i>Aristida tenuissima</i>	<i>Aristida tenuissima</i>	A.Camus	MSV1053_Aristida_tenuissima
<i>Arthraxon antsirabensis</i>	<i>Arthraxon antsirabensis</i>	A.Camus	NOP217_Arthraxon_antsirabensis
<i>Arundinella nepalensis</i>	<i>Arundinella nepalensis</i>	Trin.	MSV608_Arundinella_nepalensis
<i>Axonopus compressus</i>	<i>Axonopus compressus</i>	(Sw.) P.Beauv.	Allied with the genus <i>Phragmites</i> and added at the midpoint of the branch leading to the MRCA of

			the 2 tips belonging to this genus in the Hackel <i>et al</i> tree.
<i>Bothriochloa bladhii</i>	<i>Bothriochloa bladhii</i>	(Retz.) S.T.Blake	Added as a sister taxon to the MRCA of the 5 tips belonging to the genus <i>Bothriochloa</i> in the Hackel et al tree.
<i>Bothriochloa pertusa</i>	<i>Bothriochloa pertusa</i>	(L.) A.Camus	MSV353_Botriochloa_pertusa
<i>Brachiaria arrecta</i>	<i>Urochloa arrecta</i>	(Hack.) Morrone & Zuloaga	MSV1036_Brachiaria_arrecta
<i>Brachiaria bemarivensis</i>	<i>Brachiaria bemarivensis</i>	A.Camus	MSV936_Brachiaria_bemarivensis
<i>Brachiaria comorensis</i>	<i>Panicum comorense</i>	Mez	NOP193_Brachiaria_comorensis
<i>Brachiaria deflexa</i>	<i>Urochloa deflexa</i>	(Schumach.) H.Scholz	MSV914_Brachiaria_deflexa
<i>Brachiaria dimorpha</i>	<i>Brachiaria dimorpha</i>	A.Camus	MSV1234_Brachiaria_dimorpha
<i>Brachiaria distachya</i>	<i>Urochloa distachya</i>	(L.) T.Q.Nguyen	MSV915_Brachiaria_distachya
<i>Brachiaria epacridifolia</i>	<i>Brachiaria epacridifolia</i>	(Stapf) A.Camus	MSV722_Brachiaria_epacridifolia
<i>Brachiaria hubbardii</i>	<i>Acroceras hubbardii</i>	(A.Camus) Clayton	MSV347_Brachiaria_hubbardii
<i>Brachiaria humbertiana</i>	<i>Brachiaria humbertiana</i>	A.Camus	MSV1378_Brachiaria_humbertiana
<i>Brachiaria nana</i>	<i>Brachiaria nana</i>	Stapf	Added as a sister taxon to the MRCA of the 34 tips belonging to the genus <i>Brachiaria</i> in the Hackel et al tree.
<i>Brachiaria pseudodichotoma</i>	<i>Brachiaria pseudodichotoma</i>	Bosser	MSV942_Brachiaria_pseudodichotoma

<i>Brachiaria ramosa</i>	<i>Urochloa ramosa</i>	(L.) T.Q.Nguyen	MSV1763_Brachiaria_ramosa
<i>Brachiaria reptans</i>	<i>Urochloa reptans</i>	(L.) Stapf	MSV583_Brachiaria_reptans
<i>Brachiaria subquadrifera</i>	<i>Urochloa distachya</i>	(L.) T.Q.Nguyen	GB38-2014_Brachiaria_subquadrifera
<i>Brachiaria subrostrata</i>	<i>Brachiaria subrostrata</i>	A.Camus	MSV716_Brachiaria_subrostrata
<i>Brachiaria tsiafajavonensis</i>	<i>Brachiaria tsiafajavonensis</i>	A.Camus	MSV697_Brachiaria_tsiafajavonensis
<i>Brachiaria umbellata</i>	<i>Brachiaria umbellata</i>	(Trin.) Clayton	RCH17_Brachiaria_umbellata
<i>Brachypodium madagascariense</i>	<i>Brachypodium madagascariense</i>	A.Camus & H.Perrier	MSV735_Brachypodium_madagascariense
<i>Brachypodium perrieri</i>	<i>Brachypodium perrieri</i>	A.Camus	LRK2010_Brachypodium_perrieri
<i>Cenchrus ciliaris</i>	<i>Cenchrus ciliaris</i>	L.	Cenchrus_ciliaris
<i>Cenchrus echinatus</i>	<i>Cenchrus echinatus</i>	L.	MSV965_Cenchrus_echinatus
<i>Cenchrus polystachyos</i>	<i>Setaria parviflora</i>	(Poir.) Kerguelen	MSV334_Cenchrus_polystachyos
<i>Centotheca lappacea</i>	<i>Centotheca lappacea</i>	(L.) Desv.	Centotheca_lappacea
<i>Chasechloa madagascariensis</i>	<i>Chasechloa madagascariensis</i>	(Baker) A.Camus	Allied with the genera <i>Acroceras</i> , <i>Brachiaria</i> , and <i>Pseudechinolaena</i> and added at the midpoint of the branch leading to the MRCA of the 54 tips belonging to these genera in the Hackel <i>et al</i> tree.
<i>Chloris barbata</i>	<i>Chloris barbata</i>	Sw.	MSV579_Chloris_barbata
<i>Chloris humbertiana</i>	<i>Chloris humbertiana</i>	A.Camus	NOP206_Chloris_humbertiana
<i>Chloris pycnothrix</i>	<i>Chloris pycnothrix</i>	Trin.	MSV313_Chloris_pycnothrix
<i>Chloris virgata</i>	<i>Chloris virgata</i>	Sw.	Chloris_virgata

<i>Chrysopogon humbertianus</i>	<i>Chrysopogon humbertianus</i>	A.Camus	MSV1413_Chrysopogon_humbertiana
<i>Chrysopogon serrulatus</i>	<i>Chrysopogon serrulatus</i>	Trin.	MSV326_Chrysopogon_serrulatus
<i>Coelachne africana</i>	<i>Coelachne africana</i>	Pilg.	RCH09_Coelachne_africana
<i>Coelachne simpliciuscula</i>	<i>Coelachne simpliciuscula</i>	(Wight & Arn. ex Steud.) Munro ex Benth.	Added as a sister taxon to the MRCA of the 2 tips belonging to the genus <i>Coelachne</i> in the Hackel <i>et al</i> tree.
<i>Craspedorachis africana</i>	<i>Craspedorachis africana</i>	Benth.	RGD188_Craspedorachis_africana
<i>Ctenium concinnum</i>	<i>Ctenium concinnum</i>	Nees	RGD194_Ctenium_concinnum
<i>Cymbopogon caesius</i>	<i>Cymbopogon caesius</i>	(Hook. & Arn.) Stapf	Cymbopogon_caesius
<i>Cynodon dactylon</i>	<i>Cynodon dactylon</i>	(L.) Pers.	Cynodon_dactylon
<i>Cynodon radiatus</i>	<i>Cynodon radiatus</i>	Roth	MSV715_Cynodon_radiatus
<i>Cyphochlaena madagascariensis</i>	<i>Cyphochlaena madagascariensis</i>	Hack.	Cyphochlaena_madagascariensis
<i>Cyphochlaena sclerioides</i>	<i>Cyphochlaena sclerioides</i>	(A.Camus) Bosser	Added as a sister taxon to the MRCA of the 2 tips belonging to the genus <i>Cyphochlaena</i> in the Hackel <i>et al</i> tree.
<i>Cyrtococcum bosseri</i>	<i>Cyrtococcum bosseri</i>	A.Camus	NOP228_Cyrtococcum_bosseri
<i>Cyrtococcum deltoideum</i>	<i>Cyrtococcum deltoideum</i>	(Hack.) A.Camus	RCH10_Cyrtococcum_deltoideum
<i>Cyrtococcum multinode</i>	<i>Cyrtococcum multinode</i>	(Lam.) Clayton	NOP229_Cyrtococcum_multinode
<i>Cyrtococcum tamatavense</i>	<i>Cyrtococcum tamatavense</i>	A.Camus	RCH39_Cyrtococcum_tamatavense

<i>Dactyloctenium aegyptium</i>	<i>Dactyloctenium aegyptium</i>	(L.) Willd.	Dactyloctenium_aegyptium
<i>Dactyloctenium capitatum</i>	<i>Dactyloctenium capitatum</i>	A.Camus	MSV1393_Dactyloctenium_capitatus
<i>Dactyloctenium ctenoides</i>	<i>Dactyloctenium ctenoides</i>	(Steud.) Bosser	MSV918_Dactyloctenium_ctenoides
<i>Daknopholis boivinii</i>	<i>Daknopholis boivinii</i>	(A.Camus) Clayton	MSV925_Daknopholis_boivinii
<i>Decaryella madagascariensis</i>	<i>Decaryella madagascariensis</i>	A.Camus	MSV1398_Decaryella_madagascariensis
<i>Dichanthium annulatum</i>	<i>Dichanthium annulatum</i>	(Forssk.) Stapf	MSV582_Dichanthium_annulatum
<i>Dichanthium aristatum</i>	<i>Dichanthium aristatum</i>	(Poir.) C.E.Hubb.	MSV949_Dichanthium_aristatum
<i>Digitaria biformis</i>	<i>Digitaria bicornis</i>	(Lam.) Roem. & Schult.	MSV928_Digitaria_bicornis
<i>Digitaria debilis</i>	<i>Digitaria debilis</i>	(Desf.) Willd.	MSV631_Digitaria_debilis
<i>Digitaria didactyla</i>	<i>Digitaria didactyla</i>	Willd.	Digitaria_didactyla
<i>Digitaria glauca</i>	<i>Digitaria glauca</i>	A.Camus	MSV950_Digitaria_glauca
<i>Digitaria longiflora</i>	<i>Digitaria longiflora</i>	(Retz.) Pers.	MSV745_Digitaria_longiflora
<i>Digitaria perrottetii</i>	<i>Digitaria perrottetii</i>	(Kunth) Stapf	Added as a sister taxon to the MRCA of the 28 tips belonging to the genus <i>Digitaria</i> in the Hackel <i>et al</i> tree.
<i>Digitaria pseudodiagonalis</i>	<i>Digitaria pseudodiagonalis</i>	Chiov.	MSV1005_Digitaria_pseudodiagonalis
<i>Digitaria radicata</i>	<i>Digitaria radicata</i>	(J.Presl) Miq.	MSV703_Digitaria_radicata
<i>Digitaria sanguinalis</i>	<i>Digitaria sanguinalis</i>	(L.) Scop.	Digitaria_sanguinalis
<i>Dimeria madagascariensis</i>	<i>Dimeria madagascariensis</i>	A.Camus	MSV343_Dimeria_madagascariensis

<i>Dimeria manongarivensis</i>	<i>Dimeria manongarivensis</i>	A.Camus	Added at the midpoint of the branch leading to the <i>Dimeria madagascariensis</i> tip
<i>Echinochloa colona</i>	<i>Echinochloa colonum</i>	(L.) Link	<i>Echinochloa_colona</i>
<i>Echinochloa crus-galli</i>	<i>Echinochloa crus-galli</i>	(L.) P.Beauv.	<i>Echinochloa_crus-galli</i>
<i>Echinochloa frumentacea</i>	<i>Echinochloa colonum subsp. edulis</i>	(Honda) Banfi & Galasso	MSV636_ <i>Echinochloa frumentacea</i>
<i>Echinochloa jubata</i>	<i>Echinochloa jubata</i>	Stapf	MSV943_ <i>Echinochloa jubata</i>
<i>Echinochloa oryzoides</i>	<i>Echinochloa oryzoides</i>	(Ard.) Fritsch	MSV709_ <i>Echinochloa oryzoides</i>
<i>Echinochloa stagnina</i>	<i>Echinochloa stagnina</i>	(Retz.) P.Beauv.	RCH49_ <i>Echinochloa stagnina</i>
<i>Echinochloa ugandensis</i>	<i>Echinochloa ugandensis</i>	Snowden & C.E.Hubb.	MSV706_ <i>Echinochloa ugandensis</i>
<i>Eleusine indica</i>	<i>Eleusine indica</i>	(L.) Gaertn.	<i>Eleusine_indica</i>
<i>Elionurus tristis</i>	<i>Elionurus tristis</i>	Hack.	MSV589_ <i>Elionurus tristis</i>
<i>Enneapogon cenchroides</i>	<i>Enneapogon cenchroides</i>	(Licht.) C.E.Hubb.	NOP174_ <i>Enneapogon cenchroides</i>
<i>Enteropogon prieurii</i>	<i>Enteropogon prieurii</i>	(Kunth) Clayton	MSV964_ <i>Enteropogon prieurii</i>
<i>Eragrostis aethiopica</i>	<i>Eragrostis aethiopica</i>	Chiov.	MSV1335_ <i>Eragrostis aethiopica</i>
<i>Eragrostis aspera</i>	<i>Eragrostis aspera</i>	(Jacq.) Nees	NOP200_ <i>Eragrostis aspera</i>
<i>Eragrostis atrovirens</i>	<i>Eragrostis atrovirens</i>	(Desf.) Trin. ex Steud.	Added as a sister taxon to the MRCA of the 62 tips belonging to the genus <i>Eragrostis</i> in the Hackel <i>et al</i> tree.

<i>Eragrostis bemarivensis</i>	<i>Eragrostis bemarivensis</i>	A.Camus	Added as a sister taxon to the MRCA of the 62 tips belonging to the genus <i>Eragrostis</i> in the Hackel <i>et al</i> tree.
<i>Eragrostis boinensis</i>	<i>Eragrostis boinensis</i>	A.Camus	MSV935_ <i>Eragrostis boinensis</i>
<i>Eragrostis capensis</i>	<i>Eragrostis capensis</i>	(Thunb.) Trin.	<i>Eragrostis capensis</i>
<i>Eragrostis capuronii</i>	<i>Eragrostis capuronii</i>	A.Camus	NOP186_ <i>Eragrostis capuronii</i>
<i>Eragrostis chabouisii</i>	<i>Eragrostis chabouisii</i>	Bosser	NOP185_ <i>Eragrostis chabouisii</i>
<i>Eragrostis chapelieri</i>	<i>Eragrostis chapelieri</i>	(Kunth) Nees	MSV639_ <i>Eragrostis chapelieri</i>
<i>Eragrostis cilianensis</i>	<i>Eragrostis cilianensis</i>	(All.) Vignolo ex Janch.	<i>Eragrostis cilianensis</i>
<i>Eragrostis ciliaris</i>	<i>Eragrostis ciliaris</i>	(L.) R.Br.	MSV388_ <i>Eragrostis ciliaris</i>
<i>Eragrostis cylindriflora</i>	<i>Eragrostis cylindriflora</i>	Hochst.	<i>Eragrostis cylindriflora</i>
<i>Eragrostis gangetica</i>	<i>Eragrostis gangetica</i>	(Roxb.) Steud.	MSV968_ <i>Eragrostis gangetica</i>
<i>Eragrostis hildebrandtii</i>	<i>Eragrostis hildebrandtii</i>	Jedwabn.	MSV590_ <i>Eragrostis hildebrandtii</i>
<i>Eragrostis humbertii</i>	<i>Eragrostis humbertii</i>	A.Camus	MSV1417_ <i>Eragrostis humbertii</i>
<i>Eragrostis japonica</i>	<i>Eragrostis japonica</i>	(Thunb.) Trin.	MSV1349_ <i>Eragrostis japonica</i>
<i>Eragrostis lateritica</i>	<i>Eragrostis lateritica</i>	Bosser	MSV638_ <i>Eragrostis lateritica</i>
<i>Eragrostis macilenta</i>	<i>Eragrostis macilenta</i>	(A.Rich.) Steud.	NOP71_ <i>Eragrostis macilenta</i>
<i>Eragrostis perrieri</i>	<i>Eragrostis perrieri</i>	A.Camus	Added as a sister taxon to the MRCA of the 62 tips belonging to

			the genus <i>Eragrostis</i> in the Hackel <i>et al</i> tree.
<i>Eragrostis pilosa</i>	<i>Eragrostis pilosa</i>	(L.) P.Beauv.	MSV349_Eragrostis_pilosa
<i>Eragrostis poaoides</i>	<i>Eragrostis minor</i>	Host	MSV1394_Eragrostis_minor
<i>Eragrostis sarmentosa</i>	<i>Eragrostis sarmentosa</i>	(Thunb.) Trin.	Added as a sister taxon to the MRCA of the 62 tips belonging to the genus <i>Eragrostis</i> in the Hackel <i>et al</i> tree.
<i>Eragrostis tenella</i>	<i>Eragrostis tenella</i>	(L.) P.Beauv. ex Roem. & Schult.	MSV699_Eragrostis_tenella
<i>Eragrostis tenuifolia</i>	<i>Eragrostis tenuifolia</i>	(A.Rich.) Hochst. ex Steud.	Eragrostis_tenuifolia
<i>Eriochloa barbatus</i>	<i>Eriochloa barbatus</i>	(Trin.) S.Yadav & M.R.Almeida	MSV963_Eriochloa_fatmensis
<i>Euclasta condylotricha</i>	<i>Euclasta condylotricha</i>	(Hochst. ex Steud.) Stapf	Allied with the genus <i>Bothriochloa</i> and added at the midpoint of the branch leading to the MRCA of the 5 tips belonging to this genus in the Hackel <i>et al</i> tree.
<i>Eulalia villosa</i>	<i>Eulalia villosa</i>	(Spreng.) Nees	MSV621_Eulalia_villosa
<i>Festuca altissima</i>	<i>Festuca altissima</i>	All.	Festuca_altissima
<i>Festuca camusiana</i>	<i>Festuca camusiana</i>	St.-Yves	MSV617_Festuca_camusiana
<i>Festuca perrieri</i>	<i>Festuca perrieri</i>	A.Camus	NOP85_Festuca_perrieri
<i>Hemarthria altissima</i>	<i>Hemarthria altissima</i>	(Poir.) Stapf & C.E.Hubb.	Allied with the genus <i>Heteropholis</i> , and added at the midpoint of the branch leading to the <i>Heteropholis_sulcata</i> tip
<i>Heteropogon contortus</i>	<i>Heteropogon contortus</i>	(L.) P.Beauv. ex Roem. & Schult.	Heteropogon_contortus

<i>Heteropogon melanocarpus</i>	<i>Heteropogon melanocarpus</i>	Dewey ex J.M.Coult.	NOP139_Heteropogon_melanocarpus
<i>Humbertochloa bambusiuscula</i>	<i>Humbertochloa bambusiuscula</i>	A.Camus & Stapf	MSV956_Humbertochloa_bambusiuscula
<i>Hyparrhenia newtonii</i>	<i>Hyparrhenia newtonii</i>	(Hack.) Stapf	MSV721_Hyparrhenia_newtonii
<i>Hyparrhenia rufa</i>	<i>Hyparrhenia rufa</i>	(Nees) Stapf	MSV328_Hyparrhenia_rufa
<i>Hyparrhenia schimperi</i>	<i>Hyparrhenia schimperi</i>	(Hochst. ex A.Rich.) Andersson ex Stapf	MSV720_Hyparrhenia_schimperi
<i>Hyperthelia dissoluta</i>	<i>Hyperthelia dissoluta</i>	(Nees ex Steud.) Clayton	MSV910_Hyperthelia_dissoluta
<i>Imperata cylindrica</i>	<i>Imperata cylindrica</i>	(L.) Raeusch.	Imperata_cylindrica
<i>Isachne humbertiana</i>	<i>Isachne humbertiana</i>	A.Camus	MSV496_Isachne_humbertiana
<i>Isachne humicola</i>	<i>Isachne humicola</i>	A.Camus	MSV563_Isachne_humicola
<i>Isachne mauritiana</i>	<i>Isachne mauritiana</i>	Kunth	MSV308_Isachne_mauritiana
<i>Isachne musicola</i>	<i>Isachne musicola</i>	A.Camus	MSV597_Isachne_musicola
<i>Ischaemum heterotrichum</i>	<i>Ischaemum heterotrichum</i>	Hack.	MSV643_Ischaemum_heterotrichum
<i>Ischaemum koleostachys</i>	<i>Ischaemum koleostachys</i>	(Steud.) Hack.	Ischaemum_koleostachys
<i>Ischaemum polystachyum</i>	<i>Ischaemum polystachyum</i>	J.Presl	Added as a sister taxon to the MRCA of the 7 tips belonging to the genus <i>Ischaemum</i> in the Hackel <i>et al</i> tree.
<i>Ischaemum rugosum</i>	<i>Ischaemum rugosum</i>	Salisb.	MSV501_Ischaemum_rugosum
<i>Lasiorhachis viguieri</i>	<i>Lasiorhachis viguieri</i>	(A.Camus) Bosser	MSV1248_Saccharum_viguieri

<i>Leersia hexandra</i>	<i>Leersia hexandra</i>	Sw.	Leersia_hexandra
<i>Leptaspis zeylanica</i>	<i>Leptaspis zeylanica</i>	Nees ex Steud.	Allied with the genus <i>Pharus</i> , and added at the midpoint of the branch leading to the <i>Pharus_latifolius</i> tip
<i>Leptocarydion vulpiastrum</i>	<i>Leptocarydion vulpiastrum</i>	(De Not.) Stapf	NOP173_Leptocarydion_vulpiastrum
<i>Leptochloa panicea</i>	<i>Leptochloa panicea</i>	(Retz.) Ohwi	MSV1837_Leptochloa_panacea
<i>Lepturus anadabolavensis</i>	<i>Lepturus anadabolavensis</i>	A.Camus	NOP203_Lepturus_anadabolavensis
<i>Lepturus humbertianus</i>	<i>Lepturus humbertianus</i>	A.Camus	MSV1403_Lepturus_cf._humbertianus
<i>Lepturus radicans</i>	<i>Lepturus radicans</i>	(Steud.) A.Camus	Lepturus_radicans
<i>Lepturus repens</i>	<i>Lepturus repens</i>	(G.Forst.) R.Br.	Lepturus_repens
<i>Loudetia filifolia</i>	<i>Loudetia filifolia</i>	Schweick.	MSV1368_Loudetia_filifolia
<i>Loudetia simplex</i>	<i>Loudetia simplex</i>	(Nees) C.E.Hubb.	MSV595_Loudetia_simplex
<i>Megastachya mucronata</i>	<i>Megastachya mucronata</i>	(Poir.) P.Beauv.	Megastachya_mucronata
<i>Melinis minutiflora</i>	<i>Melinis minutiflora</i>	P.Beauv.	Melinis_minutiflora
<i>Melinis repens</i>	<i>Melinis repens</i>	(Willd.) Zizka	Melinis_repens
<i>Merxmuellera ambalavaoensis</i>	<i>Merxmuellera ambalavaoensis</i>	(A.Camus) Conert	MSV1235_Merxmuellera_ambalavaoensis
<i>Merxmuellera tsaratananensis</i>	<i>Merxmuellera tsaratananensis</i>	(A.Camus) Conert	MSV486_Merxmuellera_tsaratananensis
<i>Microchloa kunthii</i>	<i>Microchloa kunthii</i>	Desv.	MSV746_Microchloa_kunthii
<i>Microstegium nudum</i>	<i>Microstegium nudum</i>	(Trin.) A.Camus	MSV1845_Microstegium_nudum

<i>Neostapfiella perrieri</i>	<i>Neostapfiella perrieri</i>	A.Camus	JB20177_Neostapfiella_perrieri
<i>Oplismenus burmanii</i>	<i>Oplismenus burmanni</i>	(Retz.) P.Beauv.	RCH41_Oplismenus_burmanii
<i>Oplismenus burmannii</i>	<i>Oplismenus burmanni</i>	(Retz.) P.Beauv.	Oplismenus_burmannii
<i>Oplismenus compositus</i>	<i>Oplismenus compositus</i>	(L.) P.Beauv.	Oplismenus_compositus
<i>Oplismenus flavicomus</i>	<i>Oplismenus flavicomus</i>	L.	RCH25_Oplismenus_flavicomus
<i>Oplismenus hirtellus</i>	<i>Oplismenus hirtellus</i>	(L.) P.Beauv.	Oplismenus_hirtellus
<i>Oryza sativa</i>	<i>Oryza sativa</i>	NA	Oryza_sativa_Indica_Group
<i>Panicum ambositrense</i>	<i>Panicum ambositrense</i>	A.Camus	MSV736_Panicum_ambositrense
<i>Panicum andringitrense</i>	<i>Panicum andringitrense</i>	A.Camus	MSV591_Panicum_andringitrense
<i>Panicum brevifolium</i>	<i>Panicum brevifolium</i>	Jahn ex Schrank	MSV304_Panicum_brevifolium
<i>Panicum cinctum</i>	<i>Panicum cinctum</i>	Hack.	MSV1027_Panicum_cinctum
<i>Panicum cupressifolium</i>	<i>Panicum cupressifolium</i>	A.Camus	MSV1233_Panicum_cupressifolium
<i>Panicum dregeanum</i>	<i>Panicum dregeanum</i>	Nees	Added as a sister taxon to the MRCA of the 97 tips belonging to the genus <i>Panicum</i> in the Hackel <i>et al</i> tree.
<i>Panicum ibitense</i>	<i>Panicum ibitense</i>	A.Camus	RGD171_Panicum_ibitense
<i>Panicum luridum</i>	<i>Panicum luridum</i>	Hack.	MSV909_Panicum_luridum
<i>Panicum maximum</i>	<i>Megathyrsus maximus</i>	(Jacq.) B.K.Simon & S.W.L.Jacobs	Megathyrsus_maximus

