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Human pressure as an ecological force across scales and systems

By

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DECLARATION

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Caroline McKeon

ABSTRACT

Human pressure as an ecological force across scales and systems. Caroline Margaret McKeon

Historically, climate has been seen as the main driver of global vegetation patterns, but ecological paradigms have recently expanded to acknowledge human activity as a critical determinant of species biogeography. Today, human land use is the primary direct anthropogenic driver of global biodiversity decline, but not all species respond in the same way. How do species differentially respond to direct human disturbance and to climate? And how do the importance of these factors compare? I investigate these questions through the lens of species inherent characteristics (life form and life history) in different systems (flowering plants and fish) across multiple scales. Drawing on publicly available global databases, I integrate data on climate and different forms of human pressure to assess how these forces compare across dimensions of biodiversity. I investigate: how human land use compares to climate in driving plant life form occurrence and abundance (global); how cumulative human pressure compares to climate in affecting spatial patterning in endemic European plant species (continental); how climate compares to fishing pressure in affecting fish community life history strategy in the North East Atlantic (regional), and how nutrient addition and abandonment of traditional management practises impact productivity, diversity and community composition in a unique high diversity Irish grassland (hyper-local). Across scales and systems, I find that direct human influence is a factor affecting ecological patterns, and that the relative influence of different ecological drivers depends on the extent and resolution at which they are studied. Climate and human disturbance act in tandem as filters shaping the realised niches of species through space. Additionally, human disturbance may produce more divergent outcomes than climate across species inherent traits, contracting the niche of species with slower life history and expanding the niche of disturbance tolerant species. My findings highlight the urgent need to include direct human disturbance in all investigations of fundamental ecological patterns, and to explicitly consider the scale at which are ecological questions are being asked. If biodiversity is to be protected, and broad patterns of life in space and time understood, we must consider ecology within the context of pervasive human influence.

SUMMARY

Human activity has been part of the natural world for thousands of years, and our influence has been increasing dramatically in the last century, such that it is not possible to fully understand the natural world without considering our effect on it. In spite of this, it is still not the *de facto* position in ecological research to consider human influence as an ecological force. The relationship between ecological patterns and their environment is scale dependant, meaning that the signal and relative importance of ecological variables depends on how they are observed. The theme of this thesis is the explicit inclusion of human influence in investigations of ecological patterns including an additional consideration of scale with the aim of improving our understanding of patterns as they occur in today's world, and providing evidence for the ecological impacts of the main driver of global change. I use open source data, a manipulative field experiment, and Bayesian and Frequentist Hierarchical modelling to address these aims. Across different dimensions of spatial scale, I focus on how human pressure compares to climate in affecting plants across their intrinsic traits (Chapter 2) and in their patterning through space (Chapter 3). I then investigate how spatial scale affects the signal of human pressure on traits in Marine communities (Chapter 4), and how two human activities compare and interact in affecting biodiversity in a high resolution case study (Chapter 5). At all scales, I find human pressure to be affecting ecological patterns. The relative importance of human pressure compared to other ecological factors varies with the scale of investigation, and at some scales, human pressure is comparable in importance to non-human variables (i.e. climate) in its ecological impacts. Where data was available, I found species' responses to human pressure to be mediated by their intrinsic traits. Considering human influence in ecological studies is a realistic and informative step needed in understanding the natural world and in efforts to protect it in light of global change. Importantly, understanding the full suite of factors impacting ecology can be best achieved by explicitly considering the scales at which they are studied.

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Additional published or submitted work

1. Tramps in transition: genetic differentiation between populations of an iconic "supertramp" taxon in the Central Indo-Pacific. Fionn Ó Marcaigh, Darren P. O'Connell, Kangkuso Analuddin, Adi Karya, Naomi Lawless, Caroline M. McKeon, Niamh Doyle, Nicola M. Marples and David J. Kelly (2022), ***Frontiers of Biogeography*** https://doi.org/10.21425/F5FBG54512

FÓM, DOC, DJK, and NMM conceived this study. FÓM, DJK, and NMM led the writing of the manuscript. DJK, NMM, DOC, FÓM, AK, and KA carried out the fieldwork. FÓM, NL, and ND carried out the labwork. CM measured the geographic distances. FÓM analysed the data, with input from the other authors. All authors contributed to revising and improving the manuscript.

2. Twin pressures of intensification and abandonment negatively impact grassland biodiversity in the Burren. Caroline M. McKeon, Alain Finn, Maria P. Long, Ian Donohue, Yvonne M. Buckley (2022), ***Biology and Environment: Proceedings of the Royal Irish Academy***

Research was conceived and designed by CMM, AF, ID and YMB. Data were collected in the field by AF, CMM, MPL and YMB, and processed further in the lab by AF. CMM conducted the data analysis and wrote the first draft. YMB and ID provided advice on analyses. All authors provided feedback on the manuscript.

3. "Land use and climate affect plant occurrence and abundance across life forms." Caroline M McKeon, Ruth Kelly, Luca Börger, Adriana De Palma, Yvonne M. Buckley. Revised manuscript submitted in September 2022 to ***Ecology Letters***

Research was conceived and designed by CMM, RK, YMB and LB. CMM conducted the data analysis and wrote the first draft. RK and YMB provided advice on analyses. Data were contributed through TRY, BIEN and Worldclim, and through PREDICTS by LB and AP. Results were initially interpreted by CMM with advice from YMB and RK. All authors provided intellectual input and edited the MS.

4. "Synergistic solutions to climate change (renewable infrastructure) and biodiversity loss: Cass study of Ireland." Courtney E. Gorman, Andrew Torsney, Aoibheann Gaughran, Caroline McKeon, Catherine Farrell, Cian White, Ian Donohue, Jane Stout, Yvonne M. Buckley. Review for the Irish Climate Change Advisory Council, submitted May 2022 to ***Science of the total environment***

CEG and YMB carried out project administration and wrote the original draft. Conceptualization, investigation, and manuscript review and editing was carried out by AT, AG, CF, CW, CMM, ID, JS, YMB, CEG. CMM contributed visualizations. YMB carried out supervision and funding acquisition.

5. "Contribution of geographically common and rare species to spatial biodiversity patterns." Hannah White, Caroline McKeon, Robin Pakeman, Yvonne Buckley. Submitted in June 2022 to ***Global Ecology and Biogeography***

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Chapter 1 General introduction

1.1 Human influence on the N-dimensional niche

Global change is having massive impact on the natural world (Almond et al., 2020; Boyce et al., 2010; Brondizio et al., 2019; Díaz et al., 2019; Masson- Delmotte et al., 2021). Both for our fundamental understanding of ecology, and in order to protect and benefit from the natural world, it is important to understand how global change is affecting species. Climate is acknowledged as a critical factor shaping ecological patterns (Elsen et al., 2021; Foden et al., 2019; Gaston, 2003; Olson et al., 2001; Smith, 1909; Whittaker, 1970). As such, much ecological research has focused on the impacts of current and future climate across levels of biological organisation (Corlett & Westcott, 2013; Elsen et al., 2021; Malhi et al., 2020; Weiskopf et al., 2020). In addition to climate change, another more immediate component of global change is direct human pressure (Almond et al., 2020; Díaz et al., 2019; Grooten et al., 2018). In terrestrial environments, direct pressure manifests as human land use - currently the leading cause of global biodiversity loss (Almond et al., 2020; Díaz et al., 2019; Grooten et al., 2018; Newbold et al., 2015). Human pressure is highest in the most biologically productive environments (Kennedy et al., 2019; Venter et al., 2016), affecting the composition (Newbold et al., 2016) and heterogeneity (Newbold et al., 2018) of ecological communities, and interacting with climate change to affect trends in species' populations (Williams et al., 2021). In marine environments, direct human pressure appears as fishing pressure and habitat loss (Fu et al., 2012; Halpern et al., 2008; Moullec et al., 2021), which are negatively impacting marine systems (Halpern et al., 2015; Jackson et al., 2001; Sala & Knowlton, 2006).

While there is clear evidence of the largely negative impacts of recent human activity on global biodiversity trends, there is still a lack of studies integrating human influence into ecological research (Estes et al., 2018; Liu et al., 2007). Despite evidence for the pervasiveness of human impact in ecology, much work seeks to study ecology as it "would have" happened, in the absence of human influence (Ellis, 2019). Three ideas may be contributing to this disparity. Firstly, humans and nature are seen as independent i.e. there are currently places on the planet that are "wild", when in reality, excluding Antarctica, 95% of terrestrial land shows some evidence of human modification (Kennedy et al., 2019). A second more philosophical reason why "true" ecology and human influence are often separated is that humans have been seen as "outside nature", not subject to its laws. Rather than being grounded in scientific evidence, the idea of nature as untouched by and independent from people (Prümers et al., 2022), or latterly as a resource that can be optimised for extraction (Mace, 2014; McCauley, 2006) is a result of historic, colonial and capitalist ideology (Redford & Adams, 2009), and still informs much of ecological thinking (Ellis, 2019; Fletcher et al., 2021; Mace, 2014). Ecological and conservation sciences have only recently begun to view human and "natural" systems as integrated (Folke et al., 2021; Liu et al., 2007; Mace, 2014), as the inaccuracy and unsustainability of earlier views are increasingly recognised (Clement et al., 2021; Fletcher et al., 2021; Folke et al., 2021; Roberts et al., 2021). Thirdly, human influence is not viewed as an extrinsic ecological factor because pervasive human impact is often still seen as a relatively recent phenomenon. However, in the terrestrial environment, human activity has been shaping ecology globally for at least the last 12,000 years (Ellis et al., 2021; Tallavaara et al., 2015; Prümers et al., 2022; Pires et al., 2015; Sales et al., 2022; Fricke et al., 2022), with an increase in intensity in the last 300 years (Ellis et al., 2021, 2010), and a further dramatic increase during the last 70 years (Kennedy et al., 2019; Steffen et al., 2015; Venter et al., 2016). These "aboriginal" (beginning approximately 12000 to 5000 years ago - in some cases beginning 35-40000 years ago), "colonial" (beginning 500-100 years ago) and "global" (beginning in the last 100 years) periods of different intensities of human activity/extraction have also been described in the marine environment (Jackson et al., 2001). Viewing human influence as distinct from other ecological forces is therefore inaccurate and limits our understanding of ecology (Liu et al., 2007; Sullivan et al., 2017).

Just as current climate change is different from past climate changes by virtue of the *rate* rather than the magnitude of change, current human activity is markedly different to the long history of human terrestrial and marine presence that came before (Ellis et al., 2021; Fletcher et al., 2021; Folke et al., 2021; Jackson et al., 2001; Steffen et al., 2015). Human presence and activity has coincided with (Araújo, 2003; Prümers et al., 2022) or been responsible for promoting high biodiversity in many places for thousands of years (Ellis et al., 2021), (though not always, and not for all types of species (Fricke et al., 2022; Pires et al., 2015; Sales et al., 2022)). I therefore distinguish between human presence - our long history of interaction with the rest of the natural world, and human pressure – the dimension of rapid and escalating global change coinciding with drastic biodiversity trends i.e. the sixth mass extinction (Barnosky et al., 2011). Human influence, both past and present, is a pervasive and unignorable ecological force. If ecological patterns are to be properly explained and understood, and a sustainable future created for ecological systems, human influence must be integrated into the study of ecology (Ellis, 2015; Cepic et al., 2022; I. Dullinger et al., 2021; Folke et al., 2021).

1.2 Pattern and scale

At different spatial and temporal scales, factors contributing to patterns in ecology are of different relative importance (Chase, 2014; Chase & Knight, 2013) - “no single mechanism explains patterns on all scales” (Levin, 1992). Consider *Plantago lanceolata* in a field in the Burren in Ireland. The pattern of its genetic distance from other species in that field may be best explained by processes (geological, climatic, evolutionary) at a phylogenic time scale – millions of years (Spiridonov & Lovejoy, 2022). The pattern of this plant’s presence in this field in relation to its global distribution (i.e. it’s biogeographic range) may be best explained by climate on a time scale of thousands of years (maybe since the Last Glacial Maximum in Europe) (Svenning & Skov, 2007), by the movement and agricultural practises of humans (Smith et al., 2020), and by *Plantago*’s dispersal ability (Estrada et al., 2015; Sporbert et al., 2021). The relative abundance of the plant in this field might be best explained by the nuances of the human management of the field (Borer, Seabloom, et al., 2014; Dunford & Feehan, 2001) (grazing to provide disturbance) and abiotic conditions (rainfall and soil nutrients) (Parr et al., 2009) in addition to biotic interactions (Gurevitch et al., 2016), while the realised life history strategy of a plant in this field might be influenced by the suitability of climatic conditions (Csergő et al., 2017). None of these factors are the single most important factor in *Plantago* ecology, but different factors and their interactions may have more or less relevance depending on the spatial and temporal extent and resolution of ecological patterns under study (Sandel & Smith, 2009; Sporbert et al., 2020).

The relative importance of factors to ecological patterns is related to the amount of variance in these factors experienced by the ecological units being studied - “spatial and temporal variability will be a function of the size of the window used to view the world: as window size is increased, variability will decay” (Levin, 1992). There are at least four dimensions of scale to consider. Firstly, we can consider scale across time and space. Secondly, for both time and space, we can consider scale as extent, and as resolution. Extent describes the range of data under consideration, i.e. the extent of study through time could be data from 24000 years ago up until the year 2000, and the temporal resolution could be one data point every 500 years (coarser resolution), or one data point every three months (finer resolution). Similarly, the spatial extent of a study could be terrestrial Europe, bounded by 30 to 82 degrees latitude and -33 to 67 longitude, and the spatial resolution could be one the presence or absence of a species every 50 x 50km (coarser resolution), or one data point every 1km^2 (finer resolution).

Processes at one scale may feed into patterns at another scale, i.e. there can be mismatches in time and space between the ecological forces and their outcomes manifesting as ecological patterns (Sandel & Smith, 2009; Jackson et al., 2001; Chase et al., 2019). This thesis focuses on assessing the relative importance of human and climatic factors to patterns at a range of scales, from local to global. There is no objectively correct scale at which to study ecological patterns, but the scale at which the relationship between a pattern and a factor is studied should be ecologically appropriate to that pattern (Catford et al., 2022). Studying factors at different spatial and temporal scales is needed to disentangle the multifaceted and complex workings of ecology (Estes et al., 2018; Levin, 1992; Sandel & Smith, 2009; Windsor et al., 2022). As I demonstrate in chapters three and four, matching the scale at which a pattern is studied to the scale at which factors are affecting ecological processes is crucial to our ability to detect the signal of these factors, and so to our ability to understand ecological responses to global change, as its drivers - climate change, human land use, invasive species - are acting at vastly different scales (Carl et al., 2016; Newbold, 2018; Powell et al., 2013). I seek to assess and compare the relative explanatory power of ecological factors to ecological patterns across scales, in order to provide evidence for the importance of those factors (i.e. human land use) and also to better understand ecological patterns as we see them.