<i>Panicum mitopus</i>	<i>Panicum mitopus</i>	K.Schum.	RCH01_Panicum_mitopus
<i>Panicum parviflorum</i>	<i>Digitaria parviflora</i>	(R.Br.) Hughes	Added as a sister taxon to the MRCA of the 97 tips belonging to the genus <i>Panicum</i> in the Hackel <i>et al</i> tree.
<i>Panicum parvifolium</i>	<i>Trichantheceum parvifolium</i>	(Lam.) Zuloaga & Morrone	Panicum_parvifolium
<i>Panicum perrieri</i>	<i>Panicum perrieri</i>	A.Camus	MSV749_Panicum_perrieri
<i>Panicum pleianthum</i>	<i>Panicum pleianthum</i>	Peter	RCH53_Panicum_pleianthum
<i>Panicum spergulifolium</i>	<i>Panicum spergulifolium</i>	A.Camus	MSV1250_Panicum_spergulfolium
<i>Panicum subalbidum</i>	<i>Panicum subalbidum</i>	Kunth	MSV637_Panicum_subalbidum
<i>Panicum subhystrix</i>	<i>Panicum subhystrix</i>	A.Camus	MSV748_Panicum_subhystrix
<i>Panicum trichocladum</i>	<i>Panicum trichocladum</i>	Hack. ex Engl.	MSV705_Panicum_trichocladum
<i>Panicum voeltzkowii</i>	<i>Panicum voeltzkowii</i>	Mez	CF_Panicum_pseudovoeltzkovii
<i>Panicum vohitrense</i>	<i>Panicum vohitrense</i>	A.Camus	MSV1466_Panicum_vohitrense
<i>Paspalum conjugatum</i>	<i>Paspalum conjugatum</i>	P.J.Bergius	Allied with the genus <i>Phragmites</i> and added at the midpoint of the branch leading to the MRCA of the 2 tips belonging to this genus in the Hackel <i>et al</i> tree.
<i>Paspalum nutans</i>	<i>Paspalum nutans</i>	Lam.	
<i>Paspalum paniculatum</i>	<i>Paspalum paniculatum</i>	L.	
<i>Paspalum scrobiculatum</i>	<i>Paspalum scrobiculatum</i>	L.	
<i>Paspalum vaginatum</i>	<i>Paspalum vaginatum</i>	Sw.	Setaria_parviflora
<i>Pennisetum polystachion</i>	<i>Setaria parviflora</i>	(Poir.) Kerguelén	

<i>Perotis arenacea</i>	<i>Perotis arenacea</i>	(Judz.) P.M.Peterson	NOP197_Toliara_arenacea
<i>Perotis patens</i>	<i>Perotis patens</i>	Gand.	Perotis_patens
<i>Poa annua</i>	<i>Poa annua</i>	L.	Poa_annua
<i>Poa perrieri</i>	<i>Poa perrieri</i>	A.Camus	MSV1232_Poa_perrieri
<i>Pogonarthria squarrosa</i>	<i>Pogonarthria squarrosa</i>	(Licht.) Pilg.	Pogonarthria_squarrosa
<i>Pseudechinolaena perrieri</i>	<i>Pseudechinolaena perrieri</i>	A.Camus	Added as a sister taxon to the MRCA of the 5 tips belonging to the genus <i>Pseudechinolaena</i> in the Hackel <i>et al</i> tree.
<i>Pseudechinolaena polystachya</i>	<i>Pseudechinolaena polystachya</i>	(Kunth) Stapf	Pseudechinolaena_polystachya
<i>Pseudobromus breviligulatus</i>	<i>Pseudobromus breviligulatus</i>	Stapf ex A.Camus	MSV725_Pseudobromus_brevillugatus
<i>Pseudolasiacis leptomoides</i>	<i>Pseudolasiacis leptomoides</i>	(A.Camus) A.Camus	MSV983_Pseudolasiacis_leptomoides
<i>Pseudolasiacis neoperrieri</i>	<i>Pseudolasiacis neoperrieri</i>	(A.Camus) A.Camus	Added at the midpoint of the branch leading to the <i>Pseudolasiacis leptomoides</i> tip
<i>Rhytachne rottboellioides</i>	<i>Rhytachne rottboellioides</i>	Desv.	MSV592_Rhytachne_rottboellioides
<i>Rottboellia cochinchinensis</i>	<i>Rottboellia cochinchinensis</i>	(Lour.) Clayton	MSV948_Rottboellia_cochinchinensis
<i>Sacciolepis africana</i>	<i>Sacciolepis africana</i>	C.E.Hubb. & Snowden	Sacciolepis_africana
<i>Sacciolepis curvata</i>	<i>Sacciolepis curvata</i>	(L.) Chase	MSV394_Sacciolepis_curvata
<i>Sacciolepis indica</i>	<i>Sacciolepis indica</i>	Chase	Sacciolepis_indica
<i>Sacciolepis viguieri</i>	<i>Sacciolepis viguieri</i>	A.Camus	RGD190_Sacciolepis_viguieri

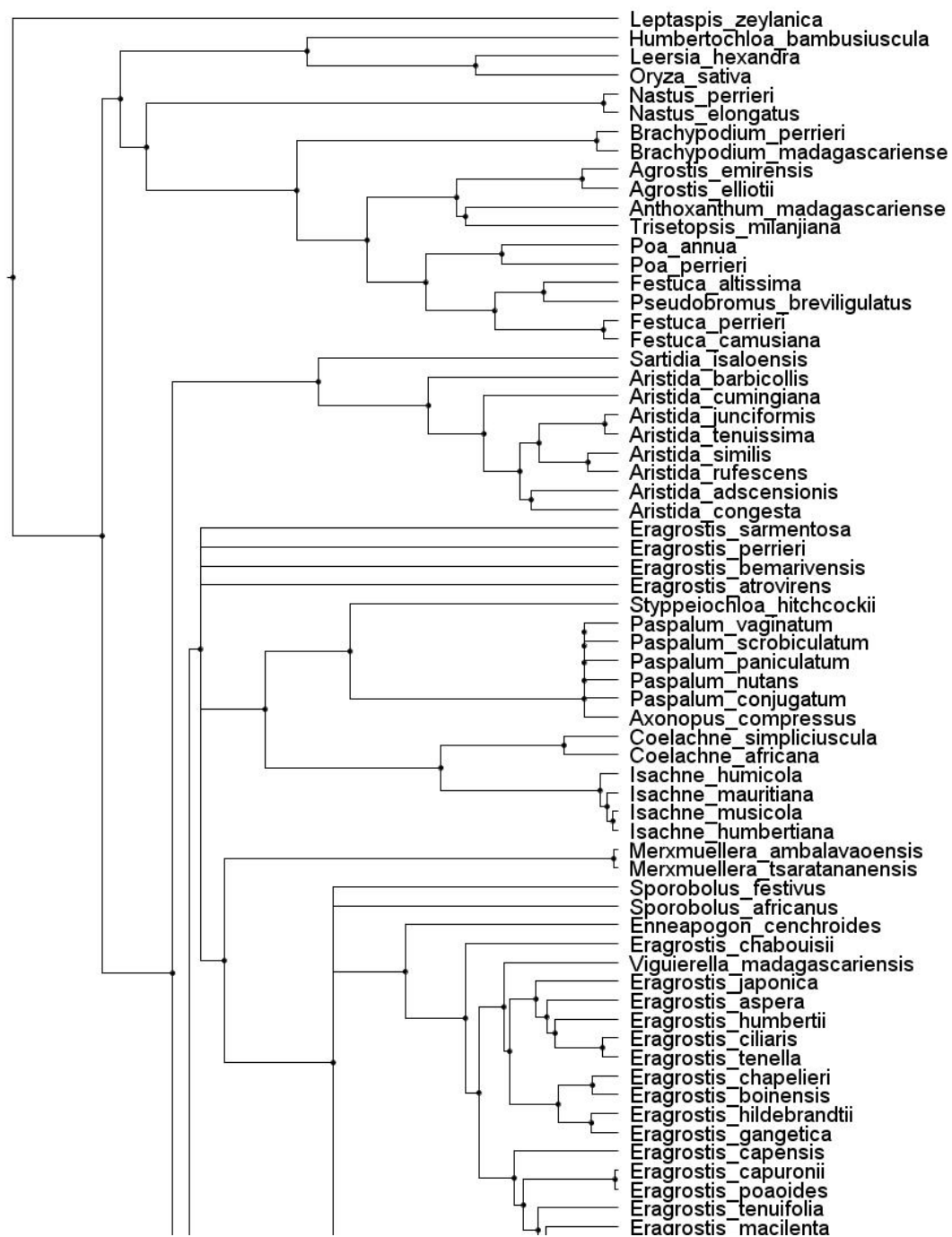
<i>Sartidia isaloensis</i>	<i>Sartidia isaloensis</i>	Voronts., Razanats. & Besnard	MSV1325_Sartidia_isaloensis
<i>Schizachyrium brevifolium</i>	<i>Schizachyrium brevifolium</i>	(Sw.) Nees ex Buse	RGD199_Schizachyrium_brevifoli um
<i>Schizachyrium exile</i>	<i>Schizachyrium exile</i>	(Hochst.) Pilg.	Added as a sister taxon to the MRCA of the 4 tips belonging to the genus <i>Schizachyrium</i> in the Hackel <i>et al</i> tree.
<i>Schizachyrium sanguineum</i>	<i>Schizachyrium sanguineum</i>	(Retz.) Alston	RGD180_Schizachyrium_sanguine um
<i>Sclerodactylon macrostachyum</i>	<i>Sclerodactylon macrostachyum</i>	(Benth.) A.Camus	NOP198_Sclerodactylon_macrost achyum
<i>Setaria barbata</i>	<i>Setaria barbata</i>	(Lam.) Kunth	Setaria_barbata
<i>Setaria humbertiana</i>	<i>Setaria humbertiana</i>	A.Camus	MSV1414_Setaria_humbertiana
<i>Setaria madecassa</i>	<i>Setaria madecassa</i>	A.Camus	MSV979_Setaria_madecassa
<i>Setaria megaphylla</i>	<i>Setaria megaphylla</i>	(Steud.) T.Durand & Schinz	Setaria_megaphylla
<i>Setaria pumila</i>	<i>Setaria pumila</i>	(Poir.) Roem. & Schult.	Setaria_pumila
<i>Setaria sagittifolia</i>	<i>Setaria sagittifolia</i>	(A.Rich.) Walp.	NOP207_Setaria_sagitifolia
<i>Setaria scottii</i>	<i>Setaria scottii</i>	(Hack.) A.Camus	MSV1041_Setaria_scottii
<i>Setaria vatkeana</i>	<i>Setaria vatkeana</i>	K.Schum.	MSV1813_Setaria_vatkeana
<i>Setaria verticillata</i>	<i>Setaria verticillata</i>	(L.) P.Beauv.	MSV1381_Setaria_verticillata
<i>Sporobolus africanus</i>	<i>Sporobolus africanus</i>	(Poir.) Robyns & Tournay	Added as a sister taxon to the MRCA of the 30 tips belonging to the genus <i>Sporobolus</i> in the Hackel <i>et al</i> tree.

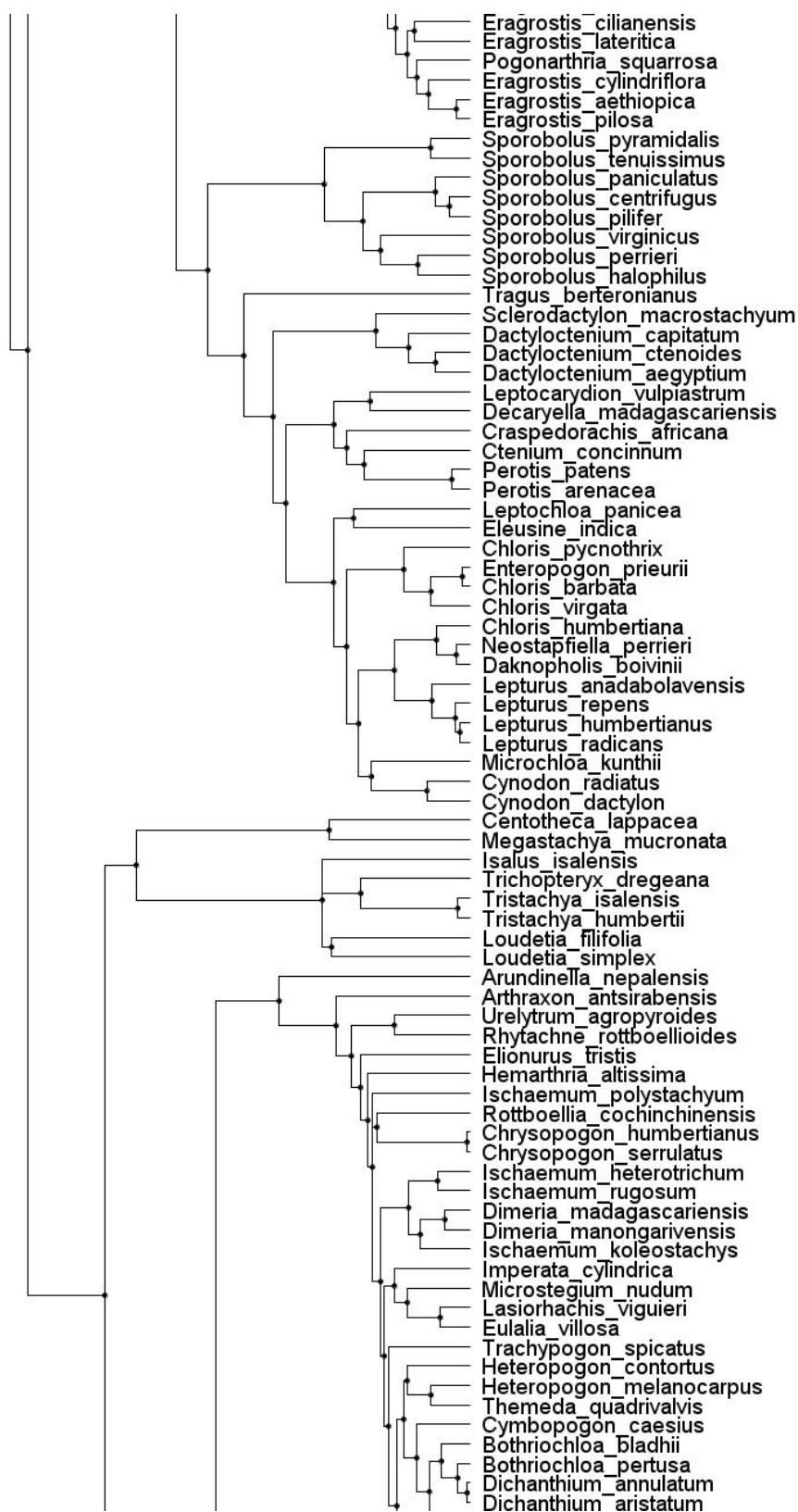
<i>Sporobolus centrifugus</i>	<i>Sporobolus centrifugus</i>	(Trin.) Nees	MSV622_Sporobolus_centrifugus
<i>Sporobolus festivus</i>	<i>Sporobolus festivus</i>	Hochst. ex A.Rich.	Added as a sister taxon to the MRCA of the 30 tips belonging to the genus <i>Sporobolus</i> in the Hackel <i>et al</i> tree.
<i>Sporobolus halophilus</i>	<i>Sporobolus halophilus</i>	Bosser	MSV585_Sporobolus_halophilus
<i>Sporobolus paniculatus</i>	<i>Sporobolus paniculatus</i>	(Trin.) T.Durand & Schinz	RGD168_Sporobolus_paniculatus
<i>Sporobolus perrieri</i>	<i>Sporobolus perrieri</i>	A.Camus	MSV1415_Sporobolus_perrieri
<i>Sporobolus pilifer</i>	<i>Sporobolus piliferus</i>	(Trin.) Kunth	MSV747_Sporobolus_piliferus
<i>Sporobolus pyramidalis</i>	<i>Sporobolus pyramidalis</i>	P.Beauv.	MSV314_Sporobolus_pyramidalis
<i>Sporobolus tenuissimus</i>	<i>Sporobolus tenuissimus</i>	(Mart. ex Schrank) Kuntze	MSV707_Sporobolus_tenuissimus
<i>Sporobolus virginicus</i>	<i>Sporobolus virginicus</i>	(L.) Kunth	Sporobolus_virginicus
<i>Stenotaphrum dimidiatum</i>	<i>Stenotaphrum dimidiatum</i>	(L.) Brongn.	Stenotaphrum_dimidiatum
<i>Stenotaphrum oostachyum</i>	<i>Stenotaphrum oostachyum</i>	Baker	MSV1042_Stenotaphrum_oostachyum
<i>Stenotaphrum unilaterale</i>	<i>Stenotaphrum unilaterale</i>	Baker	MSV1043_Stenotaphrum_unilaterale
<i>Stypeiochloa hitchcockii</i>	<i>Stypeiochloa hitchcockii</i>	(A.Camus) Cope	MSV993_Stypeiochloa_hitchcockii
<i>Themeda quadrivalvis</i>	<i>Themeda quadrivalvis</i>	(L.) Kuntze	MSV350_Themeda_quadrivalvis
<i>Thuarea involuta</i>	<i>Thuarea involuta</i>	(G.Forst.) R.Br. ex Sm.	Thuarea_involuta
<i>Thuarea perrieri</i>	<i>Thuarea perrieri</i>	A.Camus	40751_Thuarea_perrieri

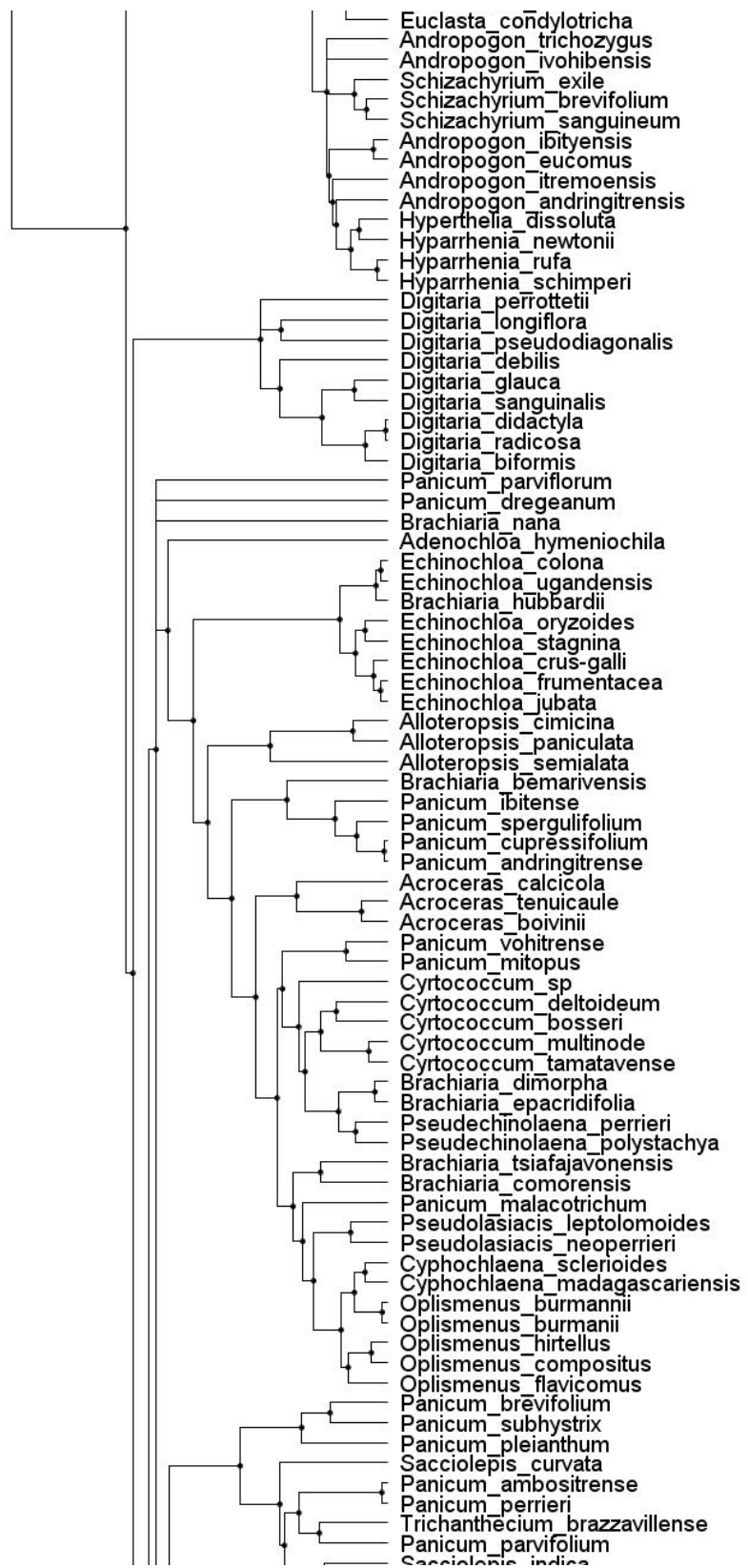
<i>Trachypogon spicatus</i>	<i>Trachypogon spicatus</i>	(L.f.) Kuntze	RGD192_ <i>Trachypogon spicatus</i>
<i>Tragus berteronianus</i>	<i>Tragus berteronianus</i>	Schult.	NOP205_ <i>Tragus berteronianus</i>
<i>Trichantheium brazzavillense</i>	<i>Trichantheium brazzavillense</i>	(Franch.) Zuloaga & Morrone	MSV1001_ <i>Trichantheium brazzavillense</i>
<i>Tricholaena monachne</i>	<i>Tricholaena monachne</i>	(Trin.) Stapf & C.E.Hubb.	<i>Tricholaena monachne</i>
<i>Trichopteryx dregeana</i>	<i>Trichopteryx dregeana</i>	Nees ex Lindl.	RGD187_ <i>Trichopteryx dregeana</i>
<i>Trisetopsis milanjana</i>	<i>Trisetopsis milanjana</i>	(Rendle) Röser & A.Wölk	Added at the midpoint of the branch leading to the <i>Trisetopsis galpinii</i> tip
<i>Tristachya humbertii</i>	<i>Tristachya humbertii</i>	A.Camus	MSV1369_ <i>Tristachya humbertii</i>
<i>Tristachya isalensis</i>	<i>Tristachya isalensis</i>	(A.Camus) Voronts. & Rakotom.	MSV1370_ <i>Tristachya isalensis</i> in ed.
<i>Urelytrum agropyroides</i>	<i>Urelytrum agropyroides</i>	(Hack.) Hack.	RGD184_ <i>Urelytrum agropyroides</i>
<i>Urochloa eminii</i>	<i>Urochloa eminii</i>	(Mez) Davidse	Added as a sister taxon to the MRCA of the 35 tips belonging to the genus <i>Urochloa</i> in the Hackel <i>et al</i> tree.
<i>Urochloa panicoides</i>	<i>Urochloa panicoides</i>	P.Beauv.	<i>Urochloa panicoides</i>
<i>Urochloa trichopus</i>	<i>Urochloa trichopus</i>	(Hochst.) Stapf	<i>Urochloa trichopus</i>
<i>Viguierella madagascariensis</i>	<i>Viguierella madagascariensis</i>	A.Camus	MSV966_ <i>Viguierella madagascariensis</i>

<i>Yvesia</i> <i>madagascariensis</i>	<i>Yvesia</i> <i>madagascariensis</i>	<i>A. Camus</i>	MSV957_Yvesia_madagascariensi s

Phylogeny







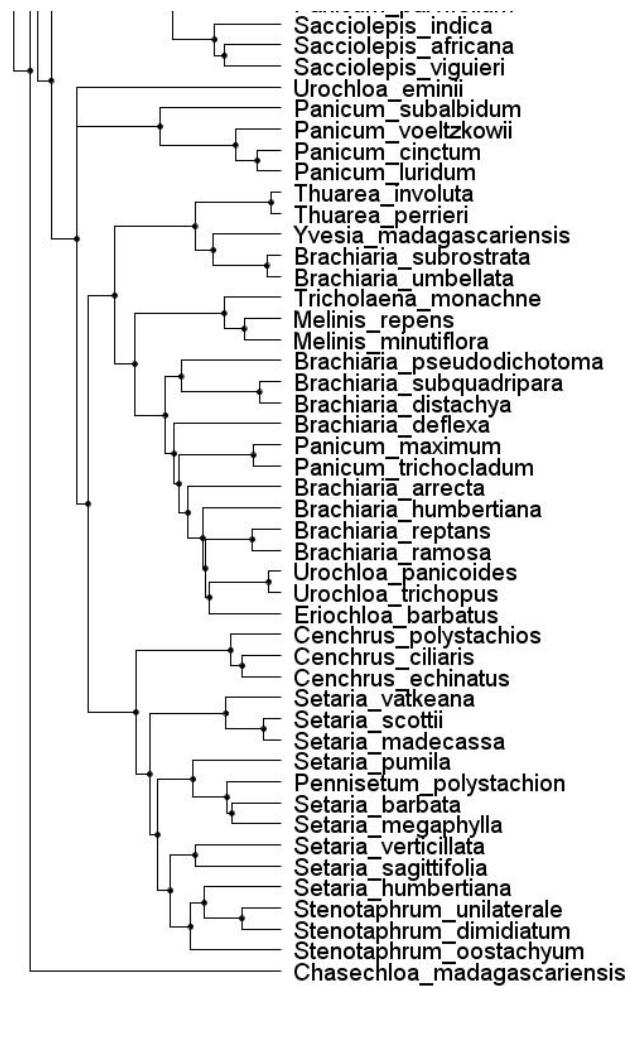


Figure S3.4. Trimmed, time-calibrated phylogenetic tree of 260 Malagasy grass species included in this study, based on Hackel et al. (2018).