1.3 Species' intrinsic traits

Globally, the aggregate effect of recent human pressure on ecological systems is negative (Díaz et al., 2019; Foley et al., 2007). However, not all species, nor all metrics of ecological health are in decline (Dornelas et al., 2014; Leung et al., 2020; McGill et al., 2015), as species differ in their responses to ecological forces, including human pressure (Newbold et al., 2018). These differing responses are mediated by species intrinsic characteristics – species traits (Funk et al., 2017; Lavorel et al., 2002; Violle et al., 2007).

In order to investigate patterns in ecology, in particular species responses to global change, it is useful to group species by their intrinsic traits (Díaz et al., 2013, 2016; Fisher et al., 2017; Garnier et al., 2007, 2018; Litchman et al., 2013; Mouquet et al., 2015). Characterizing species by their intrinsic traits provides a middle ground between low resolution information, i.e. biodiversity is in decline, and high resolution information that is resource intensive to gather, i.e. information on the individual responses of each genotype within each species. Grouping species in some biologically meaningful way allows us to investigate patterns across types of species, i.e. larger, slower lived species are less well equipped to cope with increasing anthropogenic presence (Fricke et al., 2022; Pires et al., 2015; Sales et al., 2022) and pressure (Carmona et al., 2021; Leung et al., 2020; Yackulic et al., 2011), while more generalist (Mabry & Fraterrigo, 2009) and opportunistic species (Pecuchet et al., 2017) are better equipped to cope with increased human pressure.

Characterisations of species' intrinsic traits can be considered another dimension of scale (König et al., 2019), i.e. resolution (level of detail captured by a classification system) or extent (the amount of available trait space covered by species in a study). Further, these characterisations themselves exist on a spectrum from high resolution information to high data availability. Higher resolution characterisations can provide detailed ecological information, i.e. demographic and life history data (Doak & Morris, 2010; Healy et al., 2019; Ramula et al., 2008), but are often hard to obtain at broad spatial, temporal or taxonomic extents (Salguero-Gómez et al., 2014). For data rich characterisations more information may be available (Kattge & Knöll, 2020; Maitner et al., 2018; Weigelt et al., 2019) but these traits may provide only general ecological insights i.e. plant life form (Smith, 1909), or their interpretation may depend on the ecological context, i.e. functional traits (Kelly et al., 2021). While open source data is available at unprecedented taxonomic and geographic scales (König et al., 2019), this information varies in resolutions and coverage. Trade-offs between data availability and ecological realism must therefore be considered when characterising species by their intrinsic traits.

1.4 Thesis outline

There are three broad motivations behind this thesis:

1. to explicitly include human influence in investigations of ecological patterns (**Table 1**) and compare it to other non-human factors affecting ecology;
2. to investigate these relationships across scales (**Table 1**), with an explicit consideration of how the scale at which a pattern is studied affects the signal of its relationship with ecological factors;
3. where possible, to consider how species' intrinsic traits (**Table 1**) interact with human pressure to produce divergent outcomes in species in the world today.

Through these approaches I hope to contribute to a more realistic understanding of real world patterns in living systems and provide evidence for the unignorable role of human influence as a force in ecology.

Table 1.1. Overview of the systems, patterns, scales, types of human pressure and intrinsic traits studied in this thesis.

Chapter	Study system	Pattern	Scale	Human pressure	Intrinsic traits
2	Terrestrial plant species	Occurrence and abundance	Extent: Global Resolution: < 1km2	Human land use	Raunkiaer's plant life form
3	Terrestrial endemic plant species	Metrics of range size and structure	Extent: Europe Resolution: approx. 50 x 50 km	Human footprint	
4	Marine fish communities	Community weighted mean traits	Extent: Celtic-Biscay Shelf, Resolution: 5 x 5km up to 250 x 250km	Fishing pressure	Life history traits
5	Terrestrial plant community	Biomass and biodiversity metrics	Extent: approx. 80 x 22 m Resolution: 1 m2	Nutrient addition and traditional grazing by large herbivores	

In chapter 2, I explore how Raunkiaer's plant life form produces divergent responses to human land use, and how the relationship between life form occurrence and land use compares to the relationship between life form occurrence climate.

In chapter 3, I investigate whether including human pressure along with phylogeny, and past and contemporary climate helps to explain variation in spatial patterns of endemic European plant species. I compare the effects of human pressure to other variables in the models and explore how the scale at which these spatial patterns are studied affects the strength of the signal of human pressure.

In chapter 4, I assess whether human pressure along with depth and temperature affect the community composition of life history traits in Marine fish. I compare the magnitudes of these effects across a series of spatial scales to assess how the signal of human pressure depends on the scale at which community is defined.

In chapter 5, I use a small-scale case study to investigate in detail how two human management actions interact to affect productivity and diversity in grassland plant communities.

Finally, in chapter 6, I summarise and discuss the findings on the relative importance of human pressure as an explanatory variable in ecology, how this relative importance is scale dependant, and how understanding this can help us consider the appropriate extrinsic factors at the appropriate ecological scales needed to understand how global change is producing divergent responses across species' intrinsic traits.

Chapter 2 Human land use is comparable to climate as a driver of global plant occurrence and abundance across life forms.

Running title: Human land use drives global biogeography

“Human influences are reshaping plant communities around the world through both extinctions and species gains. New work relating biodiversity shifts to rapid changes in climate and land use highlights the need for new biogeographic frameworks to understand evolutionary change in the Anthropocene.” (Ellis, 2019)

Authors: Caroline M McKeon, Ruth Kelly, Luca Börger, Adriana De Palma, Yvonne M. Buckley

Author contribution: Research was conceived and designed by CMM, RK, YMB and LB. CMM conducted the data analysis and wrote the first draft. RK and YMB provided advice on analyses. Data were contributed through TRY, BIEN and Worldclim, and through PREDICTS by LB and AP. Results were initially interpreted by CMM with advice from YMB and RK. All authors provided intellectual input and edited the MS.

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2.1 Abstract

Historically, climate has been a dominant driver of global vegetation patterns. Recently, ecological understanding has been updated to acknowledge the influence of human land use (the dominant driver of biodiversity change) in shaping global vegetation patterns. We combined data from the biodiversity and land use database PREDICTS, and plant trait databases TRY and BIEN to test whether Raunkiær’s life form, a plant classification system designed to reflect climatic drivers, affects how over 4800 species at over 300 sites globally, respond to both land use and climate. We provide evidence that human land use is comparable to climate in influencing life form occurrence, and that land use produces divergent outcomes across life forms. Combined with climatic suitability, land use acts as a filter contracting the niche of trees and expanding the niche of disturbance tolerant species. Our results highlight the fundamental role of human activity in shaping species’ distribution.

2.2 Introduction

2.2.1 Species' differing responses

Globally, biodiversity is in decline (Almond et al., 2020; Díaz et al., 2019). While the global trend is clear, not all species respond to anthropogenic pressures in the same way. Extinction risk differs across functional traits (Carmona et al., 2021) and land use drives changes in community composition (Allan et al., 2015; Maseyk et al., 2017), indicating non-uniform responses of species. Conflict in the literature (Eriksson & Hillebrand, 2019; Gonzalez et al., 2016) surrounding the rates (Grooten et al., 2018; Le Roux et al., 2019; Leung et al., 2020) and directions (Mentges et al., 2020) of trends in biodiversity, as well as the scales (Dornelas et al., 2014; Hautier et al., 2018; Suggitt et al., 2019) and metrics (Hillebrand et al., 2018; McGill et al., 2015) relevant to their measurement, supports differential species' response. What is it about species that enables some to thrive in anthropogenic environments and others to decline?

2.2.2 Drivers of global vegetation patterns

The leading cause of biodiversity loss and ecosystem change is human land use (Brondizio et al., 2019; Díaz et al., 2019). Human activities have influenced terrestrial biodiversity for at least 12,000 years (Ellis et al., 2021). This influence has increased in the last 300 years (Ellis et al., 2010), and further in the last century (Steffen et al., 2015). Currently, 75% of the earth's surface is subject to anthropogenic land use (Ellis et al., 2010; Ellis & Ramankutty, 2008; Venter et al., 2016a). Excluding Antarctica, only 5% of land shows no evidence of modification by human activity (Kennedy et al., 2019). In addition, the rate of land-use change is accelerating most rapidly in areas with highest biodiversity (Venter et al., 2016b).

While the main driver of global vegetation patterns has historically been regarded as climate (Whittaker, 1970), how species respond to land use is a determinant of contemporary species distributions and their fate in the Anthropocene. Human use of the earth's terrestrial surface is so pervasive that which biological communities occur is a result not only of climate, biotic interaction and biogeographic legacy but also to what extent humans use the landscape. We therefore consider all types of land use to be human land use, including "primary" vegetation which are classed within PREDICTS as 'forest' or 'non-forest'. We use Raunkiær's Life form, a species trait classification established to describe the influence of climate on species distributions, to investigate species' differential responses to land use, and to compare the effects of land use to climate in influencing global patterns of vegetation.

2.2.3 Life forms

"The plant itself must be the recorder of the biological value of any climate" – Raunkiær, (Smith, 1909).

In the early 20th century Raunkiær devised a plant classification system to capture the correlation between climate and vegetation (Smith, 1909). He proposed that the biological value (productivity) of a climate could not be accurately measured with physical climate parameters, as (a) different parameter values could produce the same vegetation assemblages or (b) parameter values could have different outcomes depending on other parameters. Instead he proposed biogeographers measure "biological spectra"; the relative abundance of "life forms" (**Fig 1**) as manifestations of the biological value/productivity of climate through statistical analysis of biological spectra.

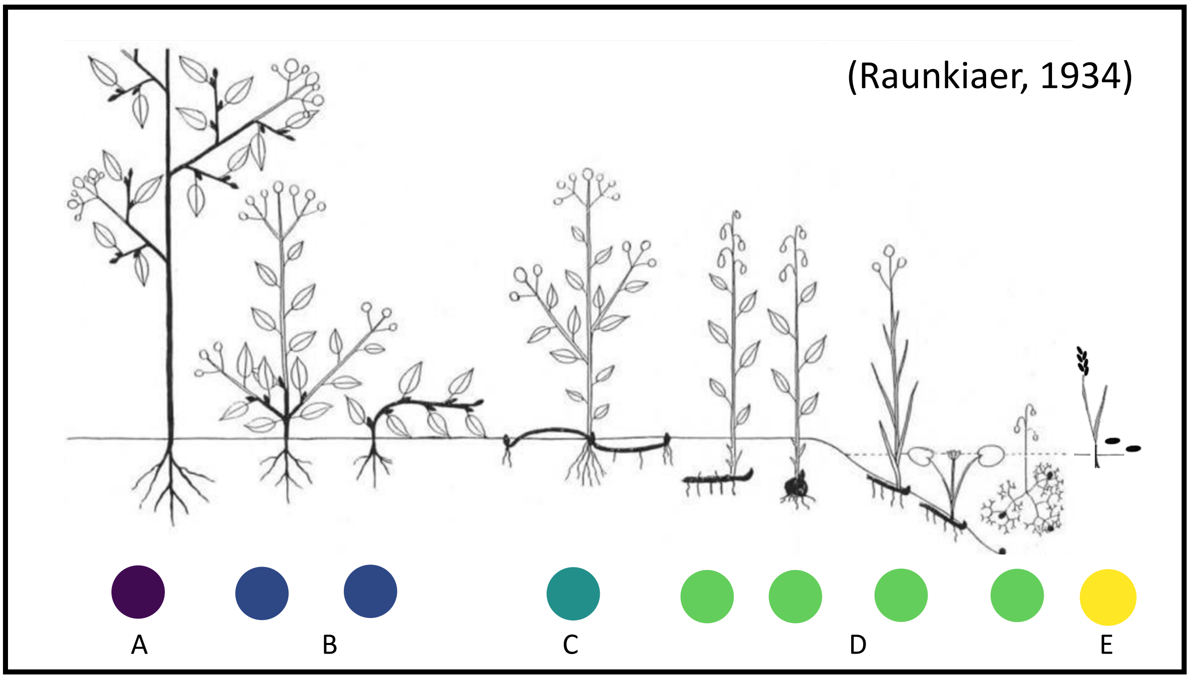

Figure 2.1. Raunkiær's Life forms.

Raunkiær classified plant "life forms" based on the location of the plant's points of regrowth, following local climatic bottlenecks. Plants regrow from apical meristems, i.e. buds, bulbs, seeds, following climatic bottlenecks least suitable for growth, i.e. the coldest/hottest/driest/flooded period. Life forms describe the vertical position of apical meristems (degree of meristem exposure) as adaptations to increasingly harsh local climatic bottle-neck conditions. Life forms can be subdivided to describe local climate at higher resolutions, but broadly they are characterised as phanerophytes (A), chameophytes (B), hemicryptophytes (C), cryptophytes (D) and therophytes (E). Phanerophytes (typically trees) have the highest degree of meristem exposure, regrowing from aerial buds suspended well above the soil surface. They are adapted to compete for space and light in warm, wet climates, but less well positioned to cope with extremes of cold and dry. Chameophytes (typically shrubs) afford more protection to their buds, regrowing from just above the soil surface. Hemicryptophytes (typically herbs) regrow from roots at or near the soil surface, cryptophytes from bulbs below the soil surface, and therophytes solely from seeds, allowing them to survive in climates with extremely harsh bottlenecks. Species can exhibit more than one life form.

Raunkiær's analysis showed the relative abundance of life forms could be used to describe vegetation assemblage, or "phyto-climates". Phanerophytes and therophytes declined with decreasing temperature, hemicryptophytes showed peak relative abundance in temperate zones, and chamaephyte relative abundance increased with falling temperature. Climate had precedence over edaphic factors in driving life form relative abundance. However, comparisons between a one and eight year old grassland showed that successional stage affected the proportions of life forms, highlighting disturbance as the only factor in Raunkiær's analysis to compete with climate as a driver of the biological spectra (Smith, 1909). Life-form is the most widely available trait-based classification of plant species, enabling differential species responses to climate and land-use to be analysed at a global scale.

2.2.4 Ecological paradigms

The framework established with Raunkiær's phyto-climates and biological spectra based on the relative abundance of life forms has been developed into terrestrial biomes (i.e. Whittaker, (1970)) and further, ecoregions (Olson et al., 2001). However, in light of the obvious and increasing human modification of the biosphere (Grooten et al., 2018; Millennium Ecosystem Assessment, 2005; Ellis et al., 2010; Le Roux et al., 2019), biodiversity patterns can no longer be studied independently of anthropogenic influence (Ellis et al., 2021; Sullivan et al., 2017). Recognising land use as an inescapable driver of ecological patterns and processes in the Anthropocene, biomes have now been described in terms of the dual filters of climate and human land use combined (Ellis & Ramankutty, 2008), though there is still a focus on the role of current and future climate (Elsen et al., 2021). We use plant life form to test the differential responses of species to drivers of contemporary biogeography: climate and land use. While climate shapes where species can occur (species' fundamental niche), we show how land use is a dominant factor in determining where they ultimately do occur (i.e., species' realised niche). This realised niche will also be influenced by other factors including biotic interactions, historic climates and dispersal, which are beyond the scope of this analysis.

2.2.5 Aims

We determine: (a) whether species differ by life form in their response to land use and climate, and (b) how land use and climate compare as correlates of life form occurrence and abundance (**Fig 2**). We combine open source databases of plant traits TRY and BIEN (Kattge et al., 2011; Maitner et al., 2018), WorldClim climate data (Fick & Hijmans, 2017), and plant population data from the PREDICTS global dataset of local biodiversity responses to land-use (Hudson et al., 2016a) for 4804 species at 323 sites worldwide (**Fig A.1**). We use frequentist mixed effects models with weighted effects coding to test whether plant species occurrence and abundance differ from the data average as a function of the interaction of life form with land use and climate. We then compare model effect sizes of climate to climatic differences between biomes and ecoregions to assess whether the modelled effects of land use on species occurrence and abundance are comparable to observed effects of climate in relation to biogeographic patterns. Given the climatic basis of the Raunkiaer life form definition we expect that occurrence of life-forms will be influenced strongly by climate, i.e. a strong life form:climate interaction. Given the dramatic effect of land use on vegetation we also expect life form to interact with land use to affect species' occurrence and abundance. We hypothesise that life form will affect species' responses to land use and climate, with life forms adapted to be more competitive in productive environments (phanerophytes – mostly trees) (Irl et al., 2020) more likely to occur in less disturbed land uses (i.e. Primary vegetation or Mature Forest), and life forms adapted to cope with patchiness of resources (hemicryptophytes, cryptophytes and, in particular, therophytes (annuals)) may be more likely to occur in disturbed land uses (Meers et al., 2008) (i.e. Cropland or Urban land uses). We provide quantitative evidence at an unprecedented scale for the relationship between life form occurrence and abundance, land use and climate, highlighting how these relationships compare to existing climate-based frameworks characterising global patterns of potential vegetation. With this work we contribute to a better understanding of the ecological impacts of a key component of global change, building on the work of others incorporating human activity as a pervasive force integral to our understanding ecological patterns in today's world.

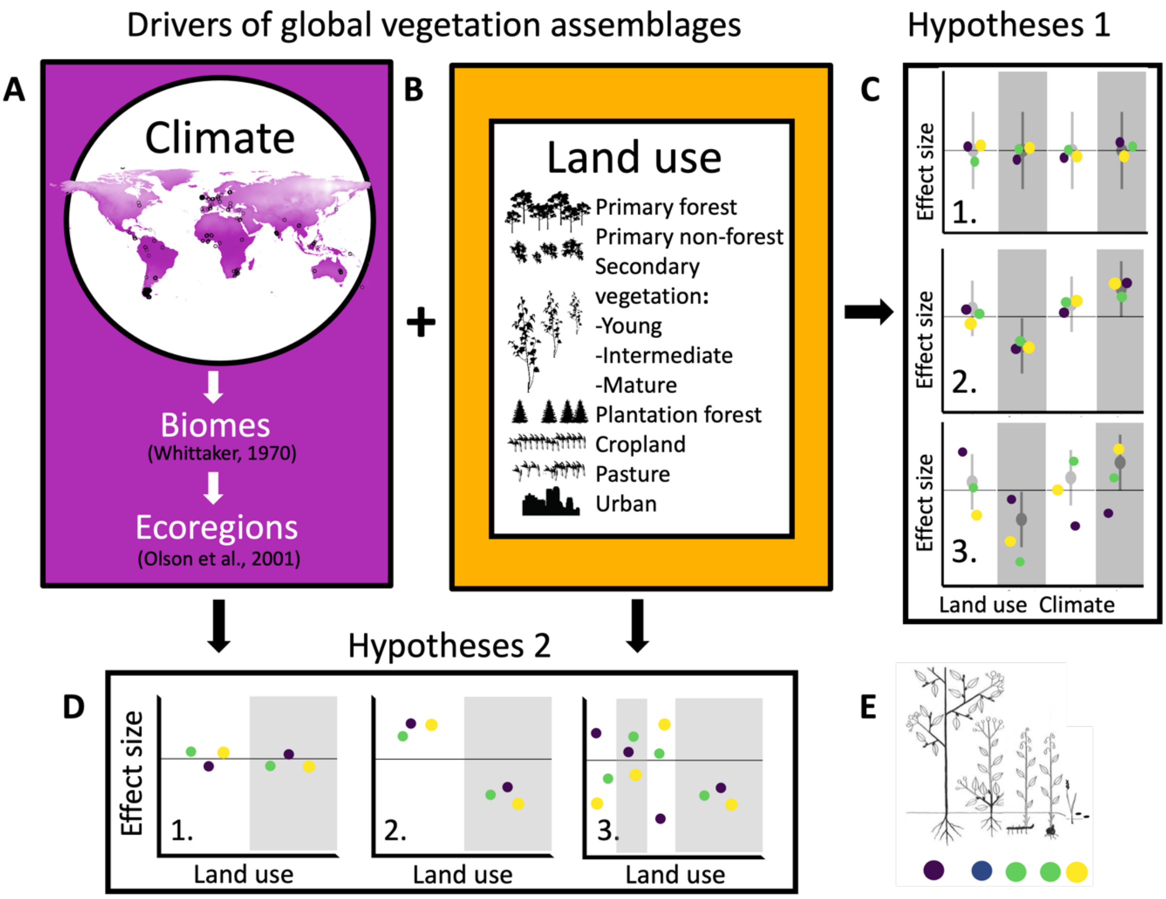

Figure 2.2 Hypothesis diagram.

Raunkiærian life form classifies plant growth strategies in relation to climate. When the classification system was devised, the relative abundance of life forms mainly described local climate (**B**). Since then, our understanding of what drives global vegetation assemblages has been updated to include human land use (**B**). Ecology has strong evidence for how life form is structured by climate, but not by land use (**D**), or how the effects of climate and land use on life form compare (**C**). We test whether land use, currently the leading driver of biodiversity change, affects life form occurrence and abundance. Additionally, we assess how the relationships between life form and land use and life form and climate compare. (**D1**) null hypothesis = land use and life form do not affect species occurrence/abundance; (**D2**) land use affects species' occurrence/abundance and **(D3**) the response of species occurrence/abundance to land use differs by life form. **(C1**) Null hypothesis, there is no effect of climate or land use on life form, **(C2**) the effects of land use and climate on life form are comparable in magnitude, **(C3**) life form occurrence/abundance is more divergent in response to land use than to climate.

2.3 Materials and Methods

2.3.1 Overview

We used PREDICTS (Hudson et al., 2016b), a global database of local biodiversity, to assess whether plant species' life form, land use in a study site, and local climate interact to affect local plant species' occurrence and abundance. Data were collected, cleaned and merged from different sources and analysed using Generalised linear mixed effects models with weighted effects coding in RStudio version 3.6.3 (R Core Team, 2019).

2.3.2 Data collection

Data on plant occurrence and abundance across land uses and site-level species richness were extracted from PREDICTS; Raunkiær life form was extracted from TRY and BIEN; and climate data was extracted from WorldClim.

The PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) database (https://www.nhm.ac.uk/our-science/our-work/biodiversity/predicts.html) gathers information from papers with occurrence/abundance records for individual species associated with land use, as well as site-level total species diversity. Land uses used in this study were: Primary forest, unknown Secondary vegetation, Mature secondary vegetation, Intermediate secondary vegetation, Young secondary vegetation, Plantation forest, Primary non-forest, Pasture, Cropland, and Urban. PREDICTS assumes space-for-time substitution in order to compare species responses across land uses (Hudson et al., 2016b). Importantly, all studies contributing data have: (a) spatial comparisons of species occurrence/abundance, (b) standardised methodology (meaning sites and species can be compared within study), and (c) motivation for recording occurrence/abundance of species at each site, i.e. absence data can be considered as "real" zeroes. "Abundance" data analysed in this study comprised non-zero percent cover data. As such, these data are a reflection of local dominance when a species is present. Scales at which the percent cover data were collected differ between studies, but are comparable within studies. For over 94% of our data, source papers' sampling target was "entire community", and sampling method and effort were comparable within studies. See **SI1** for details and **Dataset S1** for full list of studies.

TRY (Kattge et al., 2011) and BIEN (Botanical Information and Ecology Network) (*https://bien.nceas.ucsb.edu/bien/*) (Maitner et al., 2018) are open access databases containing plant trait measurements from which we obtained life form data. WorldClim version 1.4 (https://www.worldclim.org/data/v1.4/formats.html) is a global climate dataset, from which we obtained statistical summaries of climatic variables as static spatial *bioclimatic* variables at five minute resolution, calculated using monthly records for temperature and rainfall from 1970-2000 (Fick & Hijmans, 2017).

2.3.3 Data handling

Our final dataset included 4804 species, in 3830 plots at 323 sites, from 73 studies in 41 countries across the world. See Appendix **Figure A.1** for site locations and **Table A.10** for sample sizes for each land use - life form combination. These studies were conducted between 1990 and 2013. For details of the data cleaning and amalgamation processes see (see https://doi.org/10.5281/zenodo.6376554). Continuous predictor variables were scaled by subtracting the mean and dividing by one standard deviation. We calculated average climate variable averages for each of 12 Biomes (based on data from Ramankutty and Foley (1999) used in Ellis et al., (2010)) and 809 Ecoregions (based on data from (Olson et al., 2001)). We calculated the average difference between these values for each climate variable for biomes and ecoregions respectively. See https://doi.org/10.5281/zenodo.6376554 for details. See Appendix **Figures A.3 & A.4** and **Tables A.7 & A.8** for biome and ecoregion climate value summaries.

2.3.4 Statistical analysis

Generalised Linear Mixed Models (GLMMs) were used to assess the effect of life form on species response to land use. Terms included in the models can be divided into three groups; (a) categorical main effects (land use and life form), (b) continuous main effects (climate) and (c) random effects, included to account for the nested structure of the data, i.e. within and between group variation in taxonomy, sampling blocks, sites and species. Fixed terms included in the final model dataset were; land use, life form, site level species richness and four climate variables; mean annual temperature, temperature seasonality (SD), mean annual precipitation, and mean annual precipitation seasonality (coefficient of variation). Random terms included in the final dataset related to taxonomy (Class, Order, Family, Genus, Species), and data provenance (Source, Study, Site, and Block). Occurrence and abundance were modelled independently due to the different error structures of the response data. Abundance, based on non-zero percent cover data, was logit transformed and scaled, then modelled using a gaussian error distribution using the lme4 R package (Bates et al., 2015). The occurrence model (based on presence/absence from the full dataset) was modelled using a zero-inflated binomial error distribution from the "template model builder" (GlmmTMB) R package (Brooks et al., 2017).

For both occurrence and abundance, random effects structure was established using null models containing no fixed effects. All random effects were initially included (Barr et al., 2013), and random effects with low attributed variance were removed to prevent issues with model convergence. Once the random effect structure had been established, maximal GLMMs were fitted including all main effects. Model fixed effects terms were: land use, life form and their interaction, climate variables and their interaction with life form, and species richness and its interaction with life form. Species richness was included to account for differences in overall probabilities of occurrence. When accounting for species richness, we therefore compared, for example, primary forest and urban land uses from locations of similar biodiversity, to assess the effects of land use on specific life forms directly. We ran models both with and without species richness. Results of models without species richness (see **Fig A.6** & **Table A.9a and b**) show very similar patterns to those with species richness, with effect sizes of smaller magnitude, i.e. by accounting for species richness, we can see the effects of land use and life form more clearly.

We based the contrasts in our models on weighted effects coding using the “wec” package (te Grotenhuis et al., 2017a), which is more appropriate than treatment coding in this case as the latter requires a meaningful ‘reference’ factor level (te Grotenhuis et al., 2017b) (while a ‘reference’ level for land use could be chosen, it is more ambiguous for plant life form). Weighted effects coding assesses the difference between factor level means (e.g. land-use classes) and the “grand” mean (i.e., the mean of the means of all factor levels), weighted to account for differences in sample sizes between factor levels. The grand mean is therefore equivalent to the mean of the entire dataset. For weighted effects coding, the interpretation of estimates from continuous variables remains the same as in treatment coding i.e. estimates for continuous variables describe the estimated change in response variable for every 1 unit change in the continuous variable (here 1 SD change, due to scaling of variables). For more details on how we applied this method see https://doi.org/10.5281/zenodo.6376554. DHARMa (Hartig, 2018) was used for model diagnostics and ggplot2 (Wickham, 2016) for visualising model outputs. All reported models converged, and were deemed of sufficient fit using model diagnostics. All code used in this analysis is available from https://doi.org/10.5281/zenodo.6376554.

2.4 Results

Land use, life form and the interaction between them had significant effects on plant species occurrence globally (**Fig 3A & Tables A.3**). Climate also interacted with life form to affect occurrence, with temperature variation (MAT variation) having the strongest effect (**Fig 3B & Tables A.3**). With the exception of mean annual temperature variation, the magnitude of effects on species’ probability of occurrence associated with land use were comparable with those associated with a 1 standard deviation change in climate variables, (**Fig 4A & Tables A.5a & b).** Land use and climate also interact with life form to affect species abundance (**Fig 3C & 2D & Appendix Table A.4**). As with occurrence, the largest effects of land use on abundance are comparable to, or larger than, the effects of a 1 standard deviation change in climate (**Fig A.3A & Appendix Tables A.6a & b).** In our dataset, a 1 SD change in most climate variables was comparable to the average difference in climate variables between biomes or ecoregions (**Fig 5 and Appendix Tables A.7 & A.8**).