Trait-environmental model outputs

Table S3.2. *Trait-environment relationship model outputs for all 32 models within the inflorescence height model family.* Models are ranked by AIC, with lower values indicating better model fit. Coefficients for environmental predictors, along with their significance levels, are provided for each model. Log-likelihood, maximum likelihood R^2 , predicted R^2 , AIC weights, and accumulated AIC weights are also included to assess model support. Significant predictors ($P < 0.05$) are indicated with: 0-0.001 = ***, 0.001-0.01 = **, 0.01-0.05 = *, and 0.05-0.1 = . .

Model	Intercept	Mean Annual Temperature (°C)	Yearly Mean Burned Area (km ² year ⁻¹)	Global Human Modification Index	Percent Sand at 5-15cm (%)	Aridity Index	AIC	Log Likelihood	Max Likelihood R^2	Predicted R^2	AIC weights	Accumulated AIC weights
28	3.469***	0.026*	0.296*		-0.007*	-0.182	1898.274	-939.137	0.578	0.779	0.32	0.32
31	3.471***	0.026*	0.295*	-0.024	-0.007*	-0.184	1898.764	-938.382	0.578	0.778	0.251	0.571
17	3.266***	0.027*	0.306*		-0.006.		1900.662	-941.331	0.577	0.778	0.097	0.668
26	3.267***	0.027*	0.306*	-0.007	-0.006.		1901.169	-940.584	0.577	0.778	0.075	0.744
18	3.255***	0.018.	0.239*			-0.118	1901.877	-941.939	0.576	0.781	0.053	0.797
27	3.258***	0.019.	0.237*	-0.029		-0.119	1902.378	-941.189	0.577	0.781	0.041	0.838
6	3.136***	0.02*	0.258*				1903.569	-943.784	0.575	0.781	0.023	0.86
21	3.473***	0.022.			-0.005	-0.2	1903.811	-942.906	0.576	0.777	0.02	0.881
16	3.137***	0.02*	0.256*	-0.02			1904.089	-943.044	0.576	0.781	0.018	0.898
29	3.479***	0.023.		-0.064	-0.005	-0.203	1904.178	-942.089	0.576	0.777	0.017	0.915
24	3.98***		0.249*		-0.005	-0.206.	1904.435	-943.217	0.576	0.778	0.015	0.93
30	3.977***		0.251*	0.021	-0.005	-0.205	1904.886	-942.443	0.576	0.778	0.012	0.941
9	3.312***	0.017				-0.152	1905.653	-944.827	0.575	0.779	0.008	0.949
12	3.721***		0.218.			-0.158	1905.762	-944.881	0.575	0.781	0.008	0.957

Model	Intercept	Mean Annual Temperature (°C)	Yearly Mean Burned Area (km ² year ⁻¹)	Global Human Modification Index	Percent Sand at 5-15cm (%)	Aridity Index	AIC	Log Likelihood	Max Likelihood R ²	Predicted R ²	AIC weights	Accumulated AIC weights
20	3.318***	0.017		-0.063		-0.154	1906.038	-944.019	0.575	0.779	0.007	0.963
23	3.719***		0.219.	0.006		-0.158	1906.248	-944.124	0.575	0.78	0.006	0.969
8	3.256***	0.023*			-0.004		1906.571	-945.285	0.575	0.776	0.005	0.974
19	3.258***	0.024*		-0.046	-0.004		1906.992	-944.496	0.575	0.776	0.004	0.979
11	3.784***		0.257*		-0.003		1907.48	-945.74	0.574	0.777	0.003	0.982
22	3.776***		0.26*	0.042	-0.003		1907.892	-944.946	0.575	0.777	0.003	0.984
1	3.165***	0.019.					1908.014	-947.007	0.574	0.779	0.002	0.987
2	3.624***		0.236*				1908.433	-947.217	0.574	0.779	0.002	0.989
7	3.169***	0.019.		-0.051			1908.437	-946.219	0.574	0.778	0.002	0.991
15	3.915***				-0.003	-0.217.	1908.447	-946.224	0.574	0.777	0.002	0.993
25	3.919***			-0.019	-0.003	-0.218.	1908.871	-945.435	0.574	0.777	0.002	0.994
10	3.618***		0.238*	0.026			1908.9	-946.45	0.574	0.779	0.002	0.996
5	3.736***					-0.183	1908.956	-947.478	0.573	0.779	0.002	0.998
14	3.743***			-0.026		-0.185	1909.386	-946.693	0.574	0.779	0.001	0.999
4	3.711***				-0.002		1911.734	-948.867	0.573	0.775	0	0.999
32	3.625***						1912.164	-950.082	0.572	0.777	0	0.999
13	3.71***			0.004	-0.002		1912.165	-948.083	0.573	0.775	0	1
3	3.626***			-0.004			1912.61	-949.305	0.572	0.777	0	1

Table S3.3. **Trait-environment relationship model outputs for all 32 models within the culm diameter model family.** Models are ranked by AIC, with lower values indicating better model fit. Coefficients for environmental predictors, along with their significance levels, are provided for

each model. Log-likelihood, maximum likelihood R^2 , predicted R^2 , AIC weights, and accumulated AIC weights are also included to assess model support. Significant predictors ($P < 0.05$) are indicated with: 0-0.001 = ***, 0.001-0.01 = **, 0.01-0.05 = *, and 0.05-0.1 = . .

Model	Intercept	Mean Annual Temperature (°C)	Yearly Mean Burned Area (km ² year ⁻¹)	Global Human Modification Index	Percent Sand at 5-15cm (%)	Aridity Index	AIC	Log Likelihood	Max Likelihood R^2	Predicted R^2	AIC weights	Accumulated AIC weights
31	-2.337***	0.018.	0.214*	0.198	-0.004	-0.055	1329.853	-653.926	0.609	0.794	0.134	0.134
26	-2.396***	0.018*	0.216*	0.2	-0.004		1329.994	-654.997	0.609	0.795	0.125	0.259
28	-2.312***	0.019*	0.201.		-0.004	-0.061	1330.594	-655.297	0.608	0.793	0.093	0.352
17	-2.374***	0.019*	0.203*		-0.003		1330.774	-656.387	0.608	0.794	0.085	0.437
27	-2.444***	0.013	0.178.	0.189		-0.02	1331.056	-655.528	0.608	0.796	0.074	0.51
16	-2.447***	0.013.	0.183.	0.187			1331.285	-656.643	0.608	0.797	0.066	0.576
18	-2.408***	0.014.	0.168.			-0.023	1331.662	-656.831	0.608	0.796	0.054	0.63
6	-2.404***	0.013.	0.173.				1331.862	-657.931	0.607	0.797	0.049	0.679
10	-2.112***		0.182*	0.17			1333.322	-658.661	0.607	0.798	0.024	0.703
29	-2.327***	0.015		0.167	-0.003	-0.068	1333.52	-656.76	0.608	0.793	0.021	0.725
23	-2.1***		0.168.	0.193		-0.046	1333.58	-657.79	0.607	0.798	0.021	0.745
20	-2.399***	0.012		0.164		-0.045	1333.653	-657.826	0.607	0.795	0.02	0.766
2	-2.071***		0.17.				1333.738	-659.869	0.606	0.798	0.019	0.785
19	-2.404***	0.015.		0.17	-0.002		1333.819	-657.91	0.607	0.794	0.018	0.803
21	-2.305***	0.016.			-0.002	-0.072	1333.82	-657.91	0.607	0.793	0.018	0.822
22	-2.071***		0.192*	0.17	-0.001		1333.825	-657.913	0.607	0.798	0.018	0.84
30	-2.005***		0.178.	0.214	-0.002	-0.069	1333.872	-656.936	0.608	0.797	0.018	0.858
9	-2.373***	0.013				-0.048	1333.914	-658.957	0.607	0.795	0.018	0.876
12	-2.052***		0.163.			-0.03	1334.114	-659.057	0.607	0.798	0.016	0.892

Model	Intercept	Mean Annual Temperature (°C)	Yearly Mean Burned Area (km ² year ⁻¹)	Global Human Modification Index	Percent Sand at 5-15cm (%)	Aridity Index	AIC	Log Likelihood	Max Likelihood R ²	Predicted R ²	AIC weights	Accumulated AIC weights
7	-2.433***	0.013		0.164			1334.132	-659.066	0.607	0.795	0.016	0.907
8	-2.384***	0.016.			-0.002		1334.157	-659.078	0.607	0.794	0.016	0.923
11	-2.027***		0.179*		-0.001		1334.237	-659.118	0.607	0.798	0.015	0.938
1	-2.404***	0.013.					1334.387	-660.193	0.606	0.796	0.014	0.952
24	-1.967***		0.175.		-0.001	-0.045	1334.642	-658.321	0.607	0.798	0.012	0.964
14	-2.085***			0.18		-0.07	1335.923	-659.962	0.606	0.796	0.006	0.971
5	-2.034***					-0.07	1336.418	-661.209	0.606	0.797	0.005	0.976
25	-2.039***			0.185	-0.001	-0.079	1336.498	-659.249	0.606	0.796	0.005	0.981
32	-2.054***						1336.696	-662.348	0.605	0.797	0.004	0.985
3	-2.127***			0.179			1336.738	-661.369	0.605	0.797	0.004	0.989
13	-2.133***			0.185	0		1336.976	-660.488	0.606	0.796	0.004	0.993
15	-2.005***				-0.001	-0.078	1337.072	-660.536	0.606	0.797	0.004	0.997
4	-2.098***				0.001		1337.268	-661.634	0.605	0.798	0.003	1

*Table S3.4. **Trait-environment relationship model outputs for all 32 models within the leaf length model family.** Models are ranked by AIC, with lower values indicating better model fit. Coefficients for environmental predictors, along with their significance levels, are provided for each model. Log-likelihood, maximum likelihood R², predicted R², AIC weights, and accumulated AIC weights are also included to assess model support. Significant predictors ($P < 0.05$) are indicated with: 0-0.001 = ***, 0.001-0.01 = **, 0.01-0.05 = *, and 0.05-0.1 = . .*

Model	Intercept	Mean Annual Temperature (°C)	Yearly Mean Burned Area (km ² year ⁻¹)	Global Human Modification Index	Percent Sand at 5-15cm (%)	Aridity Index	AIC	Log Likelihood	Max Likelihood R ²	Predicted R ²	AIC weights	Accumulated AIC weights
28	2.452***	0.013	0.157		-0.009*	-0.153	2454.641	-1217.32	0.651	0.818	0.151	0.151
31	2.46***	0.014	0.153	-0.064	-0.009*	-0.154	2454.743	-1216.37	0.651	0.818	0.143	0.294
21	2.456***	0.011			-0.008*	-0.159	2455.937	-1218.97	0.65	0.818	0.079	0.373
29	2.468***	0.012		-0.085	-0.008*	-0.161	2455.969	-1217.98	0.65	0.818	0.078	0.45
17	2.287***	0.015	0.163		-0.009*		2456.142	-1219.07	0.65	0.816	0.071	0.521
26	2.29***	0.016	0.161	-0.044	-0.009*		2456.265	-1218.13	0.65	0.816	0.067	0.588
24	2.703***		0.133		-0.008.	-0.187	2456.742	-1219.37	0.65	0.819	0.053	0.641
30	2.714***		0.129	-0.053	-0.008.	-0.189	2456.848	-1218.42	0.65	0.819	0.05	0.691
8	2.286***	0.013			-0.007.		2457.527	-1220.76	0.649	0.816	0.036	0.727
19	2.29***	0.013		-0.064	-0.007.		2457.6	-1219.8	0.649	0.816	0.034	0.761
15	2.673***				-0.007.	-0.188	2457.765	-1220.88	0.649	0.819	0.032	0.792
25	2.689***			-0.074	-0.007.	-0.19	2457.797	-1219.9	0.649	0.819	0.031	0.824
11	2.568***		0.135		-0.007.		2458.709	-1221.35	0.649	0.816	0.02	0.843
22	2.571***		0.134	-0.018	-0.007.		2458.829	-1220.42	0.649	0.816	0.019	0.862
18	2.119***	0.006	0.09			-0.088	2459.494	-1220.75	0.649	0.819	0.013	0.875
27	2.132***	0.006	0.086	-0.085		-0.089	2459.545	-1219.77	0.649	0.819	0.013	0.888
4	2.528***				-0.006		2459.783	-1222.89	0.648	0.816	0.012	0.9
13	2.534***			-0.04	-0.006		2459.862	-1221.93	0.649	0.816	0.011	0.911
9	2.151***	0.005				-0.097	2459.905	-1221.95	0.649	0.819	0.011	0.922
20	2.163***	0.005		-0.095		-0.098	2459.911	-1220.96	0.649	0.819	0.011	0.932
12	2.266***		0.084			-0.109	2460.479	-1222.24	0.648	0.819	0.008	0.94
23	2.284***		0.079	-0.076		-0.11	2460.528	-1221.26	0.649	0.819	0.008	0.948

Model	Intercept	Mean Annual Temperature (°C)	Yearly Mean Burned Area (km ² year ⁻¹)	Global Human Modification Index	Percent Sand at 5-15cm (%)	Aridity Index	AIC	Log Likelihood	Max Likelihood R ²	Predicted R ²	AIC weights	Accumulated AIC weights
6	2.019***	0.008	0.102				2460.727	-1222.36	0.648	0.818	0.007	0.956
16	2.026***	0.008	0.099	-0.081			2460.788	-1221.39	0.649	0.818	0.007	0.963
14	2.296***			-0.088		-0.117	2460.895	-1222.45	0.648	0.819	0.007	0.969
5	2.274***					-0.116	2460.908	-1223.45	0.648	0.819	0.007	0.976
1	2.048***	0.007					2461.239	-1223.62	0.648	0.818	0.006	0.981
7	2.056***	0.007		-0.089			2461.26	-1222.63	0.648	0.818	0.006	0.987
2	2.196***		0.092				2462.014	-1224.01	0.648	0.818	0.004	0.991
10	2.212***		0.089	-0.063			2462.09	-1223.05	0.648	0.818	0.004	0.994
32	2.202***						2462.523	-1225.26	0.647	0.818	0.003	0.997
3	2.219***			-0.074			2462.546	-1224.27	0.648	0.818	0.003	1

*Table S3.5. **Trait-environment relationship model outputs for all 32 models within the leaf width model family.** Models are ranked by AIC, with lower values indicating better model fit. Coefficients for environmental predictors, along with their significance levels, are provided for*

each model. Log-likelihood, maximum likelihood R^2 , predicted R^2 , AIC weights, and accumulated AIC weights are also included to assess model support. Significant predictors ($P < 0.05$) are indicated with: 0-0.001 = ***, 0.001-0.01 = **, 0.01-0.05 = * , and 0.05-0.1 = . .

Model	Intercept	Mean Annual Temperature (°C)	Yearly Mean Burned Area (km ² year ⁻¹)	Global Human Modification Index	Percent Sand at 5-15cm (%)	Aridity Index	AIC	Log Likelihood	Max Likelihood R ²	Predicted R ²	AIC weights	Accumulated AIC weights
31	-0.708.	0.02***	0.195*	-0.208	-0.008**	-0.132.	1342.077	-660.039	0.716	0.866	0.356	0.356
28	-0.755.	0.021**	0.209*		-0.009**	-0.135.	1343.065	-661.532	0.715	0.866	0.217	0.572
26	-1.001*	0.028***	0.202*	-0.212	-0.008**		1343.62	-661.81	0.715	0.865	0.164	0.737
17	-1.033**	0.027***	0.215*		-0.008**		1344.63	-663.315	0.715	0.865	0.099	0.836
29	-0.794.	0.023**		-0.24	-0.008**	-0.13	1345.42	-662.71	0.715	0.865	0.067	0.903
21	-0.833*	0.022**			-0.008**	-0.132	1347.002	-664.501	0.714	0.865	0.03	0.933
19	-1.013*	0.026**		-0.24	-0.007*		1347.054	-664.527	0.714	0.864	0.03	0.963
8	-1.049*	0.026**			-0.007*		1348.571	-666.285	0.714	0.864	0.014	0.976
16	-1.196***	0.019***	0.137	-0.224			1350.861	-666.431	0.714	0.865	0.004	0.981
27	-1.199***	0.019***	0.137	-0.224		0.001	1351.545	-665.773	0.714	0.865	0.003	0.984
6	-1.237***	0.019***	0.153.				1352.188	-668.094	0.713	0.865	0.002	0.986
7	-1.155**	0.018***		-0.25.			1352.356	-668.178	0.713	0.865	0.002	0.988
30	-0.286		0.14	-0.169	-0.007**	-0.188*	1352.512	-666.256	0.714	0.865	0.002	0.99
20	-1.13**	0.018*		-0.24		-0.044	1352.725	-667.363	0.713	0.865	0.002	0.992
18	-1.215***	0.018**	0.148			-0.014	1352.85	-667.425	0.713	0.865	0.002	0.994
24	-0.308		0.153		-0.008**	-0.194**	1352.874	-667.437	0.713	0.866	0.002	0.995
25	-0.313			-0.197	-0.006*	-0.189*	1354.019	-668.009	0.713	0.865	0.001	0.996
1	-1.196***	0.017***					1354.279	-670.14	0.712	0.865	0.001	0.997
9	-1.167**	0.017*				-0.047	1354.296	-669.148	0.713	0.865	0.001	0.998

Model	Intercept	Mean Annual Temperature (°C)	Yearly Mean Burned Area (km ² year ⁻¹)	Global Human Modification Index	Percent Sand at 5-15cm (%)	Aridity Index	AIC	Log Likelihood	Max Likelihood R ²	Predicted R ²	AIC weights	Accumulated AIC weights
15	-0.347				-0.007*	-0.196**	1354.878	-669.439	0.713	0.865	0.001	0.998
22	-0.485		0.141	-0.163	-0.005.		1355.704	-668.852	0.713	0.863	0	0.999
11	-0.511		0.153		-0.006*		1355.978	-669.989	0.712	0.862	0	0.999
13	-0.518			-0.186	-0.004		1357.107	-670.554	0.712	0.862	0	0.999
4	-0.551				-0.005.		1357.732	-671.866	0.712	0.862	0	0.999
23	-0.709.		0.086	-0.19		-0.082	1358.164	-670.082	0.712	0.864	0	1
14	-0.695.			-0.205		-0.092	1358.338	-671.169	0.712	0.864	0	1
12	-0.757*		0.099			-0.079	1358.848	-671.424	0.712	0.864	0	1
10	-0.756*		0.096	-0.184			1359.18	-671.59	0.712	0.863	0	1
5	-0.746*					-0.089	1359.3	-672.65	0.711	0.864	0	1
3	-0.746*			-0.199			1359.545	-672.772	0.711	0.863	0	1
2	-0.801*		0.107				1359.761	-672.881	0.711	0.863	0	1
32	-0.794*						1360.385	-674.192	0.711	0.863	0	1

Table S3.6. **Trait-environment relationship model outputs for all 32 models within the leaf thickness model family.** Models are ranked by AIC, with lower values indicating better model fit. Coefficients for environmental predictors, along with their significance levels, are provided for

each model. Log-likelihood, maximum likelihood R^2 , predicted R^2 , AIC weights, and accumulated AIC weights are also included to assess model support. Significant predictors ($P < 0.05$) are indicated with: 0-0.001 = ***, 0.001-0.01 = **, 0.01-0.05 = *, and 0.05-0.1 = . .

Model	Intercept	Mean Annual Temperature (°C)	Yearly Mean Burned Area (km ² year ⁻¹)	Global Human Modification Index	Percent Sand at 5-15cm (%)	Aridity Index	AIC	Log Likelihood	Max Likelihood R ²	Predicted R ²	AIC weights	Accumulated AIC weights
29	-1.902***	-0.023*		-0.168	0.005	-0.195	1572.889	-776.445	0.515	0.739	0.14	0.14
31	-1.899***	-0.023*	0.006	-0.168	0.005	-0.194	1573.054	-775.527	0.515	0.739	0.129	0.27
21	-1.936***	-0.024*			0.005	-0.193	1573.197	-777.599	0.514	0.74	0.12	0.39
28	-1.922***	-0.024*	0.016		0.005	-0.189	1573.358	-776.679	0.515	0.739	0.111	0.501
20	-1.746***	-0.019.		-0.167		-0.237.	1574.583	-778.291	0.514	0.739	0.06	0.561
27	-1.752***	-0.019.	0.049	-0.162		-0.229.	1574.65	-777.325	0.514	0.739	0.058	0.619
9	-1.774***	-0.02.				-0.235.	1574.883	-779.441	0.513	0.739	0.052	0.671
18	-1.778***	-0.02.	0.058			-0.225.	1574.888	-778.444	0.514	0.739	0.052	0.723
19	-2.054***	-0.024*		-0.156	0.006.		1575.354	-778.677	0.514	0.739	0.041	0.764
26	-2.05***	-0.024*	0.012	-0.155	0.006		1575.469	-777.735	0.514	0.739	0.039	0.802
8	-2.068***	-0.025*			0.006.		1575.572	-779.786	0.513	0.739	0.037	0.839
17	-2.058***	-0.025*	0.022		0.006		1575.671	-778.836	0.514	0.738	0.035	0.874
25	-2.38***			-0.201	0.003	-0.19	1577.866	-779.933	0.513	0.74	0.012	0.886
30	-2.367***		0.043	-0.198	0.002	-0.185	1577.917	-778.959	0.513	0.74	0.011	0.897
23	-2.225***		0.063	-0.192		-0.208.	1578.164	-780.082	0.513	0.739	0.01	0.907
14	-2.218***			-0.199		-0.217.	1578.237	-781.118	0.512	0.74	0.01	0.917
16	-1.893***	-0.018	0.066	-0.147			1578.357	-780.179	0.513	0.738	0.009	0.926
7	-1.886***	-0.018		-0.154			1578.467	-781.234	0.512	0.738	0.009	0.934
6	-1.905***	-0.019.	0.074				1578.484	-781.242	0.512	0.737	0.009	0.943

Model	Intercept	Mean Annual Temperature (°C)	Yearly Mean Burned Area (km ² year ⁻¹)	Global Human Modification Index	Percent Sand at 5-15cm (%)	Aridity Index	AIC	Log Likelihood	Max Likelihood R ²	Predicted R ²	AIC weights	Accumulated AIC weights
24	-2.422***		0.057		0.002	-0.191.	1578.494	-780.247	0.513	0.74	0.009	0.951
15	-2.44***				0.003	-0.197.	1578.517	-781.258	0.512	0.741	0.008	0.96
1	-1.897***	-0.019.					1578.667	-782.334	0.511	0.738	0.008	0.968
12	-2.281***		0.075			-0.21*	1578.687	-781.343	0.512	0.74	0.008	0.975
5	-2.274***					-0.222*	1578.881	-782.44	0.511	0.741	0.007	0.982
22	-2.514***		0.049	-0.199	0.003		1580.294	-781.147	0.512	0.738	0.003	0.986
13	-2.531***			-0.206	0.004		1580.345	-782.173	0.511	0.738	0.003	0.989
11	-2.562***		0.064		0.003		1580.949	-782.475	0.511	0.738	0.002	0.992
4	-2.586***				0.004		1581.116	-783.558	0.511	0.738	0.002	0.994
10	-2.333***		0.078	-0.188			1581.578	-782.789	0.511	0.738	0.002	0.996
3	-2.331***			-0.199			1581.846	-783.923	0.51	0.738	0.002	0.997
2	-2.388***		0.091				1582.107	-784.053	0.51	0.737	0.001	0.999
32	-2.388***						1582.531	-785.265	0.51	0.738	0.001	1

Table S3.7. Trait-environment relationship model outputs for all 32 models within the leaf nitrogen model family. Models are ranked by AIC, with lower values indicating better model fit. Coefficients for environmental predictors, along with their significance levels, are provided for each model. Log-likelihood, maximum likelihood R², predicted R², AIC weights, and accumulated AIC weights are also included to assess model support. Significant predictors ($P < 0.05$) are indicated with: 0-0.001 = ***, 0.001-0.01 = **, 0.01-0.05 = *, and 0.05-0.1 = . .