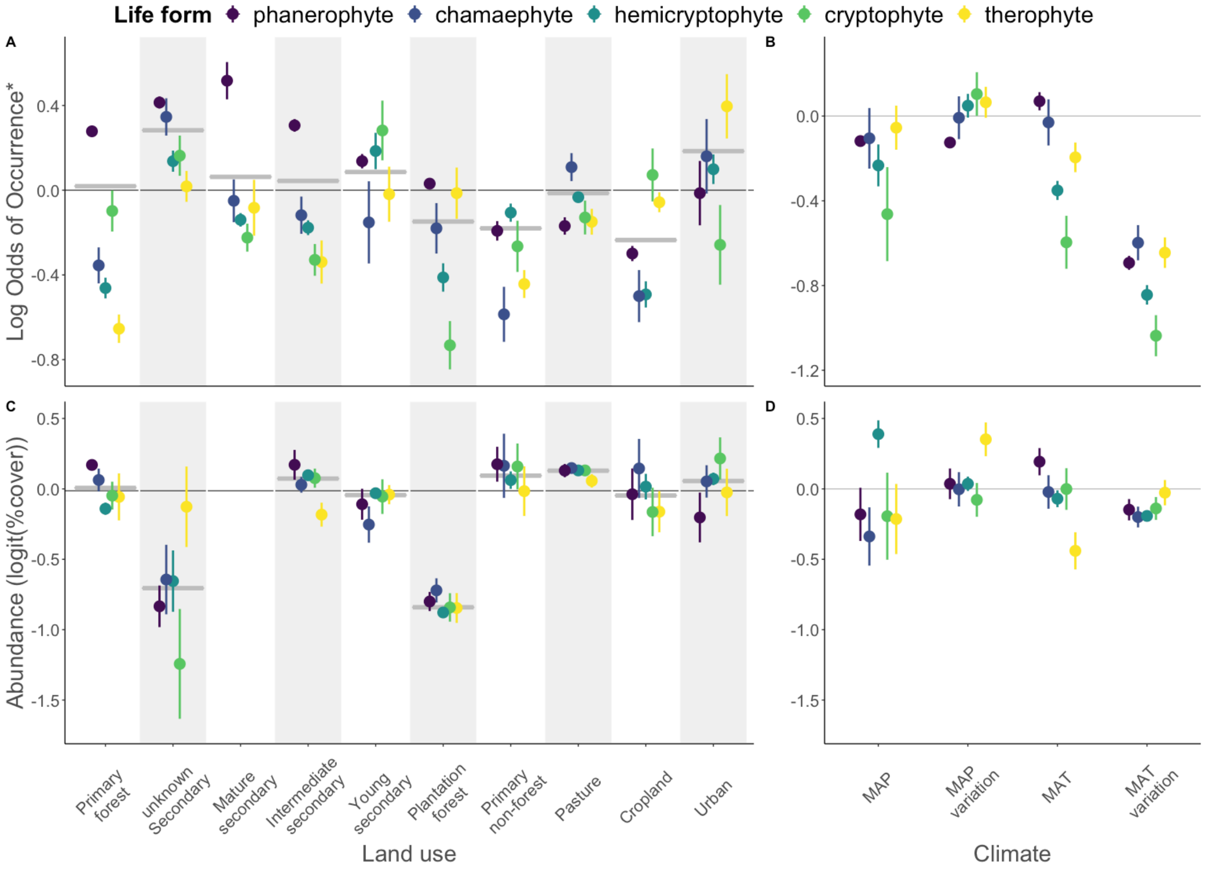

Figure 2.3. Species occurrence and abundance by land use and life form.
A) Effects of land use and life form on occurrence. B) Effects of climate and life form on occurrence. C) Effects of land use and life form on abundance. D) Effects of climate and life form on abundance. In A) and B) Y axis represents log-odds ratio (probability of occurrence) (y axis in panel A represents the log odds minus the grand mean). In A) continuous horizontal line shows the centred weighted mean log-odds ratio, i.e. average probability of occurrence when at mean values of continuous variables, in B) the continuous horizontal line represents zero (no relationship between continuous variable and response). In C) and D) Abundance data describes species' local dominance when present. Y axis represents scaled and logit transformed non-zero %cover data. In C) Horizontal line shows the weighted mean %cover, i.e. average transformed %cover when continuous variables are zero, in D) the horizontal line represents zero (no relationship between continuous variable and response). In A) and C) Horizontal line segments show land use means (across all life forms). Circular (coloured) points show "population" means, as estimated by the model, of the response variable within land uses for each life form. Points lower/higher than the horizontal line indicate that the mean probability of occurrence or abundance estimate of that particular land use*life form combination is lower/higher than the data average. In B and D) Circular (coloured) points represent the slope of relationship (change in log-odds ratio or abundance estimate), associated with 1 SD change in climate for each life form. In A-D) vertical lines represent 95% Confidence interval. CIs overlapping horizontal lines indicate that the probability of occurrence or abundance estimate is not significantly different from average. Total number of observations in occurrence model = 624,696 for 4804 species, and abundance model = 19,384 for 883 species. Note, abundance data for mature secondary forest were not available.

The divergent effects of land use on probability of occurrence within individual life forms (**Fig 4D**), are comparable to the magnitude of the effects of individual climate variables (**Fig 4E & 3C,** & Appendix **Tables A.5c & b**). For individual model estimates, p-values, biome climate averages and climate variable summary statistics, see Appendix **Tables A.5 to A.9**.

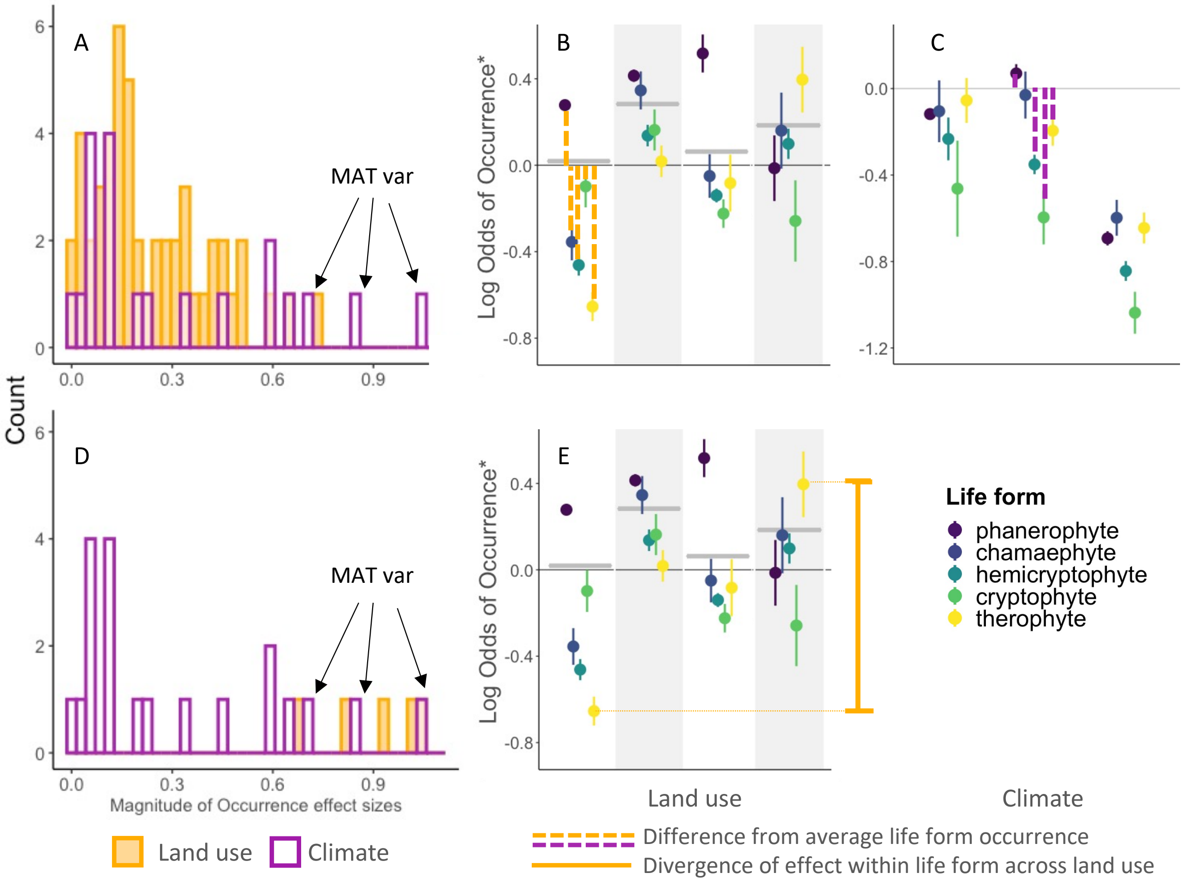

Figure 2.4. Comparison of Climate and Land use Occurrence effects.
In histograms A and D orange bars represent magnitude of land use effects, purple bars represent magnitude of climate effects. Panels B, C and E show illustrative effect sizes of land use (primary forest, unknown secondary vegetation, mature secondary vegetation, urban), and climate (MAP, MAT , MAT var) to enable interpretation of A and D. A - the distribution of effect sizes for life form by land use (dashed orange lines in B), compared to effect of 1 SD change in climate variables (dashed purple lines in C). D - the distribution of effect size range within life form across land uses (solid orange line in E), compared to effect on life form occurrence of a 1 SD change in climate variables (dashed purple lines in C). For a similar figure comparing climate and land use on abundance see **Fig 2.S5**. The largest climate effect sizes were due to Mean Annual Temperature Variation (MAT var) shown in panels A & D.

2.4.1 Land use

Species' probability of occurrence differs by life form across land uses. Phanerophytes had higher probabilities of presence in less disturbed land uses i.e. primary forest, mature, intermediate and secondary vegetation, compared to mean probability of occurrence at mean climate and species' richness values (**Fig 3A** & Appendix **Table A.3**). Though higher than average, phanerophyte probability of occurrence decreases in young secondary vegetation relative to less disturbed land uses (**Fig 3A**, 95% CIs do not overlap with estimates in other non-plantation forest land uses). Phanerophytes had lower than average probability of occurrence in more frequently disturbed land uses (pasture and cropland) and less productive environments (primary non-forest) (95% CIs do not overlap with overall mean). Phanerophyte likelihood of occurrence was not different from the overall mean occurrence of species in urban environments (95% CIs overlap with overall mean). The probability of occurrence of therophytes was higher in more disturbed land uses (**Fig 3A & Table A.3**). Therophyte probability of occurrence was lowest in primary forest and highest in urban land uses (with 95% CIs far from the overall and land use specific mean occurrences).

The abundance results show some similarities to the occurrence results. Phanerophyte abundance when present was higher than the data average in the least disturbed environments (Primary forest, Primary non-forest and Intermediate secondary vegetation), and lower in urban environments (**Fig 3C** & Appendix **Table A.4**). The differences between land uses were more pronounced than the differences within land uses for abundance data. Abundance was lower than the overall data average for all life forms in Plantation forest, and lower for all life forms except therophytes in secondary vegetation of unknown age. Abundance was higher than the data average in less disturbed land uses (Primary forest, Primary non-forest and Intermediate secondary vegetation).

2.4.2 Climate

As expected, life forms differed in their responses to climate variables (**Fig 3B** & **3D** & Appendix **Table A.3-A.4**). The effect (slope) of a climate variable is the change in occurrence or abundance associated with a change of one standard deviation in that variable. In the occurrence data, there was a consistent pattern in the response of life form to increasing precipitation, temperature and temperature variation (**Fig 3B**). Broadly, mean annual precipitation (MAP) and mean annual temperature (MAT) have negative or non-significant effects on probability of occurrence (with the exception of a small positive effect of temperature on phanerophytes) (**Fig 3B**). Mean annual temperature variation has the largest, negative effect on probability of occurrence across all life forms. Mean annual precipitation variation has a small negative effect on phanerophyte occurrence, has no effect on chamaephytes and small positive effects on hemi-, crypto- and therophyte occurrence. For abundance data, responses to climate are more similar across life forms, with some exceptions, mainly for therophytes (**Fig 3D** & Appendix **Table A.4**).

2.4.3 Climate - land use comparisons

Differences from average life form occurrence

The largest differences from average life form probability of occurrence were associated with mean annual temperature variation (**Fig 3B** & Appendix **Tables A.5a-b**). For other climate variables the effects of particular land uses on life form occurrence and abundance are similar to or greater than a 1 SD changes in climate (**Fig 4A,** Appendix **Fig A.5 & Tables A.5a-b & A.6 a-b**). For example the negative effect of Plantation forest on cryptophyte occurrence (-0.732 Log Odds) is slightly greater than the effect of mean annual temperature (-0.596 Log Odds) on cryptophyte occurrence, meaning the difference between average cryptophyte occurrence and cryptophyte occurrence in Plantation forest is similar to the effect of a mean temperature difference of 8.14 degrees C (1 SD MAT), or in terms of biomes between Open Shrubland and Tropical Evergreen Woodland biomes (delta 7.93 degrees C) (**see Fig 5** & Appendix **Tables A.5a-b, A.7 & A.8** for comparisons in terms of biomes).

Range in occurrence within life form across land use

The differences in probability of occurrence *within* life forms across land uses are similar to the differences in probability of occurrence associated with a one SD change in mean annual temperature variation (**Fig 4D**). For cryptophytes, the difference between the land uses with highest and lowest probability of occurrence (Δ1.01 Log Odds) is comparable to the effect of a 1 SD change in mean annual temperature variation (Δ1.04 Log Odds) (**Fig 4D** & Appendix **Tables A.5b-c, A.7 & A.8**). For phanerophytes, the decrease in probability of occurrence between Mature secondary vegetation and Cropland (Δ0.82 Log Odds) is slightly greater than the negative effect of mean annual temperature variation (Δ0.69 Log Odds) (1 SD MAT_var = 23.84 degrees C), i.e. difference in phanerophyte occurrence between Mature secondary vegetation and Cropland is slightly greater than the difference in occurrence associated with the change in temperature variation between Open Shrubland and Savanna biomes (delta 25.8 degrees C) (**Fig 4D** & Appendix **Tables A.5c, A.7 & A.8**).

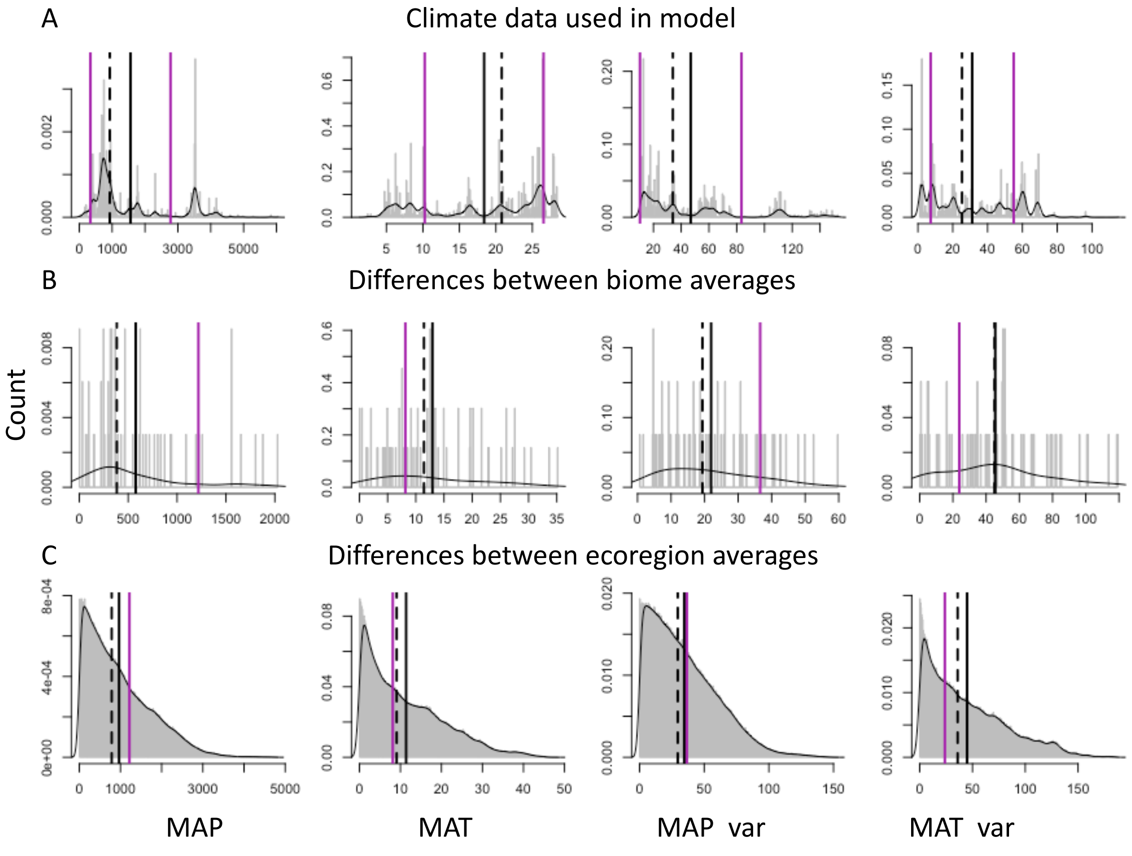

Figure 2.5. Climate variable effect size in real world terms.