Model	Intercept	Mean Annual Temperature (°C)	Yearly Mean Burned Area (km ² year ⁻¹)	Global Human Modification Index	Percent Sand at 5-15cm (%)	Aridity Index	AIC	Log Likelihood	Max Likelihood R ²	Predicted R ²	AIC weights	Accumulated AIC weights
32	0.549*						423.927	-205.963	0.293	0.439	0.075	0.075
4	0.732*				-0.004		423.932	-204.966	0.296	0.44	0.075	0.15
5	0.531*					0.037	424.492	-205.246	0.295	0.437	0.057	0.206
1	0.629.	-0.003					424.528	-205.264	0.295	0.438	0.056	0.262
8	0.728*	0			-0.004		424.528	-204.264	0.299	0.438	0.056	0.317
11	0.763*		0.096		-0.004		424.881	-204.441	0.298	0.438	0.047	0.364
15	0.742*				-0.004	-0.006	425.032	-204.516	0.298	0.438	0.043	0.407
9	0.602	-0.003				0.031	425.132	-204.566	0.298	0.436	0.041	0.448
2	0.553*		0.065				425.149	-205.574	0.294	0.438	0.041	0.489
17	0.736.	0.002	0.105		-0.004		425.444	-203.722	0.301	0.435	0.035	0.524
3	0.556*			-0.023			425.494	-205.747	0.294	0.439	0.034	0.558
13	0.731*			0.004	-0.004		425.499	-204.75	0.297	0.439	0.034	0.593
12	0.531.		0.075			0.044	425.61	-204.805	0.297	0.435	0.032	0.625
21	0.737.	0			-0.004	-0.005	425.663	-203.831	0.301	0.435	0.031	0.656
6	0.623.	-0.003	0.066				425.796	-204.898	0.297	0.436	0.029	0.686
24	0.769*		0.102		-0.004	-0.001	425.922	-203.961	0.3	0.435	0.028	0.713
14	0.538*			-0.023		0.036	426.049	-205.024	0.296	0.437	0.026	0.739
19	0.729*	0		-0.001	-0.004		426.152	-204.076	0.3	0.437	0.025	0.764
7	0.631.	-0.003		-0.015			426.152	-205.076	0.296	0.437	0.025	0.789
18	0.586	-0.002	0.077			0.039	426.302	-204.151	0.3	0.433	0.023	0.812
22	0.76*		0.099	0.024	-0.004		426.441	-204.22	0.299	0.438	0.021	0.833
28	0.736.	0.002	0.111		-0.004	0.002	426.51	-203.255	0.303	0.433	0.021	0.854

Model	Intercept	Mean Annual Temperature (°C)	Yearly Mean Burned Area (km ² year ⁻¹)	Global Human Modification Index	Percent Sand at 5-15cm (%)	Aridity Index	AIC	Log Likelihood	Max Likelihood R ²	Predicted R ²	AIC weights	Accumulated AIC weights
25	0.742*			0	-0.004	-0.005	426.589	-204.295	0.299	0.437	0.02	0.873
10	0.556*		0.064	-0.013			426.733	-205.366	0.295	0.438	0.018	0.892
20	0.604	-0.003		-0.018		0.031	426.747	-204.374	0.299	0.435	0.018	0.91
26	0.736.	0.002	0.107	0.016	-0.004		427.045	-203.522	0.302	0.435	0.016	0.926
23	0.535.		0.076	-0.012		0.044	427.182	-204.591	0.298	0.435	0.015	0.941
29	0.738.	0		-0.005	-0.004	-0.005	427.283	-203.642	0.301	0.435	0.014	0.955
16	0.624.	-0.003	0.066	-0.007			427.414	-204.707	0.297	0.436	0.013	0.968
30	0.766*		0.104	0.02	-0.004	0	427.475	-203.737	0.301	0.435	0.013	0.981
27	0.588	-0.002	0.077	-0.009		0.039	427.913	-203.956	0.3	0.433	0.01	0.991
31	0.736.	0.002	0.113	0.012	-0.004	0.002	428.113	-203.056	0.304	0.432	0.009	1

Trait coordination

Table S3.8. Regression coefficients and phylogenetic signal (d) values from Pearson's correlation analysis, including phylogeny. Estimates represent the relationship between trait variation while accounting for shared evolutionary history. P-values indicate statistical significance, with values <0.001 denoted with '***'. Phylogenetic signal (d) values indicate the extent to which each trait is constrained by phylogeny, with lower values suggesting weaker evolutionary constraints.

	Estimate	Standard Error	Z-score	P-value	Phylogenetic Signal (d)
Logged Culm Diameter (cm)	-2.118	0.047	-44.841	<0.001***	0.043
Logged Inflorescence Height (cm)	3.697	0.058	63.288	<0.001***	0.089
Logged Leaf Thickness (mm)	-2.581	0.042	-60.836	<0.001***	0.027
Logged Leaf Length (cm)	1.994	0.071	28.152	<0.001***	0.167
Logged Leaf Width (cm)	-1.054	0.054	-19.404	<0.001***	0.180
Logged Leaf Nitrogen (%)	0.347	0.043	8.031	<0.001***	0.048

Chapter 4: Intraspecific trait variation drives functional shifts in grass communities under grazing in the Scottish uplands

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Abstract

Shifting grazing regimes across Europe are altering temperate grasslands, affecting biodiversity and ecosystem services such as water filtration, nutrient cycling, and carbon sequestration. While grazing influences the structure of these grasslands, and thus the distribution of functional traits, the relative role of species turnover versus intraspecific variation (ITV) in governing trait variation of temperate grasslands is poorly understood. Improved understanding of the dynamics between species turnover and ITV with grazing regimes can enhance predictions of how grazing management influences grassland ecosystems and inform land management and conservation strategies.

We investigated the impacts of grazing on the composition and structure of grass communities within a 20-year landscape-level grazing experiment in the Scottish Uplands. Grazing intensity was manipulated through the addition or removal of sheep across three grazing treatments with replication in three locations with two drainage levels and data collected on grass composition and seven grass functional traits that represent grazing adaptations. Multivariate abundance models were fitted to determine the effect of grazing treatment, location, and plot drainage on grass community composition. We used phylogenetic linear mixed models (PLMM) to test for trait differences between plots, expecting high grazing to shift grasses towards grazing resistance (e.g. short stature, small, thin leaves) and tolerance (e.g. increased SLA, leaf nutrient contents) strategies. Grass community trait variation was decomposed to examine the relative roles of species turnover and ITV in trait responses to grazing intensities and environmental variables.

Compositional differences between plots were largely due to differences in the relative abundance of two widespread species, *Molina caerulea* and *Nardus stricta*, driven by plot location, with a marginal effect of grazing treatment. Grazing reduced plant height, leaf size and mass while increasing leaf thickness and specific leaf area. Despite compositional shifts, ITV accounted for most trait variation in response to grazing, indicating that community-level functional changes occur primarily through within-species trait adjustments rather than species turnover. The high ITV observed suggests that these

grasslands exhibit community resilience to grazing disturbances. Recognising the role of ITV in grass community responses will improve predictions of how changes in grazing management impact Scottish grassy ecosystems, informing grassland management and conservation strategies.

Keywords: plant functional traits, grazing adaptations, species turnover, community assembly, grasslands

Introduction

Over the past decades, European grasslands have changed substantially due to altered grazing regimes (Habel et al., 2013; Török et al., 2018). Grazing removal, often referred to as agricultural abandonment, can reduce plant species diversity and promote taller herbaceous or woody species, potentially resulting in grassland conversion into scrub or woodland (De Bello et al., 2006; Kuiters & Slim, 2003; Marriott et al., 2009). Conversely, intensified grazing suppresses less grazing-tolerant species (Olf & Ritchie, 1998), can increase bare ground (R. Evans, 1997), and alters plant species richness (Fischer & Wipf, 2002; Metera et al., 2010; Tóth et al., 2018). Altered grazing regimes can have profound effects on grassland-associated biodiversity, including arthropods (Littlewood et al., 2012; Morris, 2000), small mammals (Morgia et al., 2015; Schmidt et al., 2005), birds (D. M. Evans et al., 2006; Laiolo et al., 2004) and vegetation (Bullock & Pakeman, 1997; Hill et al., 1992), and key ecosystem services such water filtration, nutrient cycling, and carbon sequestration (Ford et al., 2012; Smith et al., 2014). Further, grazing impacts can be highly context-specific, varying with climate and soils, productivity, grazer type and grazing history (Blair et al., 2013; Milchunas et al., 1988; Price et al., 2022). As such, manipulative, local-scale studies enable assessments of how different grazing managements shape grassland communities.

Scottish upland grasslands (i.e., at elevations above 200 m) are of high conservation value (Usher et al., 1988), playing a central role in the country's socioeconomic, cultural, and natural heritage (Orr et al., 2008; Ratcliffe, 2012; Thompson & Horsfield, 1997). Despite their long grazing history, improperly prescribed grazing has already degraded these ecosystems, increasing soil erosion, decreasing biodiversity, reducing aquifer recharge, and increasing run-off (Hanley et al., 2008; Sansom, 1999). Climate change will likely amplify these impacts, impeding future restoration (Orr et al., 2008; Suding et al., 2004). In response, government-led initiatives such as the Agri-Environment Climate Scheme established in 2015 have promoted low-intensity grazing that supports biodiversity while maintaining economic benefits, resulting in varied grazing regimes across the landscape (MAFF, 1986; Scottish Government, 2025). As grazing regimes continue to shift across Scotland, there is a pressing need to understand how different grazing intensities shape vegetation structure and

composition in upland grassland communities, and to identify the underlying mechanisms driving these changes.

Grazing is a strong, multifaceted ecological filter, shaping species presence and functional trait variation within grassland communities (Díaz et al., 2007; W. Li et al., 2017). Functional traits- measurable morphological, physiological, or phenological attributes of individual plants- mediate species' ability to survive and reproduce under different environmental conditions (Violle et al., 2007). At the community level, changes in trait composition occur through (1) species turnover, where selection drives taxonomic composition towards species with trait values better suited to new environmental conditions and/or (2) intraspecific trait variation (ITV), where individuals within a species adjust trait values in response to environmental change through phenotypic plasticity or genetic variability (Ackerly & Cornwell, 2007; Albert et al., 2011; Kichenin et al., 2013; Lepš et al., 2011; Pigliucci, 2001).

The relative influence of species turnover and ITV reflect a community's resilience and resistance to environmental change and disturbance (Albert et al., 2011; Violle et al., 2012; Westerland et al., 2021). ITV is a predominant way individuals deal with biotic and abiotic gradients (Ackerly & Cornwell, 2007), and can be particularly important for responding to short-term, rapid change (Volf et al., 2016). High ITV within communities enhances resilience by allowing dominant species to persist by adjusting trait values rather than being replaced (Hou et al., 2019; Jung et al., 2010). However, species richness and environmental context mediate the balance between these mechanisms (Albert et al., 2011; Siefert et al., 2015). Species turnover tends to dominate in species-rich environments (Siefert et al., 2015; Violle et al., 2012), whereas historically grazed landscapes often exhibit lower turnover rates, suggesting ITV may be more advantageous in species-poor, long-grazed systems (Milchunas & Lauenroth, 1993; Niu et al., 2020; Skarpe, 1991). Because both species turnover and ITV drive functional changes at the community level, disentangling their relative roles requires examining how specific traits respond to varying grazing intensities.

Trait-based approaches are widely used to predict community and individual responses to environmental gradients and disturbances such as grazing (Díaz et al., 2001, 2004, 2007; Garnier et al., 2007; Lavorel et al., 2007; Pakeman, 2004). However, each functional trait does not function in isolation, instead forming dimensions of life history strategies, in which combinations of traits related to resource acquisition, disturbance tolerance and persistence influence a plant's ability to persist under different pressures (Laughlin, 2014; McGill et al., 2006).

In grasslands, species adopt varying strategies to avoid, tolerate or resist grazing pressures. While debate persists regarding which traits correspond to each adaptation (e.g. Briske, 1996; Pausas et al., 2017; Strauss & Agrawal, 1999), Archibald et al. (2019) defined three axes of grazing adaptation: avoidance, resistance, and tolerance. *Avoidance* traits reduce the likelihood of grazing by producing unpalatable structures less preferred by grazers, such as tougher leaves that are nutrient-poor and more tearing-resistant (e.g. high leaf carbon-to-nitrogen (leaf C:N), leaf thickness) and sparse architectures that limit biomass intake per bite (Archibald et al., 2019; Cornelissen et al., 1999; Coughenour, 1985; Grime et al., 1996). *Resistance* traits minimise defoliation impacts by limiting photosynthetic tissue loss through small stature, reduced leaf size and fragile structures (e.g. thin culms and leaves) that easily break, limiting the amount of biomass removed (Archibald et al., 2019; Drescher et al., 2006). *Tolerance* traits enhance recovery post-defoliation by promoting rapid regrowth (e.g. high leaf nutrients, high specific leaf area (SLA)), allowing grasses to quickly replace lost tissues, and flexible growth forms, enabling plants to shift between short and tall morphologies in response to grazing intensity to improve their competitive ability (Archibald et al., 2019; Díaz et al., 2001; Grime, 1994; Westoby, 1998). Successfully persisting under grazing likely requires combinations of avoidance, resistance, and tolerance traits, with the relative success of a strategy shaped by current and historical herbivory pressures and resource availability (Coley et al., 1985; Laliberté et al., 2012).

The balance between avoidance, resistance, and tolerance traits in response to changing grazing regimes influences a plant's survival and drives community trait dynamics. Under high-intensity grazing, previous studies suggest that traits shift towards strategies

allowing them to resist (e.g. short stature, small leaf area, thin culms and leaves, low leaf mass) and tolerate (e.g. increased SLA, leaf nutrient contents) grazing (Castillo-Garcia et al., 2022; Garnier et al., 2007; Lavorel et al., 2011) (Table 4.1). In contrast, no grazing releases grasses from grazing pressures, promoting traits such as increased plant height, leaf dimensions, and leaf carbon, in addition to decreased SLA (Pakeman & Marriott, 2010; Peco et al., 2005). These changes reflect a shift away from resource-acquisition strategies as, in the absence of grazing, plants can afford to invest in tougher, longer-lived aboveground structures that enhance their competitive abilities (De Bello et al., 2006; Garnier et al., 2007; Reich, 2014) (Table 4.1).

Table 4.1. *Hypothesised direction of trait shifts for our seven traits across grazing treatments.* Upwards arrows (green) indicate an increase in trait values while downwards arrows (red) indicate a decrease. Grey shading represents continuation grazing, which served as the reference condition.

	Inflorescence Height (cm)	Culm Diameter (cm)	Leaf Thickness (mm)	Leaf Area (cm ²)	Specific Leaf Area (g/cm ²)	Leaf Dry Mass (mg)	Leaf Carbon: Nitrogen (%)
High-intensity grazing	↓	↓	↓	↓	↑	↓	↓
Continuation grazing							
No grazing	↑	↑	↑	↑	↓	↑	↑

It is likely that not all plant functional traits are sensitive to grazing (Díaz et al., 2001; Ye et al., 2020). Traits such as grass height, leaf area, SLA, and leaf C:N ratios are most commonly reported to shift under different grazing pressures (Cornelissen et al., 2003; Díaz et al., 2001, 2007; McIntyre et al., 1999; Ye et al., 2020). Yet, the degree to which these traits are flexible within species, rather than shifting through species turnover, is not well understood. Whole plant-level traits, such as plant height, involving multiple plant organs

are generally more plastic than organ-level traits, such as leaf area, involving a specific, organ or isolated structure (Siefert et al., 2015). Gaining insight into whether grazing-induced trait shifts are primarily driven by ITV or species turnover can improve our understanding of how grazing shapes functional composition in Scottish grasslands.

Studies examining grazing-induced community shifts (e.g. Bullock et al., 2001; Lavorel et al., 2011; Li et al., 2017; Pakeman & Fielding, 2020) largely attribute changes to species turnover. However, ITV accounts for approximately 25% of total trait variation within communities and 32% among communities globally (Siefert et al., 2015), showing it to be a crucial yet often overlooked component of community assembly. As ITV increases with decreases in species richness, it is particularly important to include ITV when assessing community functional composition shifts in species-poor communities as it likely accounts for a larger proportion of total community functional diversity (Fajardo & Piper, 2011; Siefert et al., 2015; Violle et al., 2012). Previous studies report that ITV mediates community-level trait responses to grazing (Niu et al., 2016; Wang et al., 2023), yet its role within Scottish grasslands, where species pools are narrow, and grazing-induced compositional shifts are reported to be slow, remains unclear (Hulme et al., 1999; Pakeman et al., 2019; Ratcliffe, 2012). Therefore, incorporating ITV into trait-based analyses provides a more comprehensive understanding of how these grassland communities respond to disturbances, improving predictions of local community assembly processes (Albert et al., 2011; Jung et al., 2010; Siefert, 2012; Volf et al., 2016).

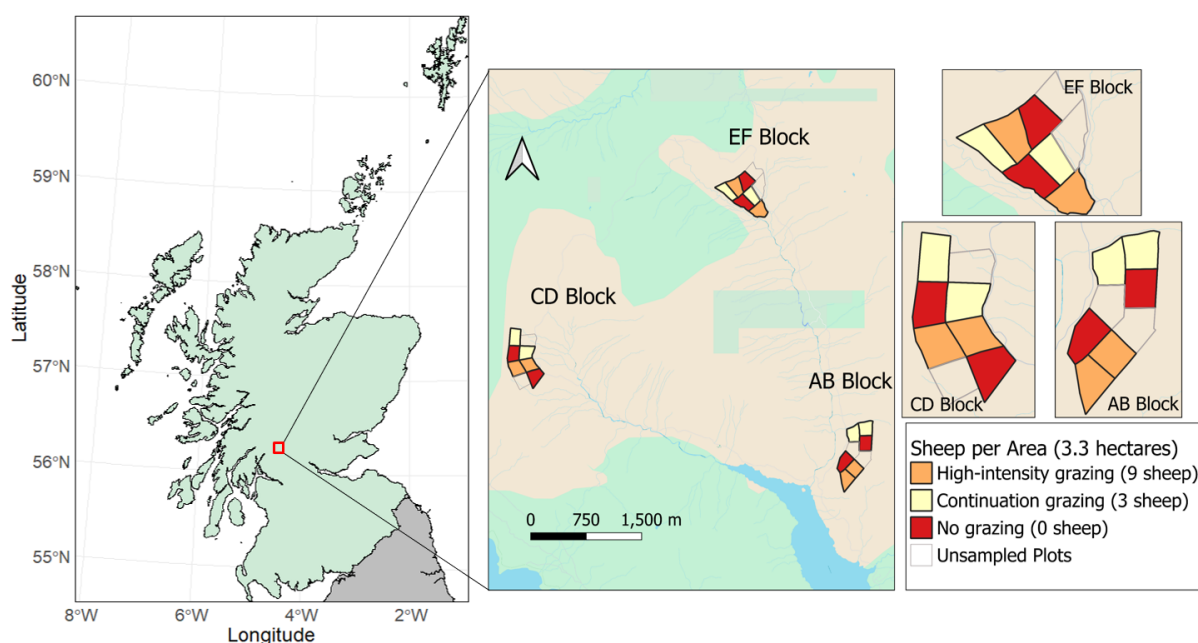
We used a 20-year grazing experiment in the Scottish Uplands to assess how grass communities change under different grazing treatments (high-intensity, continuation, no grazing) and how much of any structural changes are attributed to species turnover *versus* ITV. We focused on grasses (Poaceae) due to their long evolutionary history with grazing (Mack & Thompson, 1982; Owen & Wiegert, 1981). Additionally, concentrating on a single plant functional group minimised trait variability within sites, making patterns in trait variation more evident (Adler et al., 2004; Westoby et al., 2002). We measured seven functional traits related to avoidance, resistance, and tolerance of grazing: inflorescence height, culm diameter, leaf thickness, leaf area, specific leaf area (SLA), leaf dry mass, and

leaf carbon to nitrogen ratio (leaf C:N) (Archibald et al., 2019; Díaz et al., 2001, 2007). Specifically, we asked: (a) Does community composition change with grazing treatment? (b) Do trait values shift with grazing treatment? And do these trait shifts match expectations outlined in Table 4.1? and (c) Are differences in grass community functional composition driven by Intraspecific trait variation (ITV)?

Methods

Study location and site selection

Our study was located in Glen Finglas estate (56°16'N, 4°24'W) in the Southern Highlands, Scotland, UK (Figure 4.1), a 4039-ha estate with a long-term history of sheep and cattle grazing. The climate is cool and wet, with mean annual rainfall of 2230 mm and interpolated monthly mean temperature for January of 3.04 °C and for July of 14.12 °C (1981-2010) (Perry & Hollis, 2005). Soils are humus-iron podzols with peaty gleys (Soil Survey of Scotland Staff, 1981). Glen Finglas is a relatively species-poor environment, with only 19 grass species recorded in our study. The vegetation of the estate is a mosaic of upland (approx. 200 to 500 m elevation) unimproved plant communities that, based on the UK National Vegetation Classification (Rodwell, 1991, 1992) are: (1) Upland wet heathland - M15 *Scirpus cespitosus* (now *Trichophorum cespitosum*)–*Erica tetralix* wet heath , (2) Mire communities- M6 *Carex echinata*–*Sphagnum recurvum/auriculatum* (*Carex* mire), M23 *Juncus effusus/acutiflorus*–*Galium palustre*, and M25 *Molinia caerulea*–*Potentilla erecta* (merged with M23 into *Molinia* mire), (3) Acid grassland communities - U4 *Festuca ovina*–*Agrostis capillaris*–*Galium saxatile* (*Agrostis*–*Festuca* grassland), U5 *Nardus stricta*–*Galium saxatile* (*Nardus* grassland), and U20 *Pteridium aquilinum*–*Galium saxatile* (bracken).



Environmental Variable	Number of Levels	Levels	What does it capture?
Grazing Treatment	3	High, Continuation, No Grazing	Grazing effect
Block	3	AB, CD, EF	Topography, Aspect, Catchment, Soil Properties
Drainage	2	Uphill, Downhill	Soil Saturation

Figure 4.1. Map of study sites located within Glen Finglas, Scotland, showing three experimental blocks (AB, CD, EF), each divided into uphill and downhill subblocks (A–F). Within each subblock, three grazing treatments were applied: high-intensity grazing (orange), continuation grazing (yellow), and no grazing (red). The table (bottom) summarises the environmental variables, the number and names of levels within each, and the ecological factors they capture.

In 2003, the James Hutton Institute and SEFARI, with support from the Scottish Government, established a grazing management experiment that has now been implemented continuously for 22 years. The grazing experiment aims to assess grazing impacts on upland ecosystems and how impacts propagate through these ecosystems. The experiment comprises three blocks that represent different catchments and various aspects within the same larger watershed (AB, CD, EF). Each block is divided into uphill (B, C, F) and downhill (A, D, E) subblocks. Each subblock contains four 3.3 hectare plots, resulting in a

total of 24 plots (Figure 4.1). When the experiment was established, each plot within a subblock was randomly assigned to one of four grazing treatments: (1) high-intensity grazing, reflecting profit-driven management with nine sheep per plot (2.7 sheep/hectare); (2) continuation grazing, maintaining historical stocking rates of 3 sheep per plot (0.9 sheep/hectare) representing low-intensity grazing, and acted as a control (reference condition) for the experiment; (3) no grazing, to mimic agricultural abandonment; and (4) mixed grazing, consisting of 2 cows for 4 weeks in the autumn and 2 sheep during the full grazing period (0.6 sheep/hectare). Grazing occurred from May to November annually, with livestock removed from December to April and briefly during routine farming operations. For each treatment, there are six replicates based on the design (Figure 4.1).

To control for differences in foraging behaviour between cattle and sheep, we surveyed only grazing treatments with a consistent grazer type, removing potential grazer-specific effects. Treatments surveyed were high-intensity, continuation, and no grazing, with randomised subblocks and plots orders to minimise sampling bias. As each block differed in location, we assumed the block variable captured landscape-level environmental variation, including aspect, catchment, topography, and soil properties. Additionally, uphill and downhill subblocks were used to account for variation in soil saturation, hereafter referred to as drainage.

Within each plot, there were 25 fixed points marked on the intersections of a 40m-interval squared grid ($N_{\text{total}}=600$). We surveyed ten randomly selected fixed points per plot ($N_{\text{study}}=180$ across 18 plots) in July and August 2023, during the mid to late growing season.

Compositional surveys

The James Hutton Institute conducted compositional surveys (D. M. Evans et al., 2015; Pakeman et al., 2019; Pakeman & Fielding, 2020; Smith et al., 2014). At each of the ten fixed points within a plot, a five-pin vertical pin-frame was used to assess grass species abundance. The pin-frame was lowered through the vegetation, and all species touching a pin were identified and recorded. Species taxonomy follows Stace (2010). Species abundances were quantified as the total number of vegetation contacts per species across

all 50 pins per plot, giving plot level abundance per species. All composition surveys were conducted consistently downhill from the fixed point. Additionally, to allow for direct comparisons of species dominance between grazing treatments, the relative cover of each grass species was calculated as the proportion of vegetation contacts for that species divided by the total number of vegetation contacts for all species in that treatment.

Functional trait surveys

We measured seven traits selected based on their ecological significance in influencing plant survival, growth, and competition ability under grazing pressures and relevance to the grazing avoidance, resistance, and tolerance adaptation axes (Archibald et al., 2019): (1) *inflorescence height* (cm), indicating plant size and canopy position (Lehmann et al., 2019; Linder et al., 2018; Westoby et al., 2002); (2) *culm diameter* (mm), reflecting structural resistance to herbivory (Benvenutti et al., 2006, 2009; Drescher et al., 2006); (3) *leaf thickness* (mm), influencing digestibility and leaf longevity (Mediavilla et al., 2008; Wright et al., 2004); (4) *leaf dry mass* (mg), representing investment in leaf tissue (Pakeman et al., 2011; Wright et al., 2002); (5) *leaf area* (cm²), affecting light interception and post grazing-recovery (Crowley & Wingler, 2020); (6) *specific leaf area* (SLA; g/cm²), representing plant growth rates and resource-use efficiency (Cornelissen et al., 2003; Rees et al., 2010; Westoby et al., 2002; Westoby & Wright, 2006); and (7) *leaf carbon-to-nitrogen ratio* (leaf C:N), indicating leaf structural investment and palatability (Craine et al., 2002; Field et al., 1983; Grime et al., 1997; Reich et al., 1997; Westoby et al., 2002; Wright et al., 2004). Full details on trait selected, measurement methods, and ecological significance are provided in Table 4.2.

Table 4.2. Seven functional traits measured from grass individuals collected within each plot. Information provided on trait selected, measurement methods, ecological significance, and relevant literature.

Trait	Measurement Method	Ecological Significance	Relevant Literature
Inflorescence height (cm)	Measured as the distance from ground level to the top of the inflorescence using a ruler.	Indicates plant size and canopy position, influencing competition and light acquisition.	Lehmann et al., 2019; Linder et al., 2018; Westoby et al., 2002
Culm diameter (mm)	Measured at the thickest point of the second internode (including leaf sheath) on the tallest culm using digital callipers (± 0.01 mm).	Reflects structural resistance to herbivory by limiting the amount of plant material that can be consumed. It is positively correlated with tensile strength and negatively with digestibility.	Benvenuti et al., 2006, 2009; Drescher et al., 2006
Leaf thickness (mm)	Measured using a micrometer (± 0.001 mm) at three points on a fully grown, undamaged leaf (excluding the midrib), then averaged.	Influences digestibility and leaf longevity; thicker leaves are less digestible and longer-lived.	Mediavilla et al., 2008; Wright et al., 2004
Leaf dry mass (mg)	Leaves dried at 60°C for 48 hours and weighed (± 0.0001 mg).	Represents investment in leaf tissue, with higher leaf dry mass representing longer leaf lifespan and slower decomposition rates.	Pakeman et al., 2011; Wright et al., 2002
Leaf area (cm²)	Up to 15 full-grown, undamaged leaves were removed and scanned to calculate leaf area (cm ²) using the image software ImageJ (Rueden et al., 2017) and the R package 'LeafArea' (Katabuchi, 2015).	Affects light interception, resource acquisition, competition, and post-grazing recovery.	Crowley & Wingler, 2020

Specific leaf area (SLA; cm²/g)	Calculated as leaf area divided by dry mass. Three fully-grown, undamaged leaves per individual were scanned, dried, and weighed.	Good predictors of plant growth rate and resource-use efficiency, reflecting the return on previously acquired resources.	Cornelissen et al., 2003; Rees et al., 2010; Westoby et al., 2002; Westoby & Wright, 2006
Leaf carbon-to-nitrogen ratio (Leaf C:N)	One to fifteen fully-grown, undamaged leaves per individual were dried and weighed (As above) then ground to a fine powder using a tissue lyser (Tissuelyser II) for 10 min at 25 beats per second. Approximately 4 mg of material were placed into tin capsules and analysed using an elemental analyser Flash SMART 2000 (Thermo Fisher Scientific).	Indicates leaf structural investment, decomposition rate, and palatability. Leaf nitrogen is positively correlated with maximum photosynthetic rates and increases with the palatability of grasses, while carbon is related to structure. High C:N ratios reflect structural investment and low digestibility.	Craine et al., 2002; Field et al., 1983; Grime et al., 1997; Reich et al., 1997; Westoby et al., 2002; Wright et al., 2004

Measurements for each trait followed the protocols presented in Wigley et al., (2020) and Pérez-Harguindeguy et al. (2013). We measured one individual of each grass species present within a 2 m semi-circle uphill of each fixed point across 18 plots. For each individual, inflorescence height and culm diameter were measured *in situ* before harvesting the entire individual. Samples were then stored in a cool box with ice packs in the field for transport to the lab for processing.

In the lab, we measured leaf thickness, leaf area, leaf dry mass, leaf carbon and nitrogen content (See Table 4.2 for measurement details). To control for the potential impact of soil drainage on chemical traits, leaf nitrogen and carbon were analysed from only uphill subblocks (B,C,F). Dried and weighed leaves were ground to a fine powder and analysed using an elemental analyser Flash SMART 2000 (Thermo Fisher Scientific). Accuracy

was validated by analysing 50 replicates, yielding a R^2 of 0.99. Leaf carbon to nitrogen percentages were then used to calculate leaf C:N ratios.

Data analysis

Data were analysed in R version 4.4 (R Core Team, 2023). Trait values were log-transformed to reduce skewness and normalise distributions. Improbable outliers were removed. All trait and composition data were aggregated at the plot level. For all analyses, $p < 0.05$ was considered significant, while $0.10 > p > 0.05$ was considered marginally significant.

Composition analysis

Multivariate abundance models were used to determine how grazing treatment, block, and drainage drive compositional change at a plot level, utilising the 'mvabund' package (Wang et al., 2012). Grass abundance per species, represented by the total number of hits per grass species per plot, was used as the response matrix. Grazing treatment, block, and drainage were included as fixed effects. Models were fitted using a negative-binomial distribution, which was determined to be appropriate by inspecting residual plots.

The `manyglm()` function was used to fit models to each species, summing the test statistics to give a multivariate test statistic known as Sum-of-LR, which was evaluated for significance using resampling with 999 bootstrap iterations to account for multiple tests. The Wald test, performed automatically within the `manyglm()` function, was conducted to assess the difference in composition between plots assigned to different levels of our predictors. Predictor levels were compared against a baseline (intercept) level to assess the significance and direction of differences in trait values between levels. Since grazing treatment and block have three levels each, we ran each model twice: once with the default order of block (AB, CD, EF) and treatment (high-intensity, continuation, no grazing) and again with block (CD, AB, EF) and treatment (continuation, high-intensity, no grazing) reordered. This ensured all pairwise combinations between levels were tested. Since the pairwise comparisons that appeared in both runs yielded identical results, we interpreted each pair only once.

The `anova.manyglm()` function with a likelihood ratio test was used to evaluate the effect of the three categorical predictors on community composition across plots. To assess the contribution of individual species to between-plot differences in community composition, we used ``p.uni = "adjusted"``` within `anova.manyglm()` to conduct univariate species models which provided species-specific effect sizes and adjusted p-values for each predictor. The p-adjusted indicates which species are driving compositional differences in response to our predictors, effectively demonstrating species-specific responses.

Trait response models

Phylogenetic linear mixed models (PLMM), utilising the `pglmm()` function from the ‘*phyr*’ package, were used to test differences in individual trait responses to grazing treatment (high-intensity, continuation, no grazing), block (AB, CD, EF), and drainage (uphill, downhill) (D. Li et al., 2020). Models were constructed to assess the impact of these categorical variables on each of: inflorescence height, culm diameter, leaf thickness, leaf area, SLA, leaf dry mass, and leaf C:N. Grazing treatment, block, and drainage effects were included as fixed predictors in all models except for leaf C:N. For leaf C:N only treatment and block were included as model predictors because only uphill plots were chemically analysed.

Because species are linked by patterns of phylogenetic relationship their trait values are to some extent statistically non-independent (i.e., they show variance covariance) (de Bello et al., 2017; Verberk et al., 2013). To account for phylogenetic non-independence, phylogeny was included as a random effect in our models. A species-level phylogeny was created using sequences downloaded from GenBank and reconstructed using the software IQ-TREE (Minh et al., 2020; Sayers et al., 2020) (Figure S4.1).

As above, to understand all pairwise comparisons of predictor levels in the model outputs, we ran each model twice: once with the default order of block and treatment and again with block and treatment reordered.

Decomposing trait variation

To disentangle the effects of intraspecific trait variation (ITV) and species turnover on the functional structure of the grass communities, we followed the decomposition of sums of squares method proposed by Lepš et al. (2011) and updated by Taudiere & Violle (2016). This method partitions variation in community trait composition into three sources: (1) species turnover, (2) ITV, and (3) covariance between these two. The covariance captures the interaction between species turnover and ITV, where positive covariation suggests species turnover and ITV change in the same direction, possibly inflating community-weighted mean (CWM) (i.e. making trait shifts larger) in response to predictors (Figure 4.2A). Conversely, negative covariation effects indicate species turnover and ITV work in opposite directions, potentially minimising predictor effects on CWM (Figure 4.2B).

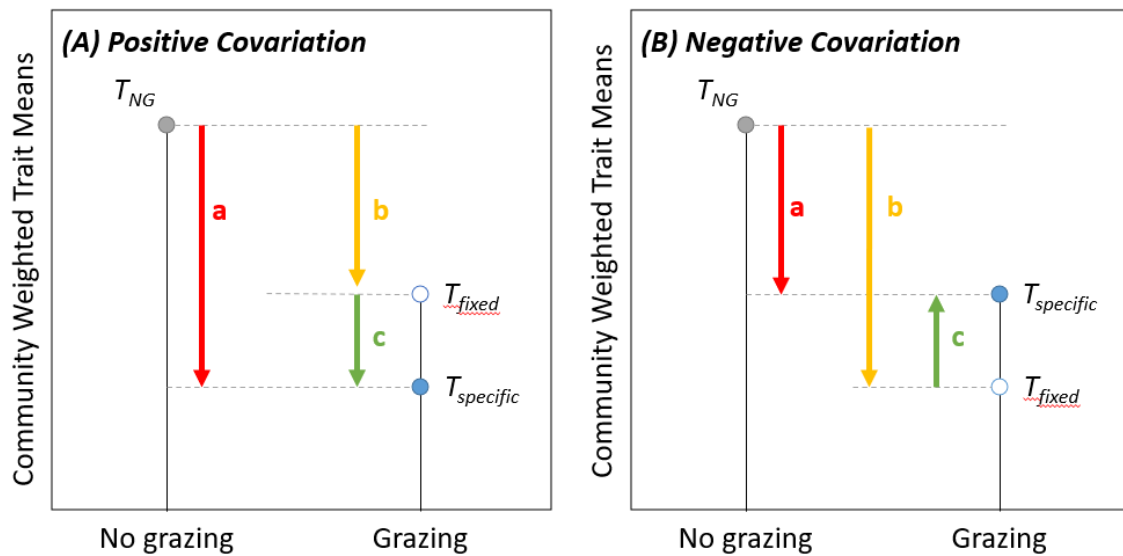


Figure 4.2. **Covariance of species turnover and intraspecific trait variations between no grazing and grazing treatments.** Adapted from Luo et al. (2023). Shows how shifts in community-weighted means (CWM) between treatments (no grazing and grazed) are driven by species turnover (yellow arrow b) and, intraspecific trait variation (green arrow c), resulting in overall trait shifts (red arrow a). For each trait (T), the CWM will shift between no grazing and grazed plots. T_{NG} (grey point) represents the trait CWM in the no grazing plots.

$T_{specific}$ (closed blue point) represents the trait CWM in grazed plots calculated using the species' trait values within each individual plot. The difference between T_{NG} and $T_{specific}$ (red arrow a) represents the overall trait shift, which is the combined result of species' turnover and intraspecific trait variation. T_{fixed} (open blue point) represents the CWM for grazed plots calculated using species' means from all grazed plots, and captures only the contribution to the trait shift of species turnover (yellow arrow b). The difference then between $T_{specific}$ and T_{fixed} represents the change in CWMs due only to intraspecific trait variation (green arrow c). Positive covariation (A) occurs when species turnover and intraspecific variation work in the same direction, amplifying trait shifts between treatments. Negative covariation (B) occurs when species turnover and intraspecific variation work in opposite directions, minimising trait shifts.

Because this approach quantifies the relative contributions of species turnover and ITV within the overall effect of an environmental variable, it does not capture contribution differences within each grazing treatment, block, or drainage level. Instead, it directly assesses how each environmental variable influences total community trait variation and decomposes this variation into species turnover and ITV components. Furthermore, as ITV can arise from either phenotypic plasticity or genetic variability (Pigliucci, 2001), distinguishing between these sources would require breeding experiments and/or genetic testing, which was beyond the scope of this study. Therefore, we refer only to ITV without differentiating its underlying causes.

For each trait we calculated three community-weighted means (explained above): (1) *Specific average*. Calculated using the species' trait values within each individual plot. This captures total trait variation due to both species turnover and ITV. (2) *Fixed average*. Calculated using species' mean trait values across all plots, representing the variation due to only species turnover; and (3) *Intraspecific variation effect*, calculated as the difference between specific and fixed averages, isolating the variation due to the ITV.

Missing trait values bias CWM by causing inconsistent weighting of average trait values. We therefore imputed 33 missing trait values for 20 individuals by assigning the

mean trait values for that species x plot combination as the missing value (Lepš et al., 2011). Leaf C:N ratios were not imputed for downhill plots as we only used uphill data for the decomposition analysis of this trait. While this imputation method may overestimate species turnover and underestimate ITV contributions by excluding some of the within-species variation, imputed traits only accounted for 0.05% of our data, making it unlikely to substantially impact results.

To quantify the contributions of species turnover, ITV, and their covariation to total trait variation, as well as how these three components varied for each predictor variable, we performed parallel three-way ANOVAs, one for each CWM parameter. We used grazing treatment, block, and drainage as variables in our ANOVA for all traits, except the leaf C:N ratio which only included grazing treatment and block. Including these variables in the ANOVAs enabled quantification of how each influenced total trait variation and to disentangle the relative contribution of species turnover, ITV, and covariation to trait shifts within each variable's effect.

From each ANOVA, we extracted the sums of squares (SS), which partitioned total trait variation (SS_{specific}) into contributions from species turnover (SS_{fixed}), ITV (SS_{ITV}) and their covariation (SS_{cov}). Covariance was calculated as $SS_{\text{cov}} = SS_{\text{specific}} - SS_{\text{fixed}} - SS_{\text{ITV}}$. Finally, we converted each SS component into relative contributions (%) to total trait variation by dividing each by the SS_{specific} and multiplying by 100. We visualised the relative contributions of species turnover, ITV, and their covariation to both total and predictor-related trait variation for each of our traits using 'ggplot' (Wickham, 2016). This analysis used portions of code from Lepš et al., (2011) and the `decompCTRE()` function from the 'cati' package (Taudiere & Violle, 2016).

Results

Across all plots, we measured 19 grass species and 1076 individual grasses. In order from most abundant to least, these 19 species (sensu Stace, 2010) were: *Molinia caerulea*, *Festuca ovina*, *Anthoxanthum odoratum*, *Nardus stricta*, *Agrostis canina*, *Agrostis capillaris*, *Deschampsia flexuosa*, *Holcus lanatus*, *Deschampsia cespitosa*, *Festuca rubra*, *Agrostis*

stolonifera, *Danthonia decumbens*, *Poa pratensis*, *Helictochloa pratensis*, *Cynosurus cristatus*, *Holcus mollis*, *Festuca vivipara*, *Poa trivialis* and *Lolium spp.*

Composition analysis

The multivariate abundance model showed that grass species abundance varied significantly between blocks ($p=0.003$) but showed only marginally significant variation in response to grazing and drainage ($p>0.08$) (Table 4.3). Results of the pairwise Wald tests showed significant compositional differences between blocks AB and CD ($p=0.001$) and between CD and EF ($p=0.002$), but not between AB and EF ($p=0.411$) (Table S4.1). Wald tests between grazing treatments showed significant differences between high-intensity and no grazing ($p=0.001$) and continuation and no grazing treatments ($p=0.046$). Differences between high-intensity and continuation treatments were marginally significant ($p=0.072$) (Table S4.1). Although multivariate models indicated a marginal effect of drainage on species composition, there were no significant pairwise differences between uphill and downhill plots ($p=0.164$).

Table 4.3. **Multivariate abundance model results for composition data.** Table shows residual degrees of freedom, degrees of freedom difference, deviance explained, and associated P-values for each predictor.

Environmental Variable	Residual DF	DF Difference	Deviance	P-value
(Intercept)	17			
Grazing Treatment	15	2	60.457	0.088.
Block	13	2	106.533	0.003**
Drainage	12	1	47.382	0.085.

Note:

P-value significance: 0-0.001 '***' 0.001-0.01 '**' 0.01-0.05 '*' 0.05-0.1 '.'

Univariate species models show that the abundance of *M. caerulea* ($p=0.009$) and *Nardus stricta* ($p=0.006$) differed significantly between blocks (Table S4.3). Blocks AB and EF had high relative cover of *M. caerulea*, with 81% and 71.1% respectively, while block CD had

a more evenly distributed grass composition, with *M. caerulea* (34.3%), *F. ovina* (16.8%), *N. stricta* (14.9%), and *A. capillaris* (11.43%) (Table S4.1.). No individual species significantly drove differences between grazing treatments or drainage. *M. caerulea* remained dominant across all grazing treatments, accounting for 80% of total grass cover under high-intensity grazing, 62.1% under continuation grazing, and 57.1% under no grazing (Table 4.4).

Table 4.4. **Total and relative species cover (%) for the 5 most abundant species in high-intensity, continuation, and no grazing treatments.** Relative cover was calculated from pin frame data as the proportion of total contacts per treatment.

Species	Species Hits	Total Hits	Relative Cover (%)
High-intensity grazing			
<i>Molinia caerulea</i>	736	1289	57.099
<i>Festuca ovina</i>	155	1289	12.025
<i>Nardus stricta</i>	132	1289	10.240
<i>Agrostis capillaris</i>	95	1289	7.370
<i>Anthoxanthum odoratum</i>	38	1289	2.948
Continuation grazing			
<i>Molinia caerulea</i>	745	1199	62.135
<i>Agrostis capillaris</i>	119	1199	9.925
<i>Festuca ovina</i>	97	1199	8.090
<i>Nardus stricta</i>	57	1199	4.754
<i>Deschampsia flexuosa</i>	50	1199	4.170
No grazing			
<i>Molinia caerulea</i>	898	1123	79.964
<i>Festuca ovina</i>	57	1123	5.076
<i>Deschampsia flexuosa</i>	36	1123	3.206
<i>Anthoxanthum odoratum</i>	31	1123	2.760
<i>Nardus stricta</i>	22	1123	1.959

Trait response models

Changes in grazing treatment resulted in shifts in all measured traits, however individual grazing treatment levels did not always differ significantly (Table 4.5).

Inflorescence height, culm diameter, leaf area, and leaf mass declined significantly with increasing grazing intensity, though culm diameter did not differ significantly between continuation and no grazing (Table 4.5: A, B, D, E). In contrast, leaf thickness, SLA, and leaf C:N increased with grazing intensity (Table 4.5: C, F, G). However, SLA and leaf C:N did not differ significantly between high-intensity and continuation nor did leaf thickness between continuation and no grazing.

*Table 4.5. **Results of Wald tests comparing grazing treatment levels for seven traits.** The direction column indicates which grazing treatment had the larger value in each pairwise comparison, where ‘>’ means the left treatment had larger trait values, and ‘<’ means the right treatment had larger trait values.*

Treatment	Direction	Treatment	Estimate	Standard Error	Z Score	P-value
(A) Logged Inflorescence Height						
High-intensity	<	Continuation	-0.101	0.018	5.537	0.000***
Continuation	<	No grazing	-0.045	0.02	2.29	0.022*
High-intensity	<	No grazing	-0.146	0.019	7.559	0.000***
(B) Logged Culm Diameter						
High-intensity	<	Continuation	-0.095	0.021	4.631	0.000***
Continuation	<	No grazing	-0.034	0.022	1.542	0.123
High-intensity	<	No grazing	-0.13	0.022	5.949	0.000***
(C) Logged Leaf Thickness						
High-intensity	>	Continuation	0.084	0.021	-3.999	0.000***
Continuation	<	No grazing	-0.017	0.023	0.735	0.463
High-intensity	>	No grazing	0.068	0.022	-3.035	0.002**
(D) Logged Leaf Dry Mass						
High-intensity	<	Continuation	-0.139	0.042	3.328	0.001**
Continuation	<	No grazing	-0.256	0.045	5.707	0.000***
High-intensity	<	No grazing	-0.395	0.044	8.944	0.000***
(E) Logged Leaf Area						
High-intensity	<	Continuation	-0.141	0.034	4.185	0.000***
Continuation	<	No grazing	-0.189	0.036	5.213	0.000***
High-intensity	<	No grazing	-0.33	0.036	9.262	0.000***
(F) Logged SLA						
High-intensity	<	Continuation	-0.002	0.017	0.113	0.910
Continuation	>	No grazing	0.057	0.018	-3.098	0.002**
High-intensity	>	No grazing	0.055	0.018	-3.048	0.002**
(G) Logged Leaf Carbon: Leaf Nitrogen						
High-intensity	<	Continuation	-0.015	0.029	0.526	0.599
Continuation	>	No grazing	0.108	0.031	-3.453	0.001**
High-intensity	>	No grazing	0.092	0.03	-3.044	0.002**

Note:

P-value significance: 0-0.001 '***' 0.001-0.01 '**' 0.01-0.05 '*' 0.05-0.1 '.'

Plot-level trait values varied between blocks and with drainage (Table S4.4- S3.10). All traits showed at least one significant pairwise comparison between blocks, though no single block differed consistently from others. Leaf C:N was the only trait that significantly differed between all blocks (Table S4.10). Uphill plots had significantly ($p < 0.05$) taller grasses with thinner, larger leaves and higher SLA than downhill plots.