Comparison of standard deviations of climate variables used in our models to differences between real world classifications of climate-based vegetation assemblages. Grey histograms represent A) climate variable data used in occurrence models, and differences between climate variable averages in B) biomes, and C) ecoregions. Purple lines represent A) +/- one standard deviation of a particular climate variable in the model data, or B) and C) magnitude of sd in model data. Solid black lines represent the mean value of each histogram (i.e. mean difference between average temperature in biomes), dashed black lines represent median value of each histogram (i.e. median difference between average rainfall in ecoregions). Biomes based on Ramankutty & Foley (1999) from Ellis et al. (2010), ecoregions based on Olson et al. (2001).

2.5 Discussion

Here we show for the first time at a global scale, life form occurrence and abundance between and within land uses is comparable to, and sometimes greater than, differences between biomes or ecoregions. Land use has a divergent effect on life form occurrence comparable to the effect of climate, with particular life forms more strongly affected than others by land use. The productivity of environments is driven mainly by climate, but which species succeed in them is also a result of land use. This means that humans are in direct competition with plant species for highly productive environments, and we find that species that have historically dominated these climates are the least able to cope with human disturbance, i.e. human pressure in highly productive climates leads to deforestation driving a lack of phanerophytes in these areas. Human land use is acting as a filter, expanding the realised niche of disturbance tolerant life forms and contracting the realised niche of others. Land use change is comparable in strength to a 1 SD change in temperature, rainfall and rainfall variation as a driver of plant life form occurrence and abundance. Life forms adapted to competition for resources in highly productive environments (i.e. phanerophytes, mostly trees) are more likely to occur, and to be locally abundant, in less disturbed, more productive land uses. Conversely, more disturbance adapted life forms (i.e. therophytes, typically annuals) are more likely to occur in more disturbed and intensive land uses.

Individually, both land use and climate are expected to have a strong influence on species occurrence and abundance (Huang et al., 2021; Allan et al., 2015; de Chazal & Rounsevell, 2009; Thuiller et al., 2006; Smith, 1909). In our models, the effect size of land uses were typically similar to, or greater than, the effect sizes of climate (the exception being the effects of temperature variation, the strongest environmental driver of global vegetation patterns (Huang et al., 2021)). A one standard deviation difference in climate variables is broadly equivalent to the average differences in climate between ecoregions (**Fig 5 & S.3**) or Biomes (Appendix **Fig A.4 & A.5 & Table A.8**). We show that land use is, at least, comparable to climate in driving distribution patterns in plant life form. The divergent effect of land use on life forms (i.e. the difference in probability of occurrence between trees in Primary forest and Cropland) is comparable to the probability of occurrence associated with a 1 SD change in climate. Land use therefore acts as an additional filter, determining successful and unsuccessful types of species in the Anthropocene.

Intensification of human land use is not uniform across different biomes. Human pressure is tightly correlated with biologically productive environments, e.g. “93.8% of the variation in average footprint values is explained by agricultural suitability [based on climate and soil factors] alone (linear model, t-value= 38.77, P<0.001)”(Venter et al., 2016a). Forest biomes (temperate broadleaf and mixed forests, tropical and sub-tropical dry broadleaf forests, Mediterranean forests, woodlands, and scrub, and mangroves) are the most highly impacted by human modification, while less productive biomes (tundra, boreal forest and taiga and desert and xeric shrubland) have the lowest levels of modification (Kennedy et al., 2019; Venter et al., 2016a). Human land use is increasing in intensity in productive climates (Kennedy et al., 2019; Venter et al., 2016a) such that “wild” habitats are now mainly in the coldest and driest, least productive, of earth’s biomes (Ellis et al., 2010). Concerningly, productive environments, in particular primary forest, support a disproportionate amount of the world’s existing biodiversity (Mannion et al., 2013; Willig et al., 2003; Barlow et al., 2007; Newbold et al., 2015; Shvidenko et al., 2005), with less than 3% of the biodiversity hotspots showing no human pressure (Venter et al., 2016).

From phyto-climates through biomes to ecoregions, ecologists have developed an understanding of how climate interacts with species intrinsic characteristics to produce vegetation assemblages. This understanding has been updated to consider how human land use changes climate based models. We contribute a more explicit understanding of which types of species are increasing and which are declining in today’s climate *and* land use driven assemblages. Trees, and to a lesser extent shrubs, are constrained by climate and land use. Hemicryptophytes and cryptophytes, neither very competitive in productive environments nor consistently successful in disturbed environments, are also less likely to occur in regions with high temperature variation. Therophytes, adapted for the necessary opportunism of less productive climates may experience competitive release for light under human disturbance which eliminates taller species.

Phanerophytes were expected to have the highest relative abundance in climates with mild climatic bottle-necks (Raunkiaer, 1934; Smith, 1909), where there is a weaker trade-off between competing for light and shielding buds from periods of harsh climate. In productive habitats, phanerophyte occurrence is high, but decreases with increasing disturbance. Human disturbance makes phanerophytes less likely to occur, i.e. land use is contracting phanerophytes’ realised niche. Therophytes, (and to a lesser extent hemicryptophytes and cryptophytes), are adapted to patchiness of resources (conditions suitable for growth and reproduction). These life forms historically had their highest relative abundances in climates unsuited to phanerophytes and species with strategies adapted to resource patchiness are able to take advantage of human disturbance. Therophytes had the largest range in probability of occurrence, indicating that human disturbance expands habitat suitable for therophytes.

Life forms differ in their occurrence depending on climate. Unsurprisingly, precipitation variation is positively associated with more disturbance tolerant life forms, hemi-, crypto- and thero-phytes, and negatively associated with phanerophytes. For precipitation, temperature and temperature variation, the pattern across life forms indicates that hemicryptophytes and cryptophytes have the strongest negative relationships with those climate variables. Higher precipitation and temperature occur in productive climates, where disturbance adapted life forms are not as competitive. The stronger negative effect of temperature variation on these life forms may reflect the length of hemi- and cryptophyte life cycles. Phanerophytes and chamaephytes, typically trees and shrubs, can live for multiple years, and may be adapted to cope with annual variation, while therophyte life cycles avoid unfavourable periods of annual temperature and moisture availability. Perennial herbs and grasses, falling in the middle of this spectrum, may be more vulnerable to intra-annual variation given their relatively short life cycle. A disproportionate increase in intra-annual climate variability is projected in more productive habitats (i.e. the Amazon) (Bathiany et al., 2018). With phanerophytes unsuited to disturbance and hemi- and cryptophytes unsuited to increased variability, therophytes may be best positioned to cope with the dual filters of land use and climate.

We show that life form affects species response to land use and provide strong evidence for land use as comparable to climate in moulding species' realised niche and creating the vegetation assemblages that contribute to the broad patterns of terrestrial life on Earth. However, explicitly testing the interaction between climate and land use, i.e. the effects of life form within land use and climatic contexts in a three-way interaction, was outside the scope of the data available for this study, as five life forms interacting with ten land uses and four climate variables would have resulted in 200 additional model terms. If data from primary forests comes mainly from the tropics, and mature secondary vegetation from temperate zones for example, or if higher temperature data comes from the tropics (rather than savanna/desert), this influences the life form occurrence within those land uses. Further research with an expanded dataset is needed on how life form is affected by land use compared to, and within climate. Land use intensity was not included in this study. We account for spatial autocorrelation through our random effects, i.e. accounting for variance associated with data within individual studies. Locations of biodiversity samples within studies were all within the same region, and in all except three studies, within the same biome. The median maximum distance between sites within a study was 24km and the mean was 80km. For further information on distances between sites within studies see Appendix **Figures A.8-11**.

The effects of temperature in our occurrence model are associated with a change of over eight degrees Celsius, a magnitude which exceeds maximum global temperature changes projected in IPCC scenarios for the rest of the twenty first century (Masson- Delmotte et al., 2021). However, it is not meaningful to extrapolate species responses to future climate conditions based on patterns observed here. Effects associated with temperature in our models describe changes in probability of occurrence in comparison to the mean temperature, so our results describe increases in tree occurrence observed when moving (for example) from temperate to tropical climates, i.e. the *current* relationship between temperature and occurrence. An increase of temperature in temperate zones to that of temperature in a rainforest is not likely to produce an equivalent increase in tree species occurrence, as vegetation in both areas are also a product of current and historic land use, along with other historic and evolutionary factors.

This study used some of the largest available datasets of species occurrence/abundance, traits (life form) and human land use, and yet coverage remains patchy, and highly correlated with areas of intensive, historical human activity. These biases are present across data collections, both ecological (Boakes et al., 2010; Dennis & Thomas, 2000; Pyšek et al., 2008) and otherwise (Arora, 2016), but must be addressed. In this study alone a broader range of site locations, particularly towards the colder climates may have enabled us to detect clearer patterns in chamaephyte occurrence and abundance. Abundance data reflected local dominance when present (see methods), rather than the habitat or landscape level relative abundance (i.e. commonness). Future work should use relative abundance data at a broader scale, capable of reflecting the vegetation composition of sampling sites or ecoregions rather than smaller scale transects and quadrats.

While Raunkiærian life form data are readily available, ecologically informative multi-dimensional trait data (Bohn et al., 2014; Funk et al., 2017; Herron et al., 2007; Lavorel et al., 2002) and demographic data (Hemrová et al., 2017; Ramula et al., 2008; Salguero-Gomez et al., 2016) are sparser (Kelly et al., 2021; Kattge & Knöll, 2020; Coutts et al., 2016; Salguero-Gómez et al., 2014). A unique advantage of life form is its relationship with climate, enabling a strong test of differences between land use and climate as drivers of biodiversity patterns. We show that life form is a useful lens through which to view biodiversity changes due to both climate and land use, including in future scenarios generated with dynamic vegetation model; however, expanded multi-dimensional trait datasets will undoubtedly prove useful in future analyses.

The most productive terrestrial habitats were historically characterised by high relative abundance of phanerophytes; life forms adapted to compete for light and space in climatically mild, undisturbed environments. Species that compete best in productive environments are now most adversely affected by human disturbance, while species that are adapted to less productive habitats are increasing. As human activity rapidly expands into productive environments, we constrain the area of suitable niche space for phanerophytes (trees), while expanding the area of suitable niche space for more disturbance tolerant species (annuals). Ecological understanding of the drivers of vegetation patterns has developed immensely since Raunkiær's life forms were first described. "Phyto-climates" have been refined into biomes, and ecoregions, and these climate-based frameworks have been updated to include the influence of human land use. Our work contributes to an emerging understanding of species divergent responses to the forces currently shaping their realised niches.

We provide for the first time and at a global scale, evidence for the effect of ten dominant categories of land use on all major plant life forms. This work formalises our understanding of which species are most vulnerable to the dominant force of global change. Land use changes towards more intensive use (i.e. away from primary or mature vegetation) in productive environments disproportionately affecting large, relatively long lived species (e.g. phanerophytes). Further, we show how human land use is associated with more divergent outcomes in species occurrence across life forms than climate, highlighting the disproportionately negative potential outcomes on species vulnerable to land use change. Climate change and its impact on species rightly receives huge research interest and investment. By providing quantitative evidence for both the obvious and surprising impacts of land use on occurrence of different life forms, and by showing how this impact can be considered comparable to the impacts of current climate, this work highlights land use as a key driver of species biogeographic distributions.

Chapter 3 Human footprint in addition to climate drives spatial patterns in European plants

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Author contribution: Research was conceived and designed by CMM, AMC and YMB. AMC provided data on species' spatial patterns. CMM obtained further data, conducted the data analysis and wrote the first draft. RK and YMB provided advice on analyses. Results were initially interpreted by CMM with advice from YMB, AMC and RK. All authors provided intellectual input and edited the MS.

3.1 Abstract

At broad spatial scales, species' occurrence through space has been shown to be driven by past and contemporary climate. However, global vegetation patterns reflect not only climate, but anthropogenic influence. We test how climate and human footprint influence six different metrics of spatial range patterning in 650 endemic European plant species. We find that climate and human footprint both correlate with measures of range size and range division, and that including human footprint in addition to climate improves our understanding of some dimensions of species' spatial patterns. The velocity of past climate change, mean annual temperature and mean human footprint had the strongest relationships with range size respectively. The relative importance of these variables was different for metrics of range division. Despite a weak positive correlation between them, mean annual temperature variation and human footprint had opposing relationships with range size, implying that climate and anthropogenic influence may influence species' spatial patterns through different mechanisms. We suggest the relatively low importance of human influence on species spatial pattern relates to the spatial resolution of data underpinning our spatial pattern metrics. Our results support the growing evidence that we cannot understand ecological patterns and the mechanisms behind them without acknowledging the influence of terrestrial anthropogenic activity.

3.2 Introduction

Fundamental research questions in ecology centre on the question of the relative influence of climatic (contemporary or past) over phylogenetic legacy, dispersal, biotic interaction and land area in driving species range distributions (Brown, 1984; Gaston, 2003; Morueta-Holme et al., 2013; Sheth et al., 2020). Given the acknowledged role that past and present climate plays in

species distributions, and facing evidence that human activity is comparable to climate in affecting patterns of global vegetation (Ellis & Ramankutty, 2008), anthropogenic influence should be considered in analyses of how species' ranges are distributed in space. Indeed, both climate and anthropogenic influence have been jointly considered in relation to; the size of individuals (Fan et al., 2020), spatial patterning and extinction risk in mammals (Yackulic et al., 2011), the contemporary and projected range of invasive aquatic plants (Kelly, Leach, et al., 2014), the expansion of invasive range edges (Lembrechts et al., 2016), forest composition (Danneyrolles et al., 2019) or, more generally; in birds (Stevens & Conway, 2020) or at small spatial scales (Machado & Oliveira-Filho, 2010). However, to our knowledge, climate and anthropogenic influence have not been directly assessed together as correlates of plant species spatial distribution across their ranges. Given the influence of human terrestrial activity in shaping contemporary ecosystems
(Brondizio et al., 2019; Díaz et al., 2019; Morris et al., 2020), we argue that species broad scale spatial patterns cannot be understood through the extrinsic lens of climate and phylogeny alone. We test whether explicitly including anthropogenic influence improves our understanding of species' patterning through space.