Species turnover *versus* intraspecific variation (ITV) analysis

Grazing treatment explained significant total trait variation in four functional traits: inflorescence height (30.82%; $p = 0.013$), culm diameter (27.91%; $p = 0.039$), leaf area (47.25%; $p = 0.003$), and leaf dry mass (53.83%; $p = 0.002$) (Figure 4.3A, & Table S4.11). When effects of grazing were decomposed, the relative contributions of ITV alone to total trait variation were more than species turnover in all traits: inflorescence height (14.80%), culm diameter (10.21%), leaf thickness (6.46%), leaf dry mass (18.32%), leaf area (12.71%), SLA (7.27%), and leaf C:N (5.23%) (Figure 4.3B). For inflorescence height, leaf area, leaf dry mass, and leaf C:N, species turnover and ITV showed positive covariation. This indicates that grazing not only selects species with particular trait values but also, through ITV, favours similar plastic responses of individuals within a species, reinforcing directional change in trait values. In contrast, covariation was negative for leaf thickness and SLA, indicating that species turnover and ITV have opposing effects on the values of these traits.

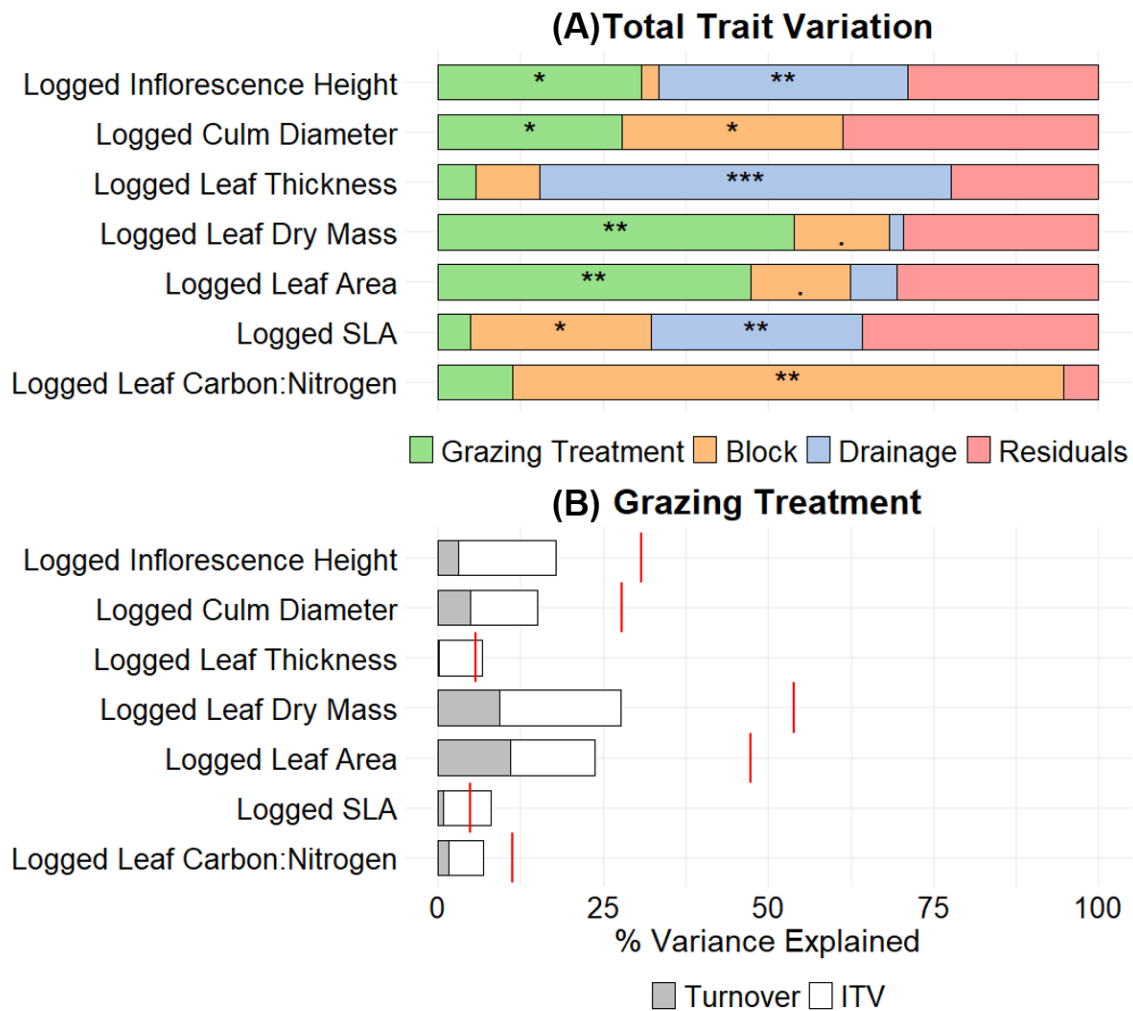


Figure 4.3. **Contributions of environmental variables to total trait variation and contributions of species turnover and intraspecific trait variation (ITV) within the grazing effects.** (A) shows the relative contributions to total trait variation across all plots of our predictors, grazing treatment (green), block (orange), and drainage (blue) as well as the residuals (red). P-value significance for predictors is denoted as follows: 0-0.001= ***, 0.001-0.01 = **, 0.01-0.05 = *, and 0.05-0.1 = . (B) shows the relative contributions of species turnover (grey) and ITV (white) to the amount of trait variation attributed to grazing treatment effects. Red bars denote total variation and correspond to the end of the green bars in (A). The space between the top of the bar and the line represents the effect of

covariation. If the bar is above the column, covariation is positive and if the bar crosses the column, covariation is negative.

Block explained significant total trait variation in culm diameter (33.34%; $p=0.024$), SLA (27.34%; $p=0.033$) and leaf C:N (83.53%; $p=0.003$) (Figure 4.3; Table S4.11). Within the significant block effects, the relative contributions of species turnover to trait variation were more than ITV in culm diameter (11.93%), leaf area (22.80%), and leaf dry mass (10.95%), while both species turnover and ITV contributed almost equally for inflorescence height (3.42%; 2.25%) and SLA (35.03%; 27.75%) (Figure S4.2 D; Table S4.11). Finally, the relative contributions of ITV were greater than species turnover in leaf thickness (12.86%) and leaf C:N (42.82%).

Drainage significantly contributed to total trait variation in inflorescence height (37.65%; $p=0.013$), leaf thickness (62.29%; $p<0.001$), and SLA (32.07%; $p=0.007$) (Figure 4.3; Table S4.11). Within drainage effects, the relative contributions of ITV were more than species turnover in six traits: inflorescence height (29.33%), culm diameter (1.86%), leaf thickness (57.08%), leaf area (1.28%), and SLA (19.41%). The relative contributions of species turnover accounted for a majority of drainage-related trait variation in leaf dry mass (1.40%) (Figure S4.2 E; Table S4.11).

Overall, the relative contributions of species turnover to total trait variation were more than ITV in only one trait: leaf area (58.48%) (Figure S4.1 A; Table S4.11). Species turnover and ITV contributed similar amounts in culm diameter (31.90%; 33.53%) and leaf dry mass (38.60%; 30.55%). For the remaining traits, ITV contributed the most to the total variation in inflorescence height (67.83%), leaf thickness (99.01%), SLA (90.99%), and leaf C:N (52.12%). There was a positive covariation between species turnover and ITV for inflorescence height (19.33%), culm diameter (34.57%), leaf area (17.47%), leaf dry mass (30.85%), and leaf C:N (38.02%), suggesting changes in species composition and within-species trait variation shift traits unidirectionally. Conversely, negative covariation was observed for vegetative height (-12.29%), leaf thickness (-3.65%), and SLA (-44.41%).

Discussion

The structure and composition of grass communities shifted with increases in grazing intensities. Composition did not differ significantly between high-intensity and continuation grazing treatments, but both treatments with grazing differed from no grazing. Increased grazing intensity resulted in shorter grasses with smaller, thicker leaves, higher leaf C:N ratios and greater capacity for regrowth, as indicated by higher SLA. ITV, rather than species turnover, made the dominant contribution to these trait changes, although the relative contributions of ITV to total trait variation varied by trait. In these temperate grasslands, it appears that changes in grazing intensity primarily alters functional composition through ITV rather than shifts in community composition, suggesting that species adjust their trait values rather than shifting their distributions. Instead, compositional shifts were most strongly influenced by plot locations across blocks. We hypothesise that block captured landscape-level variation in characteristics, such as topography, aspect, and soil properties, that filter local species pools.

Compositional change

Grass community composition differed marginally among grazing treatments, with more substantive differences in community composition with topographic position and catchment, represented by the block variable (Table 4.3). In species-poor environments like Glen Finglas (Pakeman et al., 2019) compositional shifts are constrained by the species pool (Hulme et al., 1999; Mountford & Peterken, 2003). Pakeman et al. (2019) found only small compositional changes over 20-years in Glen Finglas, resulting from grazing-associated changes in the ranking of sampled species rather than changes in which species were present.

Pairwise comparisons of grazing treatments revealed significant differences in community composition between high-intensity and no grazing, and continuation and no grazing treatments (Table S4.1). However, differences between our grazing applied treatments, high-intensity and continuation, were marginal, suggesting that grazing removal leads to grass communities' composition shifts, whereas increasing grazing intensity once

applied results in only minor changes. For example, *M. caerulea* had high relative abundance under no grazing (80%), but its cover remained relatively stable under high-intensity (62.1%) and continuation (57.1%) grazing (Table 4.4). Hulme et al. (1999) observed similar patterns in Scottish grasslands, finding grazing removal increased the abundance of grazing-intolerant species *M. caerulea* and *Deschampsia flexuosa*, while grazing intensification led to smaller differences in composition. In grasslands with long grazing histories, vegetation likely already possesses grazing adaptations, limiting further compositional changes under grazing intensification (Milchunas & Lauenroth, 1993; Skarpe & Hester, 2008). Despite shifts in *M. caerulea* dominance, no single species drove differences between grazing treatments (Table S4.3). Instead, compositional changes were likely driven by multiple species' differential responses to grazing changes. Therefore, grazing drives shifts in community functional composition rather than causing major species turnover.

While grazing effects on composition were detectable, plot location, represented by the block effect, was the primary driver of compositional differences among plots (Table 4.3), suggesting that topographic position, catchment, and soil characteristics such as fertility are important determinants of species presence and dominance in these communities. Topography- including aspect and slope- affects water availability, nutrient distributions, and soil stability, all of which shape species composition (Swanson et al., 1988). However, the lack of significant differences between uphill and downhill plots indicates that soil saturation did not significantly influence grass community composition.

M. caerulea and *Nardus stricta* drove most of these block-related compositional differences (Table S4.2), supporting the findings of Hulme et al. (1999), who reported that initial vegetation largely determined species dominance. *M. caerulea* substantially dominated over other grass species in blocks AB and EF whereas block CD exhibited a more even co-dominance among *M. caerulea*, *Festuca ovina*, *N. stricta*, and *Agrostis capillaris*. Block CD was located on an east-facing slope, which may have contributed to its more even species distribution. Slope orientation has previously been identified as a major factor structuring grassland communities (Sebastiá, 2004). In Europe, east-facing slopes typically

receive less precipitation and have lower vegetation, allowing more grass species to co-dominate (Beullens et al., 2014).

Overall, species turnover appears to be constrained by existing species pools, with landscape characteristics exerting a stronger influence on community composition than grazing intensity for the levels of grazing we explored (Proulx & Mazumder, 1998). Consequently, topographic and soil condition should be considered when assessing Scottish grasslands responses to changing grazing management, as community composition globally is shaped primarily by environmental filtering rather than grazing pressure (Lavorel & Garnier, 2002; Westoby et al., 2002).

Trait responses to grazing intensity

Increased grazing resulted in decreased height, culm diameter, leaf area, and leaf dry mass while increasing leaf thickness, SLA and leaf C:N (Table 4.5). Reductions in grass height, culm diameter, leaf dry mass, and leaf area align with grazing resistance strategies (Archibald et al., 2019), consistent with previous studies showing plant height and leaf size decrease under higher grazing intensity (Díaz et al., 2007; Li et al., 2021; Noy-Meir et al., 1989) (Table 4.1). Traits also shifted towards avoidance strategies, with increased leaf thickness and high leaf C:N suggesting greater investment in structural defences that reduce palatability and digestibility (Archibald et al., 2019; Cornelissen et al., 1999; Herms & Mattson, 1992). Notably, SLA, associated with grazing tolerance, also increased with grazing intensity, indicating an improved capacity for rapid regrowth post-defoliation (Laliberté et al., 2012; Rotundo & Aguiar, 2008; Zheng et al., 2010). However, SLA is generally negatively correlated with both leaf C: N and leaf thickness, a pattern not observed here (Díaz et al., 2016; Wilson et al., 1999). Increases in leaf C:N may be because grazed plants often allocate more carbon to above-ground parts to increase structural defences, while limited soil nutrients may constrain nitrogen uptake (Huntly, 1991). As SLA, a measure of mass per unit area, is generally lower in thicker leaves the mechanism underlying this unexpected result is unclear. While changes in grazing led to functional traits shifts, responses were not always uniform. For example, culm diameter and leaf thickness did not significantly differ between

continuation and no grazing treatments (Table 4.5) suggesting these traits are less sensitive to grazing, needing sufficient grazing pressure to shift values.

No grazing resulted in taller plants with larger leaves, low SLA, and increased leaf dry mass (Table 4.5), indicating increased competition (Prévosto et al., 2011; Westoby, 1998; Westoby et al., 2002) as taller grasses can out-compete and shade small plants, while large leaves enhance light capture by increasing photosynthetic area (Crowley & Wingler, 2020). Additionally, reduced SLA and higher leaf mass under no grazing suggest a shift towards resource retention strategies, enhanced nutrient conservation and stress tolerance (Garnier et al., 2007; Reich, 2014).

Trait variation and contributions of Species Turnover and ITV

Grazing effects contributed between 4-47% to total trait variation across all traits (Figure 4.3A), with significant contributions to inflorescence height, culm diameter, leaf dry mass and leaf area. Grass height and leaf area are traits shown to be sensitive to grazing (Díaz et al., 2007; Ye et al., 2020), which explains their strong response. Although culm diameter did not significantly differ among grazing treatments, grazing still contributed significantly to its variation, likely due its strong positive allometric relationship with inflorescence height (Liu et al., 2019). Interestingly, variation in SLA was not significantly driven by grazing, despite SLA being a grazing-sensitive trait derived from leaf dry mass and leaf area (Díaz et al., 2001). Since SLA is the ratio of leaf area to dry mass, the decline of both to increased grazing may have dampened the effect of grazing on overall SLA variation. Additionally, pairwise comparisons of grazing treatments using trait models detected differences attributed to grazing for all traits, yet variance partitioning identified grazing as a significant driver of trait variation in only four traits. The differences likely arise because partitioning of trait variance accounts for the overall effects of grazing, drainage, and block, without distinguishing among levels within each variable, potentially masking some grazing-driven differences.

ITV primarily drove grazing-induced shifts in the grass functional composition across all traits, indicating that structural changes in grass communities occur primarily through

species adapting their trait values in response to changing grazing intensity rather than shifting compositions to grazing-adapted species (Figure 4.3B). By allowing species to make flexible adjustments to trait values, ITV optimises grazing-adaptation strategies while minimising the need for species replacement, enhancing community persistence and stability (Bolnick et al., 2011; Niu et al., 2016). Additionally, ITV broadens species' ecological niches, increasing survival under grazed conditions (Jung et al., 2010; Messier et al., 2010; Nicotra et al., 2010). High ITV in response to grazing allows these communities to maintain function even under repeated disturbance (Albert et al., 2010; Jung et al., 2010; Mouillot et al., 2013; Violle et al., 2012).

Species turnover and ITV exhibited positive covariation for four traits: inflorescence height, culm diameter, leaf dry mass and leaf area (Figure 4.3B), suggesting that grazing selects both species with preferred trait values and individuals within species with similar plastic responses, reinforcing trait selection (Lepš et al., 2011; Siefert et al., 2014). For example, grasses became shorter under high-intensity grazing likely due to the plastic response of individuals shifting towards shorter heights as well as a compositional shift towards shorter species. Positive covariation suggests that at both the community and species levels, grazing promotes the dominance of shorter grasses with smaller, lighter leaves, reflecting a shared response to grazing (Fajardo & Siefert, 2018). In contrast, leaf thickness, SLA, and leaf C:N, exhibited negative covariation between species turnover and ITV, suggesting that grazing selects for species with optimal trait values, but individual plastic responses counteract these shifts, dampening the overall effect of grazing on these traits.

While landscape factors did drive compositional differences between plots, ITV was the dominant driver of community response to disturbance and overall environmental variation within Glen Finglas (Figure S4.2A). ITV explained more total trait variation than species turnover for all traits except leaf area, consistent with expectations that organ-level traits exhibit lower ITV contributions (Siefert et al., 2015). Within Glen Finglas an ecosystem with a long grazing history, limited species pools and slow compositional change (Pakeman et al., 2019), species persist by adjusting their functional traits rather than being replaced by

more grazing-adapted species (Milchunas & Lauenroth, 1993; Skarpe, 1991). The ability to respond via ITV rather than species turnover protects species from extinction, buffers for changes in species composition, and stabilises species richness (Lepik et al., 2005; Volf et al., 2016). ITV also facilitated niche differentiation, allowing plants to partition resources efficiently, promoting species coexistence (Ackerly & Cornwell, 2007; Callaway et al., 2003; Jung et al., 2010; Miner et al., 2005). The high contributions of ITV to total and grazing-induced trait variation indicates a greater resistance to environmental change as communities can remain stable during adverse conditions (Mouillot et al., 2013; Volf et al., 2016).

Here, we partitioned trait variance into species turnover and ITV but this approach does not consider phylogenetic covariances within communities. Some argue that phylogenetic corrections are unnecessary when considering ecological questions like ours (Westoby et al., 2023). However, the omission of phylogeny when decomposing trait variation may have implications as trait averages across species do not account for phylogenetic distances, with closely related species likely sharing similar trait values independent of the eco-evolutionary process (de Bello et al., 2017; Verberk et al., 2013).

Conclusion

As grazing regimes continue to shift across Europe, having direct impacts on biodiversity (Violle et al., 2012) and ecosystem functioning (de Bello et al., 2010), understanding how grazing alters the functional composition of grass communities is essential to management. In the Scottish uplands, increased grazing shifted grasses towards combinations of both avoidance and resistance traits, such as small stature and thick leaves, that make grasses unpalatable and limit biomass removal, and also tolerance traits, such as high SLA, that support rapid regrowth after defoliation. ITV played a dominant role in these responses, allowing species to persist and adapt to changing grazing intensities without shifting species distributions. Limited species pools and slow compositional shifts within Glen Finglas likely limited the role of species turnover in community responses, with

differences in community composition across plots largely shaped by landscape-level characteristics.

Effective grassland management requires an understanding of the mechanism by which communities shift in response to environmental change. ITV's dominant role in grass community adaptations to grazing within the Scottish uplands indicates it should be considered in ecological assessments of these areas. Furthermore, site-specific studies of community responses provide insight into how factors like grazing history, landscape productivity, and species availability influence ITV's role in trait response. While this study focused on grass species, future work should examine whether ITV similarly shapes trait variation in other grassland plant groups, such as forbs. Recognising the dominant role of ITV in temperate grass community responses may improve predictions of how changes in grazing management impact grassy ecosystems, informing more effective grazing management and grassland conservation strategies.

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Chapter 4 supplemental material

Phylogeny

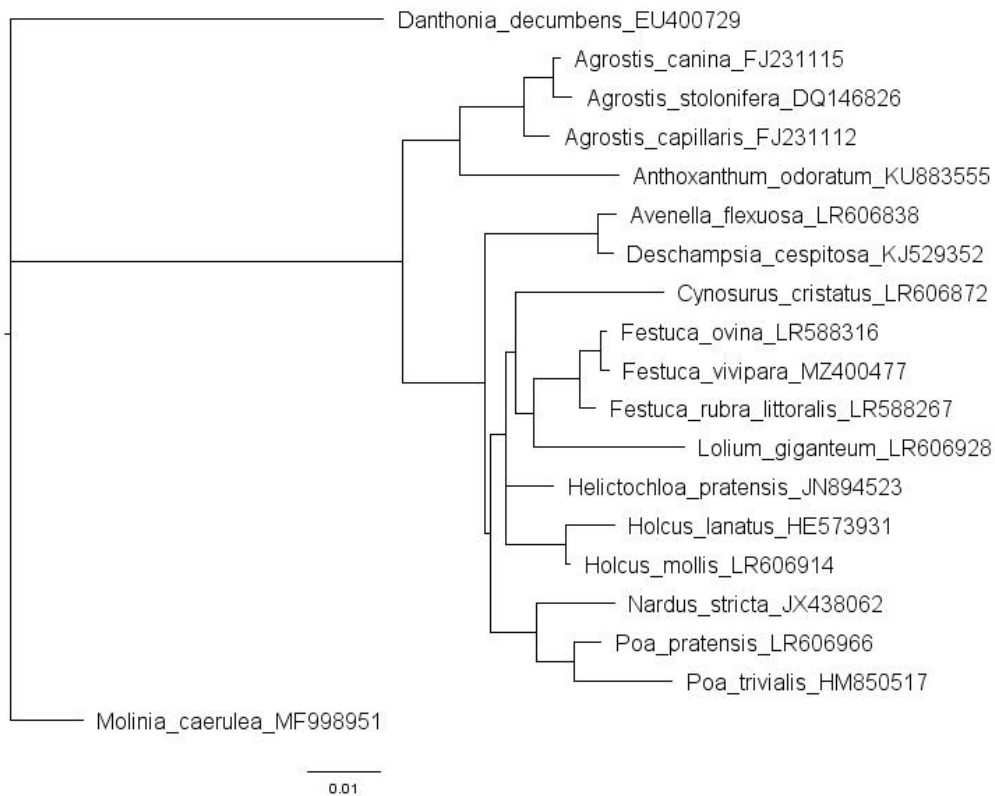


Figure S4.1. Phylogenetic tree of 19 grass species found across all plots. The tree was constructed using genes from GenBank (Sayers et al., 2020) with species names and accession numbers provided.

Composition models

Table S4.1. **Wald tests tested for pairwise differences between levels in our three predictors:** block (AB, CD, EF), grazing treatment (high-intensity, continuation, no grazing), and drainage (uphill, downhill).

Wald Test Comparisons		
Comparison	Wald Value	P-value
High-intensity vs Continuation grazing	6.068	0.072.
Continuation vs No grazing	6.036	0.046*
High-intensity vs No grazing	8.926	0.001**
Block AB vs Block CD	10.606	0.001**
Block CD vs Block EF	9.228	0.002**
Block AB vs Block EF	4.012	0.411
Downhill vs Uphill	5.641	0.15

Note:

P-value significance: 0-0.001 '***' 0.001-0.01 '**' 0.01-0.05 '*' 0.05-0.1 '.'

TableS4.2. **Relative species cover for the 5 most grass abundant species per block.** Relative cover was calculated from pin frame data as the proportion of total contacts per block.

Species	Species Hits	Total Hits	Relative Cover (%)
Block AB			
<i>Molinia caerulea</i>	1088	1344	80.952
<i>Festuca ovina</i>	76	1344	5.655
<i>Agrostis capillaris</i>	55	1344	4.092
<i>Nardus stricta</i>	31	1344	2.307
<i>Agrostis canina</i>	28	1344	2.083
Block CD			
<i>Molinia caerulea</i>	300	875	34.286
<i>Festuca ovina</i>	147	875	16.800
<i>Nardus stricta</i>	130	875	14.857
<i>Agrostis capillaris</i>	100	875	11.429
<i>Anthoxanthum odoratum</i>	56	875	6.400
Block EF			
<i>Molinia caerulea</i>	991	1392	71.193
<i>Festuca ovina</i>	86	1392	6.178
<i>Agrostis capillaris</i>	77	1392	5.532
<i>Deschampsia flexuosa</i>	76	1392	5.460
<i>Nardus stricta</i>	50	1392	3.592

Table S4.3. **Univariate abundance models result for all plots.** All species recorded in composition surveys were tested to see if their abundance significantly drove differences in abundance for each of our predictors (grazing treatment, block, drainage).

	<i>Agrostis canina</i>		<i>Anthoxanthum odoratum</i>		<i>Agrostis stolonifera</i>		<i>Agrostis capillaris</i>	
	Dev	P-value	Dev	P-value	Dev	P-value	Dev	P-value
Grazing treatment	0.417	0.989	0.945	0.977	8.284	0.298	6.153	0.468
Block	3.62	0.795	11.696	0.125	5.341	0.71	1.54	0.834
Drainage	1.073	0.987	1.199	0.987	5.126	0.57	0.189	0.995
	<i>Cynosurus cristatus</i>		<i>Deschampsia cespitosa</i>		<i>Danthonia decumbens</i>		<i>Deschampsia flexuosa</i>	
	Dev	P-value	Dev	P-value	Dev	P-value	Dev	P-value
Grazing treatment	1.83	0.977	1.371	0.977	4.705	0.68	0.237	0.989
Block	6.176	0.619	2.014	0.834	3.198	0.795	4.76	0.733
Drainage	5.545	0.511	1.098	0.987	0.143	0.995	0.058	0.995
	<i>Festuca ovina</i>		<i>Festuca rubra</i>		<i>Festuca vivipara</i>		<i>Helictochloa pratensis</i>	
	Dev	P-value	Dev	P-value	Dev	P-value	Dev	P-value
Grazing treatment	6.552	0.444	2.896	0.9	0	1	2.036	0.976
Block	4.488	0.733	3.656	0.795	0	1	5.933	0.648
Drainage	2.387	0.915	0	1	0	1	10.751	0.139
	<i>Holcus lanatus</i>		<i>Holcus mollis</i>		<i>Lolium spp.</i>		<i>Molinia caerulea</i>	
	Dev	P-value	Dev	P-value	Dev	P-value	Dev	P-value
Grazing treatment	5.804	0.475	5.03	0.672	2.398	0.983	0.319	0.989
Block	1.375	0.834	7.235	0.5	3.088	0.888	18.864	0.01
Drainage	0.418	0.988	1.046	0.987	2.772	0.914	1.055	0.987
	<i>Nardus stricta</i>		<i>Poa pratensis</i>		<i>Poa trivialis</i>		<i>Poa spp.</i>	
	Dev	P-value	Dev	P-value	Dev	P-value	Dev	P-value
Grazing treatment	8.229	0.298	1.053	0.991	2.197	0.984	0	1
Block	20.727	0.008	0.624	0.915	2.197	0.909	0	1
Drainage	6.198	0.456	6.938	0.438	1.386	0.989	0	1
	Unidentified spp.							
	Dev	P-value						
Grazing treatment	0	1						
Block	0	1						
Drainage	0	1						

Trait response models

Table S4.4. Output for Logged Inflorescence Height response PGLMM models. The table shows the comparison of levels within the predictors. The direction column indicates which environmental variable level had the larger value in each pairwise comparison, where '>' means the left level had larger trait values, and '<' means the right level had larger trait values.

Direction			Estimate	Standard Error	ZScore	P-value
High-intensity	<	Continuation	-0.101	0.018	5.537	0.000***
Continuation	<	No grazing	-0.045	0.02	2.29	0.022*
High-intensity	<	No grazing	-0.146	0.019	7.559	0.000***
Block AB	>	Block CD	0.023	0.019	-1.172	0.241
Block CD	<	Block EF	-0.039	0.018	2.14	0.032*
Block AB	<	Block EF	-0.016	0.02	0.819	0.413
Downhill	>	Uphill	0.161	0.016	-10.361	0.000***

Note:
P-value significance: 0-0.001 '***' 0.001-0.01 '**' 0.01-0.05 '*' 0.05-0.1 '.'

Table S4.5 Output for Logged culm diameter response PGLMM models. The table shows the comparison of levels within the predictors. The direction column indicates which environmental variable level had the larger value in each pairwise comparison, where '>'

means the left level had larger trait values, and '<' means the right level had larger trait values.

Direction			Estimate	Standard Error	Z Score	P-value
High-intensity	<	Continuation	-0.095	0.021	4.631	0.000***
Continuation	<	No grazing	-0.034	0.022	1.542	0.123
High-intensity	<	No grazing	-0.13	0.022	5.949	0.000***
Block AB	>	Block CD	0.097	0.022	-4.376	0.000***
Block CD	<	Block EF	-0.014	0.021	0.686	0.492
Block AB	>	Block EF	0.082	0.023	-3.626	0.000***
Downhill	<	Uphill	-0.028	0.018	1.602	0.109

Note:

P-value significance: 0-0.001 '***' 0.001-0.01 '**' 0.01-0.05 '*' 0.05-0.1 '.'

Table S4.6. **Output for logged mean leaf thickness response PGLMM models.** The table shows the comparison of levels within the predictors. The direction column indicates which environmental variable level had the larger value in each pairwise comparison, where '>' means the left level had larger trait values, and '<' means the right level had larger trait values.

Direction			Estimate	Standard Error	Z Score	P-value
High-intensity	>	Continuation	0.084	0.021	-3.999	0.000***
Continuation	<	No grazing	-0.017	0.023	0.735	0.463
High-intensity	>	No grazing	0.068	0.022	-3.035	0.002**
Block AB	>	Block CD	0.019	0.023	-0.827	0.408
Block CD	>	Block EF	0.087	0.021	-4.136	0.000***
Block AB	>	Block EF	0.106	0.023	-4.577	0.000***
Downhill	<	Uphill	-0.19	0.018	10.6	0.000***

Note:

P-value significance: 0-0.001 '***' 0.001-0.01 '**' 0.01-0.05 '*' 0.05-0.1 '.'

Table S4.7. **Output for logged leaf dry mass response PGLMM models.** The table shows the comparison of levels within the predictors. The direction column indicates which environmental variable level had the larger value in each pairwise comparison, where '>' means the left level had larger trait values, and '<' means the right level had larger trait values

Direction			Estimate	Standard Error	Z Score	P-value
High-intensity	<	Continuation	-0.139	0.042	3.328	0.001**
Continuation	<	No grazing	-0.256	0.045	5.707	0.000***
High-intensity	<	No grazing	-0.395	0.044	8.944	0.000***
Block AB	<	Block CD	-0.084	0.045	1.876	0.061.
Block CD	>	Block EF	0.163	0.042	-3.881	0.000***
Block AB	>	Block EF	0.079	0.046	-1.722	0.085.
Downhill	>	Uphill	0.047	0.036	-1.312	0.189

Note:

P-value significance: 0-0.001 '***' 0.001-0.01 '**' 0.01-0.05 '*' 0.05-0.1 '.'

Table S4.8. **Output for logged mean leaf area response PGLMM models.** The table shows the comparison of levels within the predictors. The direction column indicates which environmental variable level had the larger value in each pairwise comparison, where '>'

means the left level had larger trait values, and '<' means the right level had larger trait values.

Direction			Estimate	Standard Error	Z Score	P-value
High-intensity	<	Continuation	-0.141	0.034	4.185	0.000***
Continuation	<	No grazing	-0.189	0.036	5.213	0.000***
High-intensity	<	No grazing	-0.33	0.036	9.262	0.000***
Block AB	<	Block CD	-0.094	0.036	2.612	0.009**
Block CD	>	Block EF	0.073	0.034	-2.15	0.032*
Block AB	<	Block EF	-0.021	0.037	0.573	0.567
Downhill	>	Uphill	0.109	0.029	-3.784	0.000***

Note:

P-value significance: 0-0.001 '***' 0.001-0.01 '**' 0.01-0.05 '*' 0.05-0.1 '.'

Table S4.9. **Output for logged specific leaf area (SLA) response PGLMM models.** The table shows the comparison of levels within the predictors. The direction column indicates which environmental variable level had the larger value in each pairwise comparison, where '>' means the left level had larger trait values, and '<' means the right level had larger trait values.

Direction			Estimate	Standard Error	Z Score	P-value
High-intensity	<	Continuation	-0.002	0.017	0.113	0.910
Continuation	>	No grazing	0.057	0.018	-3.098	0.002**
High-intensity	>	No grazing	0.055	0.018	-3.048	0.002**
Block AB	<	Block CD	-0.004	0.018	0.198	0.843
Block CD	<	Block EF	-0.096	0.017	5.653	0.000***
Block AB	<	Block EF	-0.1	0.019	5.36	0.000***
Downhill	>	Uphill	0.069	0.014	-4.753	0.000***

Note:

P-value significance: 0-0.001 '***' 0.001-0.01 '**' 0.01-0.05 '*' 0.05-0.1 '.'

Table S4.10. **Output for logged leaf carbon: leaf nitrogen ratio (C:N) response PGLMM models.** The table shows the comparison of levels within the predictors. The direction column indicates which environmental variable level had the larger value in each pairwise comparison, where ‘>’ means the left level had larger trait values, and ‘<’ means the right level had larger trait values.

Direction			Estimate	Standard Error	Z Score	P-value
High-intensity	<	Continuation	-0.015	0.029	0.526	0.599
Continuation	>	No grazing	0.108	0.031	-3.453	0.001**
High-intensity	>	No grazing	0.092	0.03	-3.044	0.002**
Block AB	<	Block CD	-0.211	0.032	6.671	0.000***
Block CD	<	Block EF	-0.097	0.029	3.397	0.001**
Block AB	<	Block EF	-0.308	0.032	9.764	0.000***

Note:

P-value significance: 0-0.001 ‘***’ 0.001-0.01 ‘**’ 0.01-0.05 ‘*’ 0.05-0.1 ‘.’

ITV vs turnover

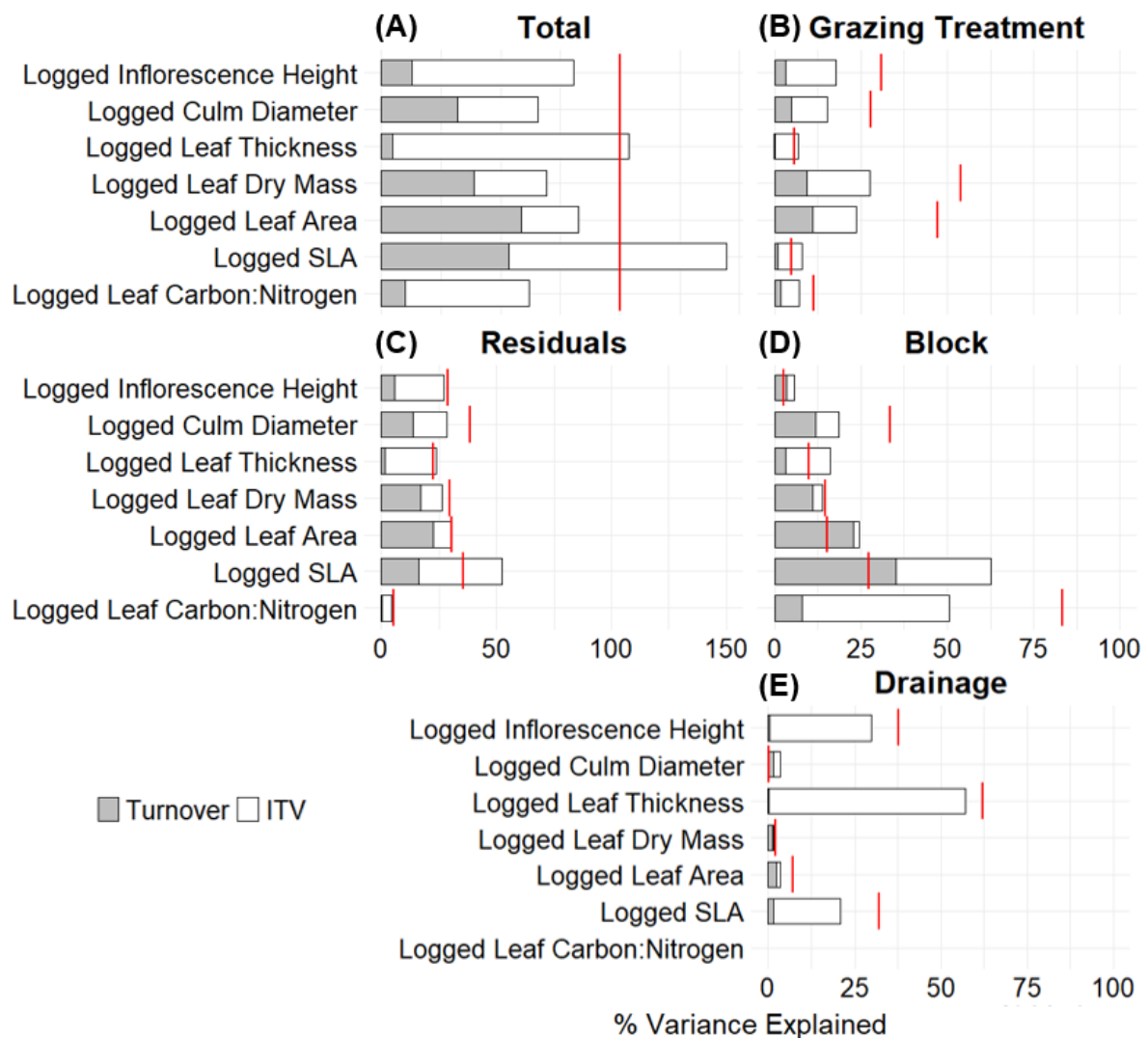


Figure S4.2. **Relative contributions of species turnover (grey) and ITV (white) to the amount of trait variation for all seven measured traits.** Trait variation was attributed to (A) total, (B) grazing treatment, (C) residual, (D) block, and (E) drainage effects. Red bars denote total variation for the specific effect. The space between the top of the bar and the line represents the effect of covariation. If the bar is above the column, covariation is positive and if the bar crosses the column, covariation is negative.

Table S4.11. ***Relative contributions of species turnover, intraspecific trait variation (ITV), and their covariation to total trait variation for seven measured traits.*** Values are presented as percentages of total variance explained. The “Total” column represents the sum of species turnover, ITV, and their covariation. P-values indicate the significance of each predictor’s contribution to species turnover, ITV, and total variation, where available.

Trait	Variation Source	Species Turnover	P-value_{Turnover}	ITV	P-value_{ITV}	Covariance	Total	P-value_{Total}
Logged Inflorescence Height	<i>Grazing Treatment</i>	3.04%	0.081	14.81%	0.043	12.98%	30.82%	0.013
	<i>Block</i>	3.42%	0.063	2.25%	0.549	-3.02%	2.66%	0.590
	<i>Drainage</i>	0.52%	0.323	29.33%	0.002	7.80%	37.65%	0.002
	<i>Residuals</i>	5.86%	NA	21.44%	NA	1.58%	28.87%	NA
	<i>Total</i>	12.84%	NA	67.83%	NA	19.34%	100.00%	NA
Logged Culm Diameter	<i>Grazing Treatment</i>	4.85%	0.160	10.21%	0.043	12.85%	27.91%	0.039
	<i>Block</i>	11.93%	0.023	6.65%	0.108	14.76%	33.34%	0.024
	<i>Drainage</i>	1.52%	0.269	1.86%	0.243	-3.37%	0.02%	0.943
	<i>Residuals</i>	13.60%	NA	14.81%	NA	10.32%	38.73%	NA
	<i>Total</i>	31.90%	NA	33.53%	NA	34.57%	100.00%	NA

<i>Trait</i>	<i>Variation Source</i>	<i>Species Turnover</i>	<i>P-value</i> <i>Turnover</i>	<i>ITV</i>	<i>P-value</i> <i>ITV</i>	<i>Covariance</i>	<i>Total</i>	<i>P-value</i> <i>Total</i>
Logged Leaf Thickness	<i>Grazing Treatment</i>	0.16%	0.500	6.46%	0.221	-0.99%	5.64%	0.259
	<i>Block</i>	3.04%	0.001	12.86%	0.067	-6.17%	9.73%	0.114
	<i>Drainage</i>	0.11%	0.330	57.08%	0.000	5.10%	62.29%	0.000
	<i>Residuals</i>	1.33%	NA	22.61%	NA	-1.60%	22.34%	NA
	<i>Total</i>	4.64%	NA	99.02%	NA	-3.66%	100.00%	NA
Logged Leaf Dry Mass	<i>Grazing Treatment</i>	9.35%	0.071	18.32%	0.002	26.17%	53.84%	0.002
	<i>Block</i>	10.95%	0.050	2.73%	0.218	0.87%	14.55%	0.091
	<i>Drainage</i>	1.40%	0.338	0.05%	0.806	0.53%	1.98%	0.389
	<i>Residuals</i>	16.90%	NA	9.45%	NA	3.29%	29.64%	NA
	<i>Total</i>	38.60%	NA	30.55%	NA	30.85%	100.00%	NA
Logged Leaf Area	<i>Grazing Treatment</i>	10.99%	0.091	12.71%	0.004	23.56%	47.26%	0.004
	<i>Block</i>	22.81%	0.015	1.72%	0.325	-9.33%	15.19%	0.089
	<i>Drainage</i>	2.31%	0.288	1.28%	0.199	3.44%	7.03%	0.122
	<i>Residuals</i>	22.38%	NA	8.33%	NA	-0.20%	30.52%	NA
	<i>Total</i>	58.48%	NA	24.04%	NA	17.47%	100.00%	NA

<i>Trait</i>	<i>Variation Source</i>	<i>Species Turnover</i>	<i>P-value</i> <i>Turnover</i>	<i>ITV</i>	<i>P-value</i> <i>ITV</i>	<i>Covariance</i>	<i>Total</i>	<i>P-value</i> <i>Total</i>
<i>Logged SLA</i>	<i>Grazing Treatment</i>	0.74%	0.763	7.28%	0.336	-3.17%	4.85%	0.466
	<i>Block</i>	35.03%	0.001	27.75%	0.034	-35.43%	27.34%	0.033
	<i>Drainage</i>	1.58%	0.299	19.41%	0.027	11.08%	32.07%	0.007
	<i>Residuals</i>	16.07%	NA	36.56%	NA	-16.89%	35.74%	NA
	<i>Total</i>	53.42%	NA	90.99%	NA	-44.41%	100.00%	NA
<i>Logged Leaf Carbon:Nitrogen</i>	<i>Grazing Treatment</i>	1.68%	0.023	5.23%	0.193	4.30%	11.21%	0.102
	<i>Block</i>	7.86%	0.001	42.82%	0.008	32.86%	83.53%	0.003
	<i>Drainage</i>	NA	NA	NA	NA	NA	NA	NA
	<i>Residuals</i>	0.30%	NA	4.09%	NA	0.86%	5.25%	NA
	<i>Total</i>	9.85%	NA	52.13%	NA	38.02%	100.00%	NA

Chapter 5: General Discussion

Introduction

Grasslands have undergone rapid transformation over the past century, with up to 49% experiencing degradation, driven by climate change, agriculture expansion, and land-use change (Egoh et al., 2009; Gang et al., 2014; Hoekstra et al., 2005). In particular, native grazer extinctions, livestock introductions, and recent rewilding practices have altered grazing regimes in many grassland ecosystems, reshaping grassland structure and function (Donlan et al., 2006; Hempson et al., 2017; Johnson, 2009). However, predicting grazing's effects and interactions with other environmental drivers, such as temperature, nutrient availability, water availability, and fire, remains difficult across spatial scales and ecological contexts (Maestre et al., 2022).

A major challenge in understanding grassland dynamics - the complex interactions among plants, animals, soils, disturbances, and abiotic conditions such as water, nutrients, and climate that shape community composition, species traits, biotic interactions, and ecosystem functions in grasslands - is the fragmented nature of grassland research. Tropical and temperate grasslands are often studied separately, limiting opportunities to identify broader ecological patterns or shared mechanisms. This disconnect also extends across spatial scales. The effects of fine-scale ecological processes such as grazing are examined at local (i.e. single site) levels (e.g. Bakker et al., 1983; Bullock et al., 2001; McIntyre & Lavorel, 2001), while broad-scale climatic drivers such as temperature and precipitation are typically assessed globally (e.g. Gao et al., 2024; Lehmann et al., 2019). At the global scale in particular, complex environmental interactions that shape grasslands are often studied in isolation, simplifying their effects (e.g. Bade et al., 1985; Baird et al., 2021), or in an overly aggregated way, potentially obscuring meaningful independent contributions (e.g. Crowley & Wingler, 2020; Jardine et al., 2020). Furthermore, many studies exclude within-species variation and phylogenetic relationships from analysis, despite their importance in shaping grassland community assembly (Signet 2015, de Bello et al., 2017; Xu et al., 2017). This fragmentation - across biome types, spatial scales, and biological levels- limits our

understanding of grassland dynamics, hindering our ability to predict community responses to environmental change.

In my thesis, I sought to bridge these gaps- including the separation of tropical and temperate grassland ecology, limited cross-scale assessments, oversimplification of complex environmental driver interactions, and the neglect of evolutionary and intraspecific variation and evolution- to improve the understanding of the ecology and biogeography of grassland ecosystems. Across three research chapters, I progressed my research from global to regional to local spatial scales, enabling me to assess how drivers interact and impact grassland dynamics at different spatial scales. I also drew on diverse data sources, including published literature, herbarium specimens, phylogenies, and field-collected data, to assess how grazing interacts with key environmental drivers of temperature, nutrient availability, water availability, and fire to shape grass functional traits, life history strategies and community composition across environmental contexts (Table 5.1). This cross-scale approach allowed me to link broad-scale environmental patterns with local-scale processes while integrating within species trait variation and evolutionary history, offering a more nuanced understanding of grassland dynamics. In this discussion chapter, I summarise and evaluate the key results of my primary research to consider emergent findings, positioning these findings within the wider literature and suggesting future research directions.

Table 5.1. Summary of data types used across chapters, including their sources and the spatial or temporal scales they capture.

Chapter	Data Utilised	Data Source	Scales Captured
2	Literature-derived vegetation and herbivore data	Species lists	Local
	Herbivore biomass	Trait database	Regional or Global
	Climatic data	Remote sensing	Global
3	Herbarium-derived trait data	Herbarium trait data	Local or Regional
	Environmental proxies data	Remote Sensing	Regional or Global

	Phylogeny	Molecular analysis	Evolutionary
4	Field-collected trait data	Field surveys	Local
	Field-collect composition data	Field surveys	Local
	Landscape data (Treatment, Block, Drainage)	Field surveys	Local
	Phylogeny	Molecular analysis	Evolutionary

Chapter summaries

Chapter 2: Grazing lawns are globally distributed and include a wide range of taxonomic associations

Grazing is an important ecological process that shapes ecosystems globally (Allen et al., 2010). In Chapter 2, I developed an attribute-based framework, based on McNaughton (1984) and Hempson et al. (2015), to identify grazing lawns- short-statured vegetation communities maintained via positive feedback with grazers - on a global scale. Applying this framework, I identified 108 case studies of terrestrial and aquatic grazing lawns across six continents, including both previously recognised (author-identified) and unrecognised (attribute-identified) examples. I showed that terrestrial grazing lawns occur across a broad range of temperature and precipitation regimes but were absent from extreme climates, likely due to the interaction of grazing with vegetation dynamics under such conditions (Eldridge et al., 2022; Maestre et al., 2022). The most frequently identified grazing lawns were dominated by C₄ grasses and grazed by macroherbivores (100-1000 kg). Lawn vegetation included a variety of herbaceous plant functional types (C₃ grasses, C₄ grasses, forbs, and sedges). Grazers associated with lawns spanned five orders of magnitude in body size and included Mammalia, Aves, Reptilia, Pisces, and Gastropoda. Regardless of this diversity, grazing lawn persistence depended on a balance in grazing intensity, ensuring vegetation recovery while maintaining supporting open, herbaceous swards (Hempson et al., 2022; Teague et al., 2011; van de Koppel et al., 1997).

This study was the first attempt to provide a standardised framework for grazing lawn identification based on objective criteria. While grasslands and large herbivores, likely due to their long co-evolution (Stebbins, 1981), may be the most efficient combinations for sustaining grazing lawns, my findings demonstrate that similar positive feedbacks can arise from various vegetation-grazer associations under different environmental contexts, underscoring the cross-ecosystem relevance of grazing at a global scale. Furthermore, this chapter highlighted some of the biases in global grazing research, with grazing lawns more frequently recognised in tropical and subtropical C₄ grasslands dominated by large mammalian herbivores. By demonstrating that grazing can shape different ecosystems in similar ways, my findings emphasise the need for a broader, cross-ecosystem, scale-independent perspective on grazing dynamics.

Chapter 3: Functional variation in grasses across Madagascar in response to environment

Building on Chapter 2, which established grazing as a cross-ecosystem process shaping grazing lawns globally, Chapter 3 examined how top-down (fire, grazing) and bottom-up (temperature, nutrient availability, water availability) drivers combine to influence six functional traits related to size and leaf economics, shaping grass life history strategies at a regional scale. Using Madagascar's grassy flora as a case study, I generated and analysed herbarium-derived trait data for 1,616 individuals from 260 species—representing 47% of the island's grassy flora. By comparing herbarium- and field-collected datasets, I demonstrated that data for herbarium specimens are a viable substitute for field-collected data, emphasising their potential value for trait analysis.