The scale at which spatial pattern is studied is relevant to which ecological patterns or processes are under investigation (Carl et al., 2016; Chase, 2014; Levin, 1992; Sandel & Smith, 2009; Sporbert et al., 2021; Whittaker et al., 2001), so various metrics exist describing species' patterns in space at different scales. At broad scale i.e. scales encompassing all instances of species occurrences, a commonly used metric of spatial pattern is species range size (Estrada et al., 2015; Gaston, 2003; Gaston & Fuller, 2009; Sheth et al., 2020). Range size can be defined as the minimum convex polygon around occupied habitat grid cells (Extent of Occurrence) or the sum of the area of all occupied habitat patches (area of occupancy) (Gaston & Fuller, 2009; Csergő et al., 2020). Species' range size has been linked to trends over large spatial and temporal scales (Svenning & Skov, 2004). Range size has been linked to extrinsic and intrinsic factors (Estrada et al., 2015; Sheth et al., 2020; Svenning & Skov, 2004), and describes an important dimension of species' vulnerability to change (Mace et al., 2008). Through species' intrinsic traits, range size has been linked to species' ability to track climate change (Estrada et al., 2015, 2016, 2018), and in an absolute sense, the smaller a species range, the more vulnerable it is to stochastic extinction (Gaston, 2003; Staude et al., 2020). However, range size may be largely decoupled from other metrics of range structure (Csergő et al., 2020) and does not necessarily relate to rarity (Rabinowitz, 1981) or fragmentation (Hanski et al., 2013) within the range. A lack of knowledge on drivers of range structure limits our understanding of how processes affecting spatial patterns operate on species at smaller scales, i.e. human land use (Carl et al., 2016; Newbold, 2018). When assessing how anthropogenic influence might improve our understanding of species patterns in space, it is therefore important to consider not only range size, but also range structure.

3.2.1 Realised niche as spatial pattern

Species' realised niches manifest as patterns of occurrence and abundance through space (Colwell & Rangel, 2009). Species' niches, and therefore species' spatial patterns, are shaped by combinations of intrinsic and extrinsic factors (Gaston, 2003; Kelly, Leach, et al., 2014; Urban et al., 2020; Wisz et al., 2013). Spatial pattern describes anything from occurrence on continents to regional abundance to local density within a quadrat, and the relative importance of various intrinsic and extrinsic factors may differ across these spatial scales (Sporbert et al., 2021; Pulliam, 2000; Thomas & Kunin, 1999; Riibak et al., 2020; Carl et al., 2016; Levin, 1992). For example, at small spatial scales, mutualisms or competition might be the main drivers of plant local abundance (Gurevitch et al., 2016). At slightly larger scales, reproductive strategy might be more relevant to species' ability to colonise new areas or recolonise patches within their range (Baker, 1955; Laenen et al., 2015). At continental or global scales, niche breadth (range of external conditions a species can tolerate), and intrinsic ability to disperse and establish, (Estrada et al., 2015; Sheth et al., 2020), biogeographic barriers, past climate change velocity and present climate have been shown as key factors in shaping spatial patterns (Huang et al., 2021; Morueta-Holme et al., 2013; Sandel et al., 2011; Svenning & Skov, 2004). Differences in these patterns and the drivers behind them are of interest both theoretically, and from a management and conservation perspective (Gaston, 2003; Gaston & Fuller, 2009; Sheth et al., 2020); ecologists are interested in understanding the evolutionary and ecological processes behind spatial patterns (Sandel et al., 2011; Svenning & Skov, 2007; Urban et al., 2020), and in using spatial patterns to determine species vulnerability to anthropogenic pressure (Foden et al., 2013, 2019; Thomas et al., 2004).

3.2.2 Extrinsic drivers of large scale spatial scales

One of the most important drivers of species' large scale spatial patterns is climate (Huang et al., 2021; Lee-Yaw et al., 2016; Li et al., 2016; Liang et al., 2021; Morueta-Holme et al., 2013; Thomas, 2010; Yu et al., 2017). We distinguish between contemporary climate - stable conditions which determine contemporary persistence, and past climate - the temporal development of climate which has shaped the longer term range-wide dynamics. Climate in Europe has been relatively stable for the past 1000 years (Osman et al., 2021), following warming since the Last Glacial Maximum (LGM) approximately 19000 years ago (Clark et al., 2009; Gowan et al., 2021). Here, we consider "past" climate as referring to conditions between the LGM and the mid 20th century, and "contemporary" climate to describe the period between 1970 and 2000; the temporal range used to calculate Worldclim's bioclimatic variables (Fick & Hijmans, 2017).

Range size has been shown to be determined primarily by the legacy of past climate (specifically past climate change velocity) and contemporary climate (climate variability) in approx. 85 000 New World plants (Morueta-Holme et al., 2013). In analyses of whether range filling was driven by contemporary or past climate, Svenning and Skov (2004) found that the legacy of the LGM accounts at least in part for the spatial patterning of European tree species, and that post-glacial dispersal limitation in large part drives patterns of tree diversity in Europe (Svenning & Skov, 2007). Further, freezing resistance (ability to tolerate temperature minima) is shown to be related to range size in north Mexican trees and shrubs (Pither, 2003).

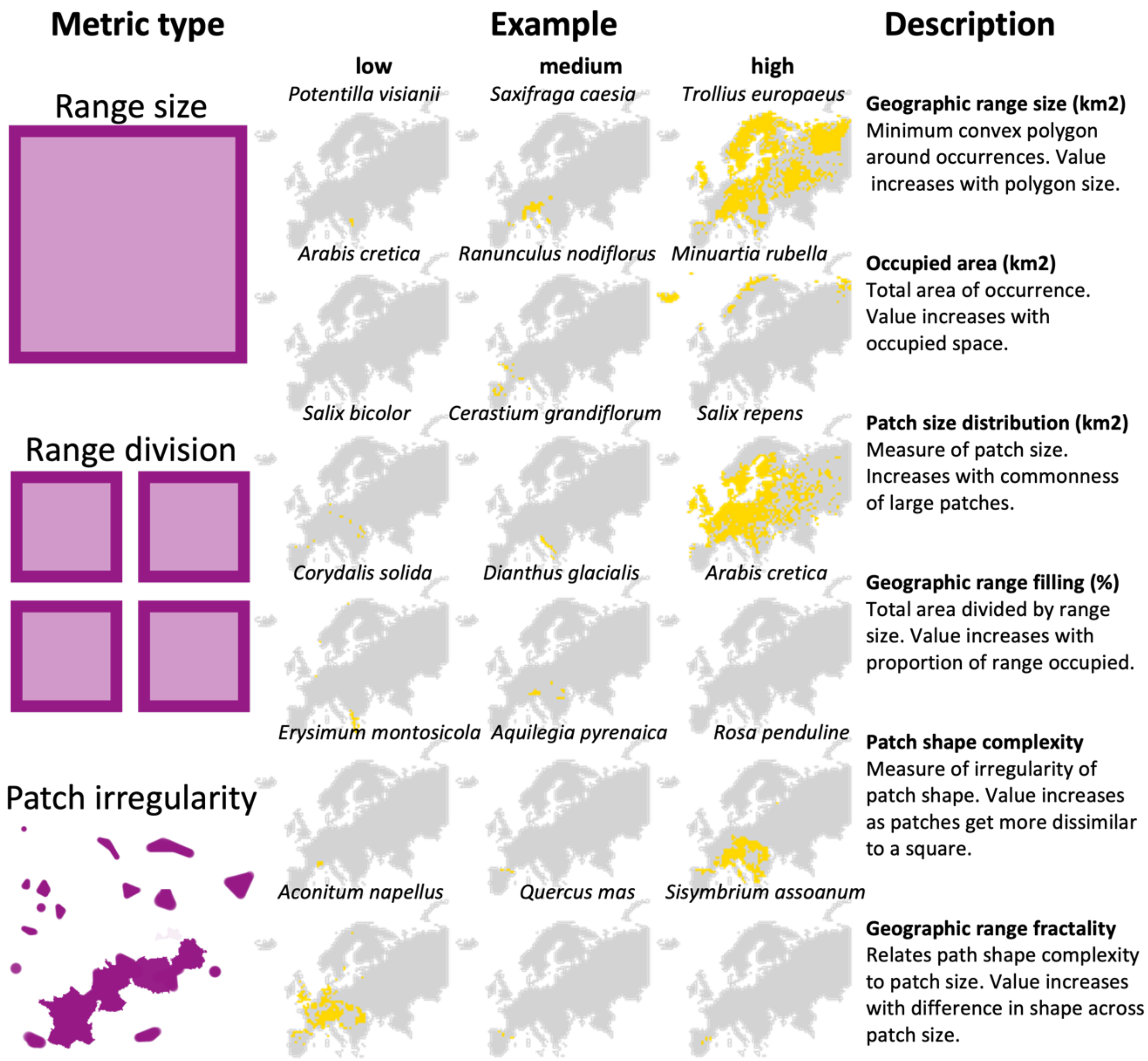
In light of worsening global climate change, in particular, forecasts of increasing temperature variability (Masson- Delmotte et al., 2021), there is naturally huge interest in species' responses to ongoing and imminent changes in global climate (Corlett & Westcott, 2013; Elsen et al., 2021; Huntley et al., 2021; Malhi et al., 2020; Weiskopf et al., 2020). Specifically, many studies have looked at how changes in climate will affect species through space (Beyer & Manica, 2020; Chen et al., 2011; S. Dullinger et al., 2012; Early & Sax, 2011; Estrada et al., 2018; Foden et al., 2013; Lenoir & Svenning, 2015; Lynn et al., 2021; MacLean & Beissinger, 2017; Mason et al., 2015; McCarty, 2001; Thomas et al., 2004; Warren et al., 2013; Weiskopf et al., 2020). However, climate change is not the only, or even currently the most pressing, driver of biodiversity loss (Almond et al., 2020; Díaz et al., 2019; Kennedy et al., 2019; Newbold, 2018).

Evidence is now consolidating for how anthropogenic influence rivals climate as a driver of species patterns, both globally (Ellis, 2019; Ellis & Ramankutty, 2008; Newbold, 2018, Chapter 2) and at smaller spatial scales. Anthropogenic influence has been shown to be of similar magnitude to biotic and climate factors in influencing global plant population dynamics (Morris et al., 2020), and global patterns in occurrence of life forms (Chapter 2), and direct anthropogenic influence has been shown to be more important than climate to long term compositional changes in northern forests (Danneyrolles et al., 2019). Species occurrence through space is expected to be related to human presence in Europe, with this relationship moderated by endemism and species' range size (Araújo, 2003). Land use and climate are expected to interact in their effects on species dynamics (Lembrechts et al., 2016; Platts et al., 2019; Williams et al., 2021; Williams & Newbold, 2021), and it is further evident that past human activity has been shaping biomes for thousands of years (Ellis et al., 2021).

Europe has been and continues to be subject to extensive human land use (Thompson, 1994), with up to 80% of its terrestrial surface currently human dominated (Kennedy et al., 2019; Venter et al., 2016). We hypothesised that rather than viewing spatial pattern purely through the lens of non-human factors, explicitly including anthropogenic activity as an extrinsic ecological factor will improve our understanding of biogeographic range patterns in endemic European plants.

3.2.3 Different dimensions of spatial patterns

Focusing on descriptors of broad scale patterns of occurrence (approx. 50 x 50km resolution), we look at six metrics of species spatial patterns describing the size, division and patch irregularity of species' ranges in Europe (**Figure 3.1.**)



Geographic range size (km2)
Minimum convex polygon around occurrences. Value increases with polygon size.

Occupied area (km2)
Total area of occurrence. Value increases with occupied space.

Patch size distribution (km2)
Measure of patch size. Increases with commonness of large patches.

Geographic range filling (%)
Total area divided by range size. Value increases with proportion of range occupied.

Patch shape complexity
Measure of irregularity of patch shape. Value increases as patches get more dissimilar to a square.

Geographic range fractality
Relates path shape complexity to patch size. Value increases with difference in shape across patch size.

Figure 3.1. Range metrics used in this study.
We use two metrics related to range size – occupied area and geographic range size, and four related to range structure. Range structure metrics either relate to measures of range division (patch size distribution and geographic range filling), or to measures of patch irregularity (patch shape complexity and geographic range fractality). Range metrics were calculated based on Atlas of Florae Europaeae species' occurrences at approx.. 50 x 50 km grid cell resolution. Further descriptions of how each metric was calculated can be found in Csergő et al. (2020) Supplementary material.

3.2.4 Aims

There is evidence of a relationship between climate and range size. Does including anthropogenic influence as an extrinsic factor affecting species' niche improve our understanding of species' spatial patterns?

Within our data, we test whether:

- Including human footprint along with climate and phylogeny improves our understanding of drivers of range size, division and patch irregularity
- Climate and human footprint effects vary across different dimensions of species spatial patterning, i.e. range size, division and patch irregularity.

We assessed these questions using; a) comparison of the explanatory power of models through DIC and Bayesian R^2, and b) comparison of effect sizes of model terms.

It is expected that contemporary and past climate change relate to species range size and occupied area in Europe (Estrada et al., 2015; Csergő et al., 2020; Svenning & Skov, 2004), and that explicitly including human footprint improves understanding of ecological patterns (Seiferling et al., 2014). Given the levels of past and present human activity in Europe (Ellis et al., 2010, 2021; Ellis & Ramankutty, 2008; Kennedy et al., 2019; Tallavaara et al., 2015; Venter et al., 2016), and the link between anthropogenic influence and changes in the biotic environment (Araújo, 2003; Díaz et al., 2019; IPBES, 2019; Newbold et al., 2015), in particular to species ranges (Sales et al., 2022), we expect that including human influence will improve climate-and-phylogeny-based models of species' spatial patterns. As anthropogenic pressure acts at finer spatial resolutions than climate (Carl et al., 2016), we expect that human footprint will be more relevant to spatial patterning within the range (metrics of range structure) compared to range size.

3.3 Methods

We modelled two measures of each of range size, range division and patch irregularity (**Figure 3.1.**) as a function of human footprint, climate and their interaction for endemic European plant species. Range size and structure data was available for 691 European endemic species from Csergo et al. (2020). Contemporary climate data was obtained from bioclim (Fick & Hijmans, 2017) and data from Sandel et al. (2011) was used to describe past climate change velocity. Human footprint data was collected from SEDAC (Venter et al., 2018) and phylogenetic data was obtained from Smith et al. (2018). Data were cleaned and merged prior to analysis (see https://github.com/cmmckeon/STR_tr8). Data cleaning involved matching species names between range metric dataset and phylogeny, creating raster of occurrences for each species, and obtaining average covariate values where each species occurred. Analysis was then carried out on a subset of species for which phylogenetic data was available, using Bayesian linear models in R version 3.6.3 (R Core Team, 2020).

3.3.1 Climate data

To describe contemporary climate, we used four variables; mean annual temperature, mean annual temperature variation (SD*100), mean annual precipitation and mean annual precipitation variation (coefficient of variation). These data came from global climate dataset WorldClim version 2.1 (https://www.worldclim.org/data/v1.4/formats.html) from which we obtained statistical summaries of climatic variables as static spatial *bioclimatic* variables at 30 second resolution (approx. 1km^2), calculated using monthly records for temperature and rainfall from 1970-2000 (Fick & Hijmans, 2017). To describe past climate we used climate change velocity data from (Sandel et al., 2011), which describes “the local average displacement rate of mean annual temperature since the Last Glacial Maximum”, available at 24.122 km resolution.

3.3.2 Human footprint

SEDAC (Socioeconomic Data and Applications Center) (https://sedac.ciesin.columbia.edu) aims to facilitate interdisciplinary work between earth and social sciences by creating data products centring around human interaction with the environment. SEDAC’s data products include “human footprint value”, a metric comprised of the sum of eight variables weighted by relative levels of human pressure (Sanderson et al., 2002): extent of built environments, crop land, pasture land, human population density, night-time lights, railways, roads; and navigable waterways (Venter 2016). This metric describes “cumulative human pressure on the environment” (Venter 2018).

3.3.3 Phylogeny

Of the 827 species in the Csergő et al. (2020) data set, 304 were identified to subspecies; this level of detail was not available in our phylogenetic data. Retaining only the binomial species identification reduced the dataset to 691 species. We created a phylogenetic tree for 570 of these species using the phylogeny from Smith et al. (2018). A further 80 species from our dataset were added into this phylogeny at random points on branches of matching genera using r package phytools (Revell, 2012), creating a tree with a maximum of 650 species (for further details see https://github.com/cmmckeon/STR_tr8).

3.3.4 Collinearity

Environmental variables, in particular climate variables, are often colinear, which is sometimes considered a problem in ecology (Dormann et al., 2013), therefore colinear terms are sometimes excluded from analysis (e.g. (Pecuchet et al., 2017)). Issues arise from collinearity when collinearity is extreme, when the focus of the modelling effort is prediction into other datasets with different collinearity structures (Dormann et al., 2013), or when sample size is small, as collinearity reduces the amount of information available to the model (Morrissey & Ruxton, 2018). Multiple regression provides informative estimates of the direct relationship between each co-variate and the response. i.e. what change in response can be expected with a one standard deviation change in a particular variable *when all other variables are held constant at their mean* (Morrissey & Ruxton, 2018). Retaining relevant variables in analyses which are not intended for prediction, with large sample size and collinearity of less than 70% is therefore preferable to excluding co-linear covariates (Morrissey & Ruxton, 2018). As the above issues do not apply to our analysis, we do not exclude any covariates on the basis of collinearity.

3.3.5 Data handling

For all 50 x 50 km grid cells occupied by each species, we calculated the mean value for human footprint, and each of our five climate variables. After data were cleaned and compiled, all variables were a) log transformed to address kurtosis where appropriate, and b) scaled (mean centred and divided by one standard deviation). Scaling ensures that the slopes of relationships directly represent correlation between continuous variables.

3.3.6 Statistical analysis

We used phylogenetically corrected Bayesian linear mixed models (Hadfield, 2010; Guillerme & Healy, 2014) to investigate the relationship between human footprint, climate and species' range metrics. We ran six sets of six models of varying complexity (**Table 3.1**) , investigating the relationship between each range metric and;

1) An intercept of 1 (null model)
2) All contemporary climate variables in interaction (two, three and four way interactions)
3) Human footprint value
4) All contemporary climate variables, human footprint value and all interactions (up to five way interaction)
5) All contemporary climate variables and past climate change velocity and all interactions (up to five way interaction)
6) All climate variables (contemporary and past climate change velocity), human footprint value and all interactions (up to six way interaction)

Table 3.1. Descriptions of sets of models.
Each of the six range metrics was used as a response variable in a set of the six models described below. Response = one of the six range metrics: occupied area, geographic range size, patch size distribution, geographic range filling, patch shape complexity or geographic range fractality. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. All models include phylogeny as a random effect.

Type of model	**Model formula**	**Description of model terms**
Null model	response ~ 1	An intercept of 1 (null model)
Human footprint model	response ~ hf	Human footprint value
Contemporary climate model	response ~ map * mat * map_var * mat_var	All contemporary climate variables in interaction (two, three and four way interactions)
Contemporary climate and human footprint model	response ~ hf * map * mat * map_var * mat_var	All contemporary climate variables, human footprint value and all interactions (up to five way interaction)
All climate model	response ~ vel * map * mat * map_var * mat_var	All contemporary climate variables and past climate change velocity and all interactions (up to five way interaction)
Maximal model	response ~ vel * hf * map * mat * map_var * mat_var	All climate variables (contemporary and past climate change velocity), human footprint value and all interactions (up to six way interaction)

Five sets of models converged and were deemed of sufficient fit based on model diagnostics using CODA (Plummer et al., 2006), models with geographic range fractality as a response did not have satisfactory diagnostics (this model had a smaller sample size due to missing data). Diagnostic checks included visual inspection of trace plots, plotting autocorrelation within the chains, comparing duplicate models using the Gelman and Rubin Multiple Sequence Diagnostic to check for convergence, plotting scatter plot matrices to check that parameters where not confounded, calculating measures of the phylogenetic signal in the models, and plotting histograms to check for the amount of variance explained by the random effects. Parameter expanded priors were used to improve the estimation of phylogenetic signal (Hadfield, 2010). All code used in this project is available from https://github.com/cmmckeon/STR_tr8.

Results were evaluated in two phases. Firstly, we used Deviance information criteria (DIC) to determine which of our models best explained the data. Comparisons with the null model allowed us to assess whether our models were explaining the data in any absolute sense. Fit for the best models was then further evaluated using Bayesian R^2 (Nakagawa & Schielzeth, 2013; Mac Nally et al., 2018). Effect sizes were assessed in the best performing models to infer the direction and magnitude of the relationship between the joint effects of climate and human footprint on species range size, division and patch irregularity.

3.4 Results

Human footprint and climate were both correlated with the spatial patterning of endemic European plant species. Including human footprint *and* climate, rather than evaluating either of these factors alone, improved models of range size and range division for the metrics: geographic range size, patch size distribution and geographic range filling (**Figure 3.2**). Climate and human footprint showed little relationship with metrics of patch irregularity.

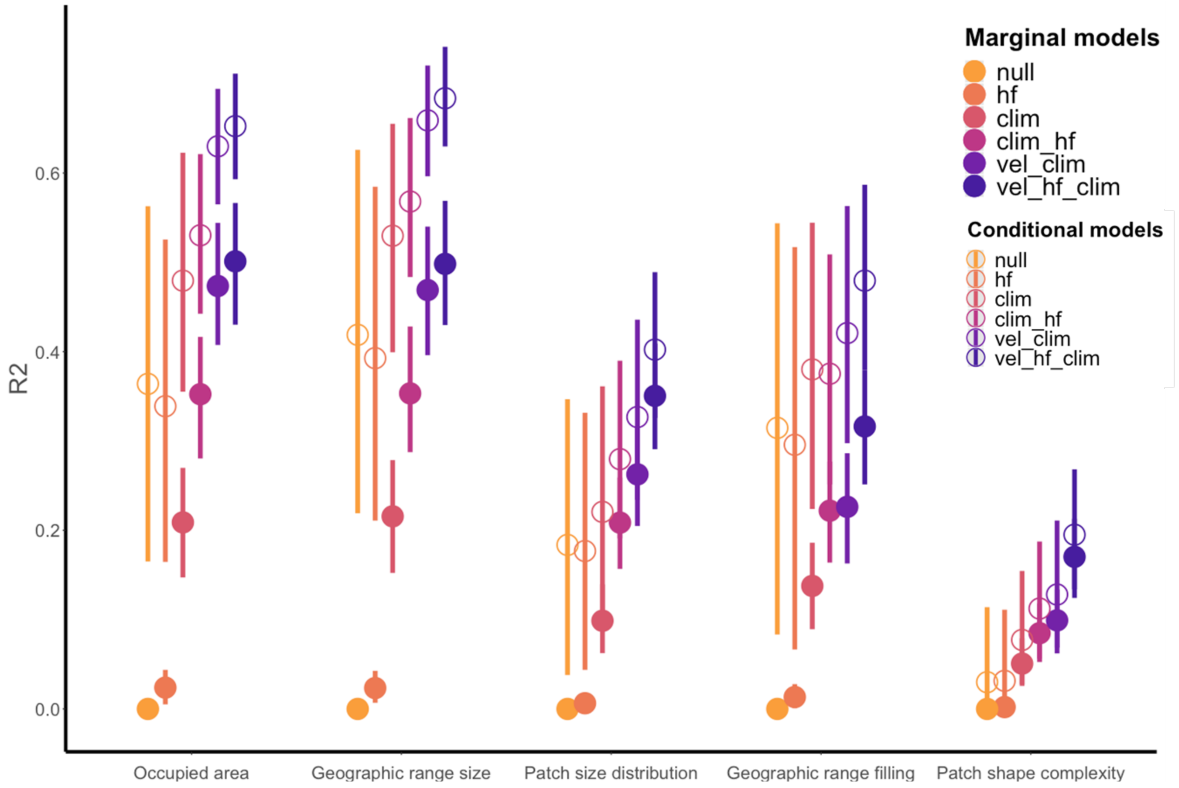


Figure 3.2 Model evaluation.

Circles represent the mean Bayesian R^2 values after Nakagawa et al (2017), vertical lines represent 95% credibility intervals. Empty circles represent the conditional mean, i.e. variance explained by the full model (including the variance explained by phylogeny). Solid circles represent the marginal mean, i.e. variance explained by the fixed effects only (excluding variance explained by phylogeny). Null = intercept only models, hf = models with only human footprint, clim = models with four interacting contemporary climate variables (mean annual precipitation, mean annual precipitation variation, mean annual temperature and mean annual temperature variation), clim_hf = models with four contemporary climate variables and human footprint all interacting, vel_clim = models with four contemporary climate variables and past climate change velocity all interacting, vel_hf_clim = maximal models with all main effects interacting. All models include phylogeny as a random effect. The geographic range fractality model was not deemed reliable based on diagnostic tests.

Metrics of range size were most strongly correlated with terms involving past climate change velocity, mean annual temperature, and mean annual temperature variation (**Figure 3.3**).

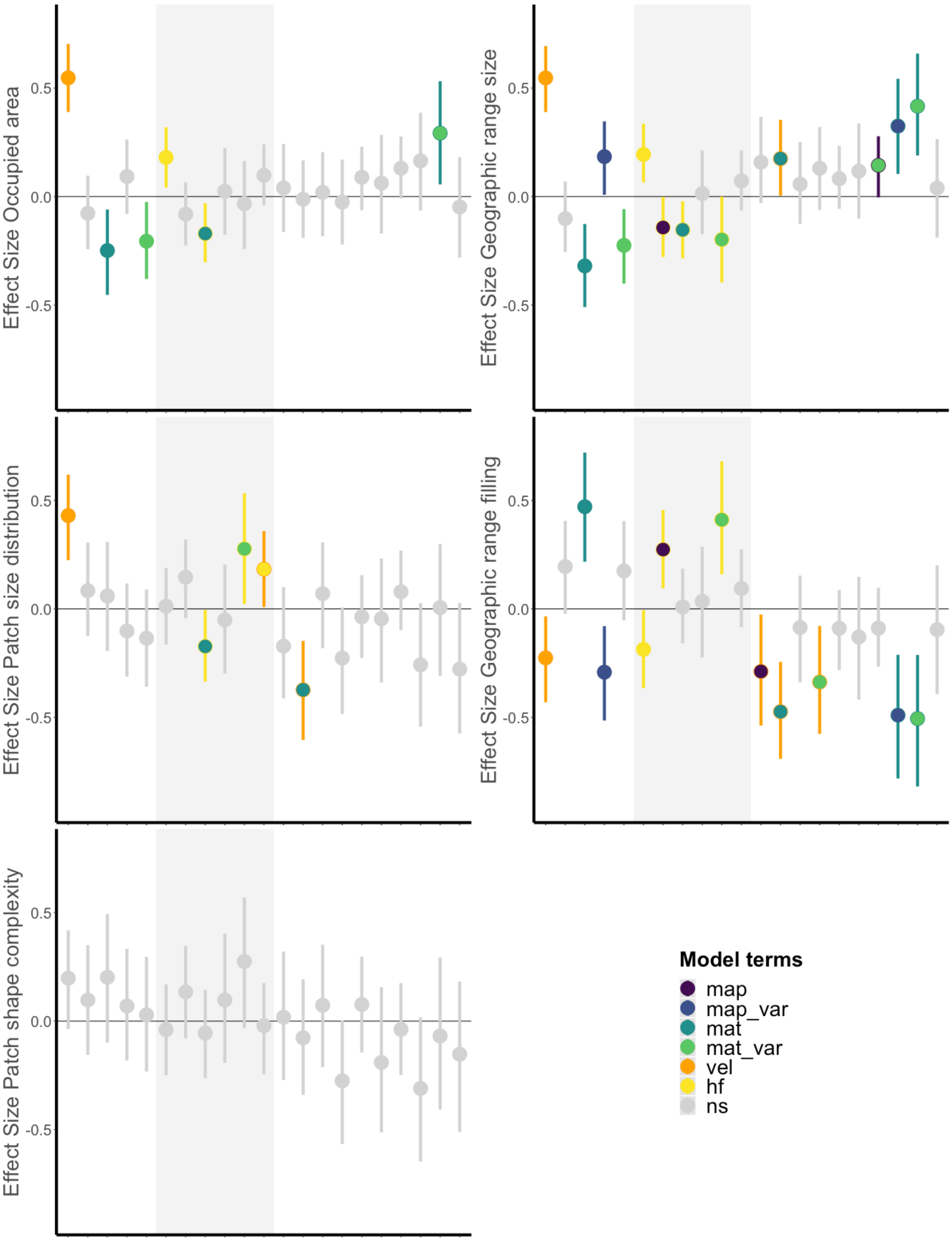


Figure 3.3 Effect sizes for main effects and two way interactions from maximal models showing the strength of the correlation between Climate and Human footprint, and Range Metrics. Solid circles represent the slope of relationship, i.e. change in range metric associated with 1 SD change in climate or human footprint value. Vertical lines represent 95% credibility interval. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity, ns = non-significant. The colour of points and vertical lines refers to the terms in the model. If a point and vertical line are the same colour, this represents a main effect. If point and vertical line are different colours, this represents the interaction between two main effects as per the legend. Non-significant model terms (pMCMC > 0.05) are shown in grey. Light grey vertical bar highlights terms associated with human footprint.

Significant effects have been coloured for clarity. For graphic with colours corresponding to all effects regardless of significance see Appendix Figure B.1. The geographic range fractality model was not included as it was not deemed reliable based on diagnostic tests.