Using phylogenetic mixed modelling, which controlled for contributions to trait values of species' shared evolutionary history, I found that temperature, nutrient availability, and fire occurrence were consistently strong predictors for most measured traits, while water availability only had a relative influence on leaf width and thickness. In contrast, leaf nitrogen showed no discernible relationship with any environmental predictors, suggesting that the selected proxies did not fully capture the environmental drivers influencing this trait. Additionally, the proxy I used for grazing (Global Human Modification Index) was not significantly correlated with any measured traits. I found that all six traits significantly co-varied, with size-related traits (e.g. inflorescence height, culm

diameter, and leaf length) showing strong positive correlations, while leaf economic traits (e.g. leaf thickness and leaf nitrogen) had moderate negative correlations. Within multivariate space, trait coordination aligned with the size and leaf economic spectra, two globally recognised axes of trait variation (Díaz et al., 2016; Grime, 1977; Jardine et al., 2020; Sandel et al., 2016). The persistence of these two axes at regional scales provides strong evidence that these trade-offs are fundamental mechanisms underlying plant life history strategies while suggesting that grasses optimise different aspects of their life history strategies across environments, reinforcing well-documented ecological trade-offs and responses (Colesie et al., 2020; Grime, 1977; Reich, 2014; Wingler & Sandel, 2023).

My carefully structured analysis enabled me to identify quantitative patterns and inter-relationships between multiple environmental drivers and key size and leaf economic traits. Overall, this chapter advances our understanding of grass life history strategies, how environmental drivers shape them and how traits are coordinated within them, improving predictions of grass differentiation along environmental gradients and responses to global change.

Chapter 4: Intraspecific trait variation drives functional shifts in grass communities under grazing in the Scottish uplands

In Chapter 3, I found that grazing effects are difficult to capture via remote-sensing data at a regional scale. Therefore, Chapter 4 examined how grass communities respond to changes in grazing intensities and the mechanisms driving these responses at a local scale. To do this, I analysed trait and composition data from a 20-year grazing experiment in the Scottish uplands, assessing whether functional shifts in the grass communities were driven by species turnover or intraspecific trait variation (ITV). Using data from 18 plots covering three grazing treatments, three locations, and two drainage levels- including 1076 individuals from 19 grass species- I found that plot location, rather than grazing, drove most of the compositional differences between plots, with grazing inducing only minimal shifts in species composition.

Although grazing did not strongly alter species composition, it induced significant trait shifts, reducing grass height, culm diameter, leaf dry mass, and leaf area, while

increasing leaf thickness and C:N ratios, reflecting grazing resistance and avoidance strategies (Archibald et al., 2019; Cornelissen et al., 1999; Herms & Mattson, 1992). Grazing also increased SLA, indicating enhanced grazing tolerance with an improved regrowth capacity post-defoliation (Laliberté et al., 2012; Rotundo & Aguiar, 2008; Zheng et al., 2010). Using the decomposition of sums of squares method developed by Lepš et al. (2011), I found that ITV rather than species turnover primarily drove these trait shifts, indicating that trait responses to grazing occur primarily through shifts in within-species trait variation rather than turnover between species with different mean trait values. The high ITV observed suggests these grasslands exhibit resilience to grazing disturbances, as species can flexibly adjust their traits without requiring community turnover, enhancing community persistence and stability (Bolnick et al., 2011; Niu et al., 2016).

This chapter is the first to recognise ITV as the main mechanism driving grass community responses to grazing in the Scottish grasslands. These findings suggest that within these species-limited grasslands, ITV plays a dominant role in maintaining functional diversity under grazing, buffering communities against further environmental change (Ackerly & Cornwell, 2007; Mouillot et al., 2013; Volf et al., 2016). Therefore, incorporating ITV into more grazing research may improve predictions of community responses to changes in grazing management, enhancing our understanding of disturbance responses and local community assembly processes in the Scottish uplands (Albert et al., 2011; Jung et al., 2010; Siefert, 2012; Volf et al., 2016).

Synthesis and emerging research opportunities

Grazing impacts and detection across spatial scales

Grazing is an important ecological process that maintains grassland ecosystems through herbivore-vegetation feedbacks, shaping biodiversity (Gao & Carmel, 2020; McNaughton, 1983; Yuan et al., 2016) and community structure (Sala et al., 1986; Zainelabdeen et al., 2020). As grazing regimes continue to shift globally, there is an increasing need to develop tools to investigate how herbivores have influenced ecological functions and resilience across ecosystems and over time (Blois et al., 2013; Estes et al., 2011; Wisz et al., 2013). However, grazing is inherently variable spatially and temporally (Bruehlheide et al., 2018). Its effects are highly context-dependent, varying with climate,

herbivore density, and evolutionary grazing history (Cingolani et al., 2003, 2005; Hobbs, 1996; Milchunas et al., 1988; Olff & Ritchie, 1998). As a result, grazing impacts are more easily detected at local scales, where high resolution data on herbivore densities and vegetation responses can be collected. In contrast, at regional and global scales, increasing environmental variability and methodological limitations obscure its effects, making broad-scale detection and quantification more challenging.

Despite the difficulty of detecting grazing effects at broad scales, the widespread distribution of grazing lawns in geographic and climatic space (Chapter 2) indicates that grazing shapes vegetation in analogous ways across ecosystems globally. However, these broad-scale patterns could only be identified by compiling local-scale studies. While these local studies provide valuable insights into grazing-environment interactions, their findings are difficult to scale up to broader environmental gradients. Since the frequency and intensity of grazing required to maintain open grassland ecosystems are likely influenced by vegetation (i.e. intrinsic growth rates and forms, species composition), historical (i.e. grazing history), environmental (i.e. resource availability) and spatial characteristics (i.e. area to be maintained) (Briske, 1996; Burkepile, 2013; Hempson et al., 2022; Leonard et al., 2010; Milchunas et al., 1988; Pakeman, 2004), scaling up grazing data would improve our ability to assess how these factors interact to shape grassland structure and distributions (Mucina, 2019).

Remote sensing offers a promising approach for studying grazing responses across spatial scales (Blanco et al., 2009; Reiner mann et al., 2020). However, at regional and global scales, available data on grazing remains limited. While efforts have been made to map livestock (e.g. Castro et al., 2020; Malek et al., 2024; Robinson et al., 2014) and large wild herbivore densities (e.g. Hempson et al., 2015), existing datasets are often geographically, taxonomically, or temporally restricted. Many of these datasets fail to integrate seasonal movements and variations in grazing intensity over time, lacking sufficient resolution for large-scale analyses. Recent work in China has quantified livestock grazing across the country, providing high-resolution grazing intensity data (Wang et al., 2024), a step towards scaling up grazing datasets. However, challenges remain in standardising measurements and improving the resolution of grazing intensity, duration, and timing data (Fetzel et al., 2017).

In Chapter 3, while some trait-environmental relationships were detectable for environmental proxies like temperature and fire, no significant trait-environmental relationships were detected for my coarse grazing proxy (i.e. Global Human Modification Index). This may reflect a genuine absence of grazing effects at a regional scale, or it may indicate the proxy lacked sufficient resolution to capture localised variation in herbivore densities and seasonal grazing patterns - underscoring the challenge of quantifying grazing over larger spatial scales. It remains unclear whether the apparent lack of consistent grazing effects across scales reflects a genuine ecological pattern, where grazing is less influential relative to other drivers at broader scales, or simply a methodological limitation. If the latter, then developing better tools and datasets to quantify grazing intensity, timing, and distribution at broader spatial scales will enhance our ability to model trait and ecosystem responses, ultimately advancing our understanding of how grazing shapes grassland dynamics.

Currently local scale studies remain the most informative for understanding grazing dynamics, capturing fine-scale ecological processes often obscured at broader spatial scales. In Chapter 2, I compiled local grazing lawn studies to identify analogous grazing patterns across broad spatial scales, demonstrating how local data, when aggregated, can reveal broad-scale ecological trends. In contrast, Chapter 4's grazing experiment enabled me to isolate the functional mechanisms underpinning community changes, finding that intraspecific trait variation plays an important role in how Scottish upland grass communities respond to grazing. While local studies offer valuable insights into the mechanisms shaping community responses, their context-specific nature limits their broader applicability across spatial scales and environmental contexts. Bridging this gap requires methods that can effectively scale up local insights while maintaining ecological relevance (Van Cleemput et al., 2025; Wiens, 1989). Developing better grazing proxies and employing multi-scale approaches should enhance our ability to connect broad-scale patterns with their underlying ecological drivers, ultimately improving our ability to model and predict grazing impacts on grassland ecosystems.

The role of herbaria in ecological research

Herbaria, with extensive collections spanning diverse geographical regions and periods, offer a potential resource for functional trait data (Heberling, 2021). In Chapter 3, I utilised herbarium specimens from collections at the Royal Botanic Garden, Kew and Paris Natural History Museum to assess functional trait coordination in responses to key environmental drivers. By comparing herbarium and field-derived data for the same species, I found strong correlations for leaf length, leaf width, leaf thickness and leaf table height. While specific leaf area was not measured in this study, previous research has demonstrated its strong correlation with field-derived data in both grasses and woody species (Jardine et al., 2020; Perez et al., 2020). Collectively, these findings confirm that herbarium specimens can be a reliable alternative to field-collected data, supporting their broader applicability for functional trait analyses.

Herbarium collections can sometimes offer an effective alternative to database-derived trait data, particularly for studying trait-environmental relationships. Compared to large-scale studies that utilise database-derived data (e.g. Gao et al., 2024; Li & Prentice, 2024), herbarium collections allow for regionally specific trait measurements, which may better capture local ecological variation (Cordlandwehr et al., 2013). By preserving historical and geographically diverse records of within and between species trait variation, herbaria may enable researchers to examine trait dynamics and variability over broader spatial and temporal scales (Queenborough, 2017). Furthermore, they facilitate trait-based research in regions lacking long-term field data, allowing for wider geographical analysis in areas with fewer further collection efforts (Heberling, 2021).

The digitisation of herbarium specimens is further enhancing access to these collections, enabling researchers to extract trait data from digital images (Hedrick et al., 2020; Soltis, 2017). For instance, spikelet morphological traits have already been successfully analysed from specimen scans using image-processing software (McAllister et al., 2019). Additional traits - such as leaf length, leaf width, culm diameter, and inflorescence height - may also be extractable using tools like ImageJ, though this remains to be formally tested. However, while digitisation increases accessibility, repositories of images typically have high financial costs (Haston et al., 2012, 2012), with individual institutions setting their

own funding and digitisation priorities (Berendsohn & Seltmann, 2010). Moreover, herbarium collections and digitisation efforts are unevenly distributed, with a majority of herbarium specimens stored in the Global North and access to herbarium collections and associated data limited in the Global South (Park et al., 2023).

Despite the advantages, the use of herbarium specimens for trait research presents several challenges. Herbarium collections are often taxonomically and geographically biased, with specimens disproportionately collected for unique species or from roadsides, rivers, and other easily accessible areas (Daru et al., 2018; Kadmon et al., 2004; Pyke & Ehrlich, 2010). For example, in Chapter 3, herbarium collections underrepresented the wettest parts of Madagascar, especially along the eastern coast, where access to forest understories can be difficult and other plant families take collection priority. This spatial bias may have constrained the trait-environment models' ability to detect relationships between water availability and certain traits, such as leaf length and inflorescence height, by failing to capture the full range of environmental conditions and trait variation across the island. Such limitations and biases should be considered when analysing and interpreting trait-based model results, and future collection efforts should aim to improve both geographic and taxonomic representation.

Additionally, the effective use of herbarium-derived traits for trait-environmental analyses requires identifying appropriate proxies that can capture environmental variation. While proxies for temperature, nutrient availability, and fire explained much of the trait variation for our traits of interest in the Malagasy grass flora, finer-scale processes like grazing were not detected through our selected proxy. This reflects a broader challenge in trait-based ecological research, as remote sensing data often fails to capture fine-scale ecological processes and environmental variations (See section *Grazing impacts and detection across spatial scales*).

The role of intraspecific trait variation in grassland ecology

Intraspecific trait variation (ITV) is widely recognised as an important mechanism in species coexistence, community assembly, niche differentiation, and ecosystem functions (Bolnick et al., 2011; Courbaud et al., 2012; Nicotra et al., 2010; Violle et al., 2012; Wright et

al., 2016). Despite accounting for approximately 25% of total trait variation within plant communities and 32% among communities (Siefert et al., 2015), ITV is often not accounted for or assessed in many multi-species trait-based studies, which typically rely on species means. This approach can obscure meaningful variation in both functional differentiation and community-level responses (Albert et al., 2011). By integrating ITV into the analyses in Chapter 3 and 4, I provided a more nuanced understanding of how grassland communities respond to environmental drivers.

Trait variation is frequently excluded from studies on multi-species life history strategies, where species means are used to assess differentiation along functional trait axes (e.g. Díaz et al., 2016; Jardine et al., 2020; Wright et al., 2004). This approach assumes differences between species are greater than within-species variation (McGill et al., 2006) and has guided much of our understanding of plant differentiation across scales. However, some research has questioned whether species-level trait differentiation along axes, such as the leaf economic spectrum (LES), applies at intraspecific levels as some traits, such as plant height, are more plastic than others (Anderegg et al., 2018). In my assessment of the Malagasy grass flora (Chapter 3), I incorporated ITV by analysing individual trait responses to environmental gradients rather than relying on species means. Even when within-species variation was included, grasses still differentiated along two axes, one being the LES, demonstrating these species-level patterns persist at the individual level. By capturing within-species covariation, this approach provided a more detailed understanding of how grass life history strategies differentiate along environmental gradients. Therefore incorporating ITV can improve our understanding of within-species variability and its role in shaping life history strategies in response to environmental factors (Westerband et al., 2021).

Studies examining plant community shifts in response to environmental drivers, such as grazing (e.g. Bullock et al., 2001; Lavorel et al., 2011; Li et al., 2017; Pakeman & Fielding, 2020), primarily attribute functional shifts to species turnover, overlooking or being unable to quantify the role of ITV in community dynamics (Violle et al., 2012; Weiher & Keddy, 1995). However, ITV can have an important role in community responses to disturbances (Niu et al., 2016; Wang et al., 2023). I found that intraspecific adjustments, rather than

species turnover, drove functional shifts in Scottish Uplands grass communities (Chapter 4), underscoring ITV's importance in maintaining functional diversity and community stability in response to grazing within these grasslands. Given ITV's negative relationship with species richness, it may be particularly relevant in species-poor communities where it likely accounts for a larger proportion of total functional diversity (Fajardo & Siefert, 2018; Siefert et al., 2015; Violle et al., 2012). Furthermore, ITV is increasingly recognised as an important factor in ecosystem resilience, with higher intraspecific variation enhancing the ability of communities to withstand and recover from disturbance and environmental stress (Hou et al., 2019; Jung et al., 2010). Therefore, incorporating ITV into community assessments will help clarify the mechanisms driving functional shifts and may provide further insights into community responses to grazing across environmental contexts and spatial scales. Examining ITV along environmental gradients will help us disentangle the factors controlling when ITV versus species turnover dominates.

While ITV's ecological significance has been widely reviewed (e.g. Albert et al., 2011; Bolnick et al., 2011; Jung et al., 2010; Lepš et al., 2011; Shipley et al., 2016; Siefert et al., 2015; Violle et al., 2012; Westerland et al., 2021), major gaps remain in understanding how it influences ecological processes such as species interactions and ecosystem resilience across spatial scales and environmental contexts. Some studies suggests ITV is most relevant at local scales, short environmental gradients, and in species-poor environments (Siefert et al., 2014, 2015), while others argue that ITV contribute significantly to trait variation across spatial scales and should be considered in regional and global studies, particularly in highly heterogeneous environments (Kuppler et al., 2020; Westerland et al., 2021). By incorporating ITV into both individual trait response (Chapter 3) and community assembly (Chapter 4) analyses, my research demonstrates its broader relevance across ecological contexts. Future work should focus on integrating ITV into more trait-based analyses to improve understanding of functional differentiation, community assembly, and ecosystem resilience (Albert et al., 2011; Jung et al., 2010; Siefert, 2012; Volf et al., 2016). Additionally, more research is needed in underrepresented geographic regions (e.g. Africa) and biomes (e.g. deserts) where ITV remains poorly studied (Siefert et al., 2015).

Disconnects between tropical and temperate grassland ecology

My thesis explored how environmental drivers shape grass communities across both tropical and temperate environments. However, as I investigated these systems, a disconnect between tropical and temperate grassland ecology became evident. For example, the trait-based framework I used to assess grazing responses (Archibald et al., 2019) was developed within tropical grasslands, where both grazing and fire strongly shape life history strategies. While I chose this framework as it represented the most recent update to grazing trait classification, its relevance in temperate systems, where fire can play a lesser role and grazing dynamics may differ, is uncertain. Other work developed in temperate grasslands, such as frameworks by Briske (1996), categorise certain traits differently. For example, short stature is considered a grazing-avoidance trait in Briske's framework, but a grazing-resistance trait in Archibald et al.'s. Whether these differences reflect an updating of understanding of grass trait responses or fundamental differences in how trait functions operate across systems remains unclear. To determine whether grazing trait responses are truly analogous across tropical and temperate systems, direct comparisons of grazing experiments across these regions are needed. Such studies could clarify whether trait responses align under the updated Archibald et al. (2019) framework or whether temperate systems require a distinct, revised classification of grazing strategies.

Tropical and temperate grasslands share key ecological processes that shape them in similar ways. Ward et al. (2020) found that temperate and subtropical grasslands exhibited consistent long-term vegetation patterns under comparable fertilisation, mowing, and fire treatments, suggesting shared community assembly rules despite differences in species pools and climate conditions. Similarly, my examination of grazing lawns revealed that positive vegetation-herbivore feedbacks create analogous habitats, demonstrating grazing's ability to similarly shape grasslands across environmental contexts. However, research on tropical and temperate grasslands remains largely separate. This separation hinders the identification of cross-system processes and limits our understanding of how broad environmental factors influence grassland composition, function, and biogeography. While some studies have attempted to reconcile this disconnect - examining variations in soil stoichiometry (Hernández-Romero et al., 2024), CO₂ responses (Hall et al., 1995), and

productivity (Mott, 1983) across both - cross-system comparisons are rare. Therefore, a more integrated research approach across tropical and temperate grasslands is needed to uncover the fundamental drivers of grassland dynamics and better predict their responses to environmental change.

Future work

A key challenge in ecology is determining generalisability - the extent to which patterns observed at individual sites also apply across spatial scales and environmental conditions. This challenge has particularly hindered grassland and grazing ecology as the interactions between and importance of environmental drivers likely shift between ecosystems. While this thesis explored trait dynamics across both tropical and temperate grasslands, the extent to which my findings generalise to other systems is still unknown. Therefore, we need to develop research that explores key themes in multiple regions over a range of spatial and temporal scales, using a coordinated and consistent set of methods. Doing so would enable us to develop global models that better explain environmental factors affecting biological processes across spatial and temporal scales and ecological contexts (Denny & Benedetti-Cecchi, 2012; Levin, 1992). Existing local study networks, such as the Nutrient Network (Borer et al., 2014) and the Global Grassy Group plot network (Lehmann et al., 2022), provide standardised datasets that facilitate comparisons across systems and environmental gradients. For instance, analysing how the relative roles of intraspecific trait variation and species turnover shift along rainfall gradients would provide more information on the contexts in which intraspecific trait variation is the dominant mechanism driving community responses. Expanding plot network efforts and conducting more explicit comparisons between tropical and temperate grasslands and across wide environmental gradients will help to clarify both shared and divergent processes governing grassland ecosystems, ultimately providing a better understanding of grassland dynamics as a whole.

Plant-soil interactions are a fundamental component of grassland ecosystems, shaping grassland community composition (e.g. Marrs, 1993; Sebastiá, 2004), life history strategies (e.g. Anderson et al., 2006; Ordoñez et al., 2009), and responses to disturbances (e.g. Cousins, 2009; S. Zheng et al., 2015). Furthermore, grassland community composition

and disturbance regimes shape soils, altering soil properties and processes such as microbial activity and nutrient cycling (Abdalla et al., 2018; Augustine & McNaughton, 2006; Castillo-Garcia et al., 2022; Neary & Leonard, 2020; Parker et al., 2012). Across my three chapters, soils emerged as an important but under-quantified factor influencing grassland dynamics. For example, soils likely influenced grazing lawn creation and persistence (Chapter 2), with soil conditions, along with rainfall, potentially playing a key role in maintaining the grazing lawn state and preventing overgrazing (Hempson et al., 2022). Across Madagascar, soil sand content - my proxy for nutrient availability - was associated with variation in inflorescence height and leaf length, width and thickness (Chapter 3), highlighting the role of soils in functional differentiation. In my Scottish upland plots, compositional differences between plots may have been driven by unmeasured variations in soil conditions (Chapter 4). While Chapter 3 included a coarse proxy for nutrient availability, one important aspect of soils, the absence of direct soil data across all chapters limited my ability to fully assess the role of soils in structuring grassland communities. Therefore, future work should incorporate soils either directly through sampling or through the inclusion of proxies that capture key aspects of soil properties - such as available nitrogen, available phosphorus, organic carbon, soil moisture, and texture - to better understand how soils drive grassland trait responses and community assembly.

While this thesis focused primarily on grasses, forbs - non-graminoid, herbaceous angiosperm species - are an important component of grassland ecosystems (Bond & Parr, 2010). In semi-arid savannas, forbs can contribute up to 78% of the species richness (Siebert & Scogings, 2015), while in temperate wet grasslands, such as the Pacific Northwest Bunchgrass Prairie, they can comprise as much as 83% (Averett & Endress, 2022). Forbs are also a key component of many herbivores' diets due to their high nutritional value, having the highest nitrogen and phosphorus tissue concentrations among plant functional types (Bråthen et al., 2021; Niinemets et al., 2015). I demonstrated that forbs can be an important component of some grazing lawns, having high palatability and the capacity to tolerate repeated grazing (Posse et al., 2000; Prins et al., 1980; Vaieretti et al., 2013). Despite their importance in herbivores' diets and dominance in many grazing lawns globally, our understanding of forb responses to disturbances in grasslands remains limited (Bråthen et

al., 2021). Studies increasingly suggest that forbs and grasses may show differing functional responses to rainfall, fire, grazing and fertiliser treatments, possibly due to distinct trait trade-offs (Segrestin et al., 2023; Van Coller et al., 2018; Zhang et al., 2022). How these differences impact community assembly is also not well understood. In Chapter 4, I focused on the role of intraspecific trait variation and species turnover in shaping grass community responses to grazing, due to their long evolutionary history with grazing (Mack & Thompson, 1982; Owen & Wiegert, 1981) and to minimised trait variability within sites, making trait variation patterns more apparent (Adler et al., 2004; Westoby et al., 2002). Forbs, though present, were not included in this analysis (Pakeman et al., 2019). This exclusion highlights remaining important questions: are the mechanisms underlying trait-based community responses in grasses shared by forbs within the same system? and do these patterns of community assembly hold when assessing the grassland community as a whole? Understanding whether forbs follow similar or distinct patterns of trait differentiation and community assembly in response to disturbances like grazing is an important next step for building a more complete picture of grassland dynamics.

Conclusion

My thesis demonstrated how integrating local and large-scale approaches reveals patterns of grassland community assembly and functional differentiation that would be overlooked at a single spatial scale. In doing so, it provided valuable insights into the ecology of grassland ecosystems by presenting global-scale evidence of grazing as a key driver of vegetation dynamics globally (Chapter 2), examining the influence of multiple environmental drivers on grass differentiation at a regional scale (Chapter 3), and assessing the specific mechanisms underpinning community responses at a local scale (Chapter 4). Together, these findings enhance our understanding of how key top-down and bottom-up drivers shape grasslands, deepening our knowledge of grassland dynamics across contexts.

However, major questions remain about how grassland dynamics vary across environmental gradients and ecological contexts, requiring further research to disentangle the factors driving this variation. In the coming decades, climate change is expected to alter grassland compositions and distributions (Jones, 2019; Zhu et al., 2024) - likely leading to C_4 grasses outcompeting and replacing C_3 grasses (de Deus Vidal et al., 2021; Havrilla et al.,

2023). At the same time, rewilding and livestock practices continue to alter grazing regimes (Donlan et al., 2006; Hempson et al., 2017). These shifts make a clear and predictive understanding of grassland dynamics increasingly urgent. Therefore, the approaches and insights developed in this thesis can help guide conservation efforts, inform grazing management and improve predictions of shifts in ecosystem structure and function under future climate scenarios, contributing to the broader goal of preserving grassland biodiversity and ecosystem functions across systems.

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