The effects of climate and human footprint differed between metrics of range size and range division. For range size, human footprint had relatively small effect sizes as a main effect, and was not significant as a main effect for metrics of range division. Mean annual temperature and human footprint showed a weak positive correlation (Appendix Figure B.2a), but had opposite correlations with species' range metrics, implying that climate and human footprint may be related to species' spatial patterns through different mechanisms. Climate and human footprint exhibit different variability across spatial resolutions and extent (**Figure 3.4**).

3.4.1 DIC

The climate only model had the lowest DIC for the range size metric Occupied area. For one metric of range size (Geographic range size) and both metrics of range division, models including interactions between climate and human footprint terms had the lowest DIC, implying that effects of human activity depend on the climatic context. For metrics of patch irregularity, all DICs were either the same or greater than DICs for the null models (**Table 3.2**).

Table 3.2. Model comparisons.
Delta DIC refers to the difference between best performing model and the null model. DIC values for the best performing models appear in bold. All models include phylogeny as a random effect. Contemporary climate = model with four interacting contemporary climate variables; mean annual precipitation, mean annual precipitation variation, mean annual temperature and mean annual temperature variation. Human footprint = model with only human footprint as a main effect. Contemporary climate and Human footprint = model with contemporary climate terms, human footprint and all interactions. All climate = model with contemporary climate terms, past climate change velocity and all interactions. Maximal model = model with contemporary climate terms, past climate change velocity, human footprint and all interactions. Null model = intercept only model. All models include all interactions of main effects, i.e. contemporary climate models have two, three and four way interactions of the four contemporary climate variables. Maximal model contains all interactions up to six way interaction between all main effects.

Metrics	Contemporary climate	Human Footprint	Contemporary climate and Human footprint	All climate	Maximal model	Null model	Delta DIC
range size							
Occupied area	1899.3	2075.72	1779.02	**1586.21**	1593.44	2095.04	508.83
Geographic range size	1870.61	2071.84	1751.88	1560.47	**1556.15**	2091.3	535.15
range division							
Patch size distribution	2100.04	2139.85	2047.96	1989.18	**1958.8**	2142.22	183.42
Geographic range filling	2046.9	2135.7	2009.45	1992.56	**1952.6**	2144.28	191.68
patch irregularity							
Patch shape complexity	2175.6	2173.86	2192.8	2179.57	2201.2	**2172.39**	0

3.4.2 Model explanatory power

In all cases, models including both climate and human footprint had the highest R^2 (**Table 3.3**). Comparison of the marginal and conditional R^2s for null models show that phylogeny accounts for approximately 36-40% of the variance in metrics of range size, and 18-31% of the variance in metrics of range division (**Figure 3.2**).

Table 3.3. Model evaluation.

Table of mean Bayesian R^2 values after Nakagawa et al (2017). *Mar* and *cond* denote marginal and conditional R^2s respectively. Marginal R^2 refer to variance associated with the main effects only. Conditional R^2 refer to variance associated with the main effect and the random effects (i.e. including phylogeny). Contemporary climate = model with four interacting contemporary climate variables; mean annual precipitation, mean annual precipitation variation, mean annual temperature and mean annual temperature variation. Human footprint = model with only human footprint as a main effect. Contemporary climate and Human footprint = model with contemporary climate terms, human footprint and all interactions. All climate = model with contemporary climate terms, past climate change velocity and all interactions. Maximal model = model with contemporary climate terms, past climate change velocity, human footprint and all interactions. Null model = intercept only model. All models include all interactions of main effects, i.e. contemporary climate models have two, three and four way interactions of the four contemporary climate variables. Maximal model contains all interactions up to six way interaction between all main effects.

Metrics		**Null model**	**Human footprint**	**Contemporary climate**	**Contemporary climate and Human footprint**	**All climate**	**Maximal model**
range size							
Occupied area	*mar*	0.000	0.024	0.209	0.352	0.473	0.501
	cond	0.364	0.339	0.479	0.530	0.630	0.652
Geographic range size	*mar*	0.000	0.023	0.216	0.353	0.469	0.498
	cond	0.419	0.393	0.530	0.568	0.659	0.684
range division							
Patch size distribution	*mar*	0.000	0.006	0.099	0.209	0.263	0.350
	cond	0.184	0.177	0.221	0.280	0.327	0.402
Geographic range filling	*mar*	0.000	0.013	0.138	0.222	0.226	0.316
	cond	0.315	0.296	0.380	0.375	0.421	0.479
patch irregularity							
Patch shape complexity	*mar*	0.000	0.002	0.051	0.085	0.099	0.170
	cond	0.030	0.031	0.077	0.112	0.128	0.195

3.4.3 Effect sizes

Species' range spatial patterns had the strongest relationships with terms involving climate change velocity and mean annual temperature, (as well as mean annual precipitation variation for geographic range filling) (**Figure 3.3**); species with higher climate change velocity where they occurred occupied more area, had higher geographic range size and had larger average patch size. Species with lower mean temperature where they occurred occupied less area, had smaller geographic range size and had higher range filling. Mean annual temperature interacted with human footprint and past climate change velocity to affect patch size, and had the greatest relative importance as a main effect size on range filling. Higher mean human footprint was correlated with higher total area occupied, larger ranges and lower range filling. As a main effect, human footprint was most strongly correlated with metrics of range size. Human footprint interacted with contemporary climate variables to negatively affect metrics of range size and to positively effect geographic range filling. Human footprint was correlated with decreased patch size at higher contemporary temperature, and increased patch size at more variable temperature. For full tables of posterior means and credibility intervals see Appendix Tables B.1.1 to B.1.5.

3.5 Discussion

For geographic range size, patch size distribution and geographic range filling, including human footprint together with phylogeny, past climate change velocity and contemporary climate improves explanatory models of species' spatial pattern in endemic European plants. Occupied area was best explained by models with climate only. While species range size and range division were well explained by models of either climate or climate and human footprint, metrics of patch irregularity were not. Effect sizes of variables and their interactions differed between metrics of spatial pattern, supporting the idea that processes producing species' patterns through space differ in importance across dimensions of spatial patterns (Carl et al., 2016; Sporbert et al., 2020). While the effect sizes of human footprint were modest, especially in comparison to climate change velocity, human footprint was consistently important across metrics of spatial pattern in interaction with other climate variables, indicating that the effects of human footprint on species spatial patterns depend on the climate context. We suggest that the relatively low importance of human footprint to species spatial patterns is a result of the spatial resolution of the occurrence data used to produce our spatial pattern metrics. Higher resolution data are needed in order to fully quantify the relationship between anthropogenic influence and spatial pattens of endemic European plants. Our results demonstrate that considering contemporary human footprint together with past climate change velocity and contemporary climate is relevant to our understanding of broad scale spatial patterns of endemic plant species in Europe. Human footprint should therefore be included with climate in considerations of which factors drive species' spatial patterns and assessments of species spatial patterns regarding their vulnerability to global change.

3.5.1 Climate

High mean climate change velocity is associated with higher occupied area, geographic range size and patch distribution. This supports the idea that range size in Europe is at least partially explained by the ability to recolonise land following deglaciation (Estrada et al., 2015, 2018;

Svenning & Skov, 2004, 2007). Temperature variability, both past and present, is often associated with large range species (Mannion et al., 2013). Temperature variability, followed by climate change velocity were the most important predictors in explaining variation in mean range size in 85000 New World plants (Morueta-Holme et al., 2013), and small range species are absent from areas with high “glacial- interglacial climate-change velocity” (Sandel et al., 2011). In opposition to this trend, our results find that contemporary temperature variability is not the most important climatic variable, and that it is associated with smaller range size. This can be explained by methodological differences between studies. Studies relating temperature variability to species distribution have linked climate values to instances of species’ occurrence (Huang et al., 2021) or evaluated the average range size of all species present per cell (Morueta-Holme et al., 2013), allowing an investigation of how certain dimensions of species’ spatial pattern relate to the full range of climate values associated with a species’ presence. In seeking to examine metrics of range size and range internal structure, our study collapses available climate information into one value per species (by obtaining mean climate and human footprint values across all occupied cells for each species). This is important to consider in interpreting the results. If a species occurs across a wide range of temperatures, the average temperature within its range will be neither very high nor very low. In our data, if a species occurs across a range of temperature variability (i.e. in some locations with constant temperature and others where mean annual temperature variability is high), the *average* value for temperature variability in this species range will be neither very high nor very low. Therefore, in our dataset, only species which occur primarily in areas with highly variable temperature will have high average temperature variability. This means that in our data, high average temperature variability is found in cold habitat specialists, restricted to cold, variable areas, where species that occur both in cold, variable habitats, but also in less variable habitats may be more generalist in their thermal niche and therefore have larger ranges (Liang et al., 2021; Morueta-Holme et al., 2013; Pither, 2003; Pulliam, 2000). *Schivereckia podolica* an alpine steppe plant (Friesen et al., 2020) has low range size, low occupied area, high average temperature variability, as do *Dianthus pseudoversicolor* and *Potentilla arcticai* (see Appendix Figure B.3 for maps). Therefore, in both our study and in studies finding a positive relationship between range size and temperature variation, methodological differences mean that these superficially opposing relationships all support a likely link between large range size and broad thermal niche.

Further, evidence for temperature variability as a driver of plant distribution patterns comes from studies conducted at a global scale (Huang et al., 2021 and citations therein). Huang et al (2021) show that climate variability is the most important driver of plant species broad-scale distribution at low latitudes, but that climate extremes are more important in northern latitudes. Europe as a whole has high temperature variability compared to equatorial regions (Appendix Table B.2). It may therefore be that at a global scale, temperature variability relates to larger range size, but at a smaller (continental) scale, there is more nuance to the relationship. In light of these key differences between our methods and other studies, we do not find our result of higher average temperature variability across species' occurrences to be in conflict with evidence showing small ranged species occur in invariable temperatures. Instead, we suspect that these findings - positive relationships between range size and temperature variability at a global scale, and smaller range size relating to higher average temperature variability within the range of European endemics - are again both likely driven by the breadth of species' thermal niches.

Our results show positive relationships between temperature and range filling. This finding may also relate to the negative relationship between range size and filling (-0.67, $p < 0.001$) (see Appendix Figure B.2b). A positive relationship between high average temperature and smaller ranges, and with greater range filling could reflect species facing dispersal limitation from glacial refugia. For example, *Silene mollissimais, Silene sieberi* and *Papaver purpureomarginatum*, species with high average temperature, high range filling and low range size, are island endemics native to Baleares, Kriti, and the Aegean Islands respectively (see Appendix Figure B.3 for maps).

3.5.2 Human footprint

Though human footprint had a lower relative importance than was expected (Sales et al., 2022), it still showed significant relationships with species spatial patterns. In our data geographic range size and occupied area were correlated (Appendix B.2b), so we expect factors related to large occupied area to relate to large range size. Human footprint correlates positively with occupied area, and range size, and is negatively correlated with geographic range filling. There may be several reasons for this. Species' potential for dispersal is expected to mediate spatial patterns within their range, i.e. range filling and local patterns of occurrence (Estrada et al., 2018; Riibak et al., 2017; Svenning & Skov, 2007). However, human activity reduces the importance of species' dispersal ability (Riibak et al., 2017) through human mediated dispersal (Kelly, Lundy, et al., 2014; Smith et al., 2020). Human mediated dispersal may contribute to large range size, with human disturbance then limiting range filling. We expect that due to the prevalence of terrestrial anthropogenic influence in Europe , the only species that still retain large high occupied area are species able to cope with anthropogenic influence (Newbold et al., 2018). Additionally, species that may have had large European ranges driven by other factors (e.g. species that were the most competitive in the most wide spread climate conditions) but that were unable to persist with human land use may have been relegated to "marginal" areas with lower levels of anthropogenic influence. On the surface, the negative relationship between range filling and human footprint may seem in contrast to Araújo (2003) who found a positive relationship between human population density and species richness in plants, mammals, amphibians and reptiles in Europe. However, as with Moretua-Holme (2013), and Huang (2021), Araújo investigated this relationship at the level of species richness, rather than through metrics of the spatial patterns of individual species. Finally, the negative relationship between human footprint and range filling could be partially driven by the negative relationship between range filling and range size, the metric best explained by our climate and human footprint variables.

3.5.3 Metrics

The main effects of climate variables and human footprint showed similar relationships across occupied area and geographic range size, but both the patterns in the effect sizes of the main effects and the two way interactions between these variables differ considerably for metrics of range division (patch size and geographic range filling). This implies that climate and human footprint have different importance to the processes affecting species' occurrence across the different dimensions of spatial pattern. For example, climate change velocity as a main effect has the largest effect size of any model term for metrics of range size, whereas it is the second smallest significant effect for range filling. Large range shifts happen over a longer time scale (Svenning & Skov, 2004) whereas spatial patterning within a species' range is responding to processes acting on a shorter timescale (Buckley & Puy, 2022; Gurevitch et al., 2016), possibly resulting in increased relative importance of contemporary climate to range filling. It may be that the effects of past climate change i.e. the relationship between range boundaries and dispersal limitation is most evident at the broadest spatial scales, while the processes driving spatial pattern within the range i.e. factors resulting in fragmentation are more evident at shorter temporal scales. Species' in fragmented ranges with larger patches are expected to be less negatively affected by the fragmentation (Hanski et al., 2013; MacArthur, 1967), and higher range filling relates directly to less fragmentation within the range. The decoupling of the pattern in effect sizes between patch size distribution and range filling is of particular interest, as these metrics capture different dimensions of fragmentation within the range. The opposing direction of relationships between these metrics and the climate and human footprint variables is unexpected, and suggest that these relationships are driven at least in part by the relationships between metrics of range division and metrics of range size.

3.5.4 Scale

The signal of the relationship between environmental variables and ecological patterns are dependent on the scale at which the patterns is measured (Levin, 1992; Sandel & Smith, 2009). As such, crucial to the interpretation of our results are the differing spatial scales over which our covariates vary, the resolution of our response variable and the temporal scale at which our covariate shape species spatial patterns. Because species occurrence is recorded at 50 x 50km, there is a mismatch between the scales at which human footprint varies (sub 50 x 50km resolution) and the information we have about species' occurrence. Human footprint varies a lot within a 50 x 50km cell (**Figure 3.4.**), and so average human footprint values between two distant 50 x 50km cells are likely to be quite similar. On the other hand, past climate change velocity varies little over small spatial scales, but a lot over large spatial scales (**Figure 3.4.**) i.e. values from two 50 x 50km cells at either end of a species range are likely to be quite different . Given the evidence that human footprint acts on ecology at smaller spatial scales that climate (Carl et al., 2016; Newbold, 2018), we suggest that if these patterns were investigated with higher resolution occurrence data, human footprint would show a greater relative importance to species' spatial patterns. Interestingly, the covariate describing variability at the greatest temporal scale – past climate change velocity – had the greatest relative importance to these low resolution spatial patterns. Spatial scale at which we are measuring our response means the signal that is clearest to us is of a variables acting at large temporal scales (past climate change velocity acts over approx. 24000 years) (Sandel et al., 2011). The large amount of variance accounted for by phylogeny alone also indicates that the forces of high relative importance to the spatial patterns at these large scales are acting at large temporal scales.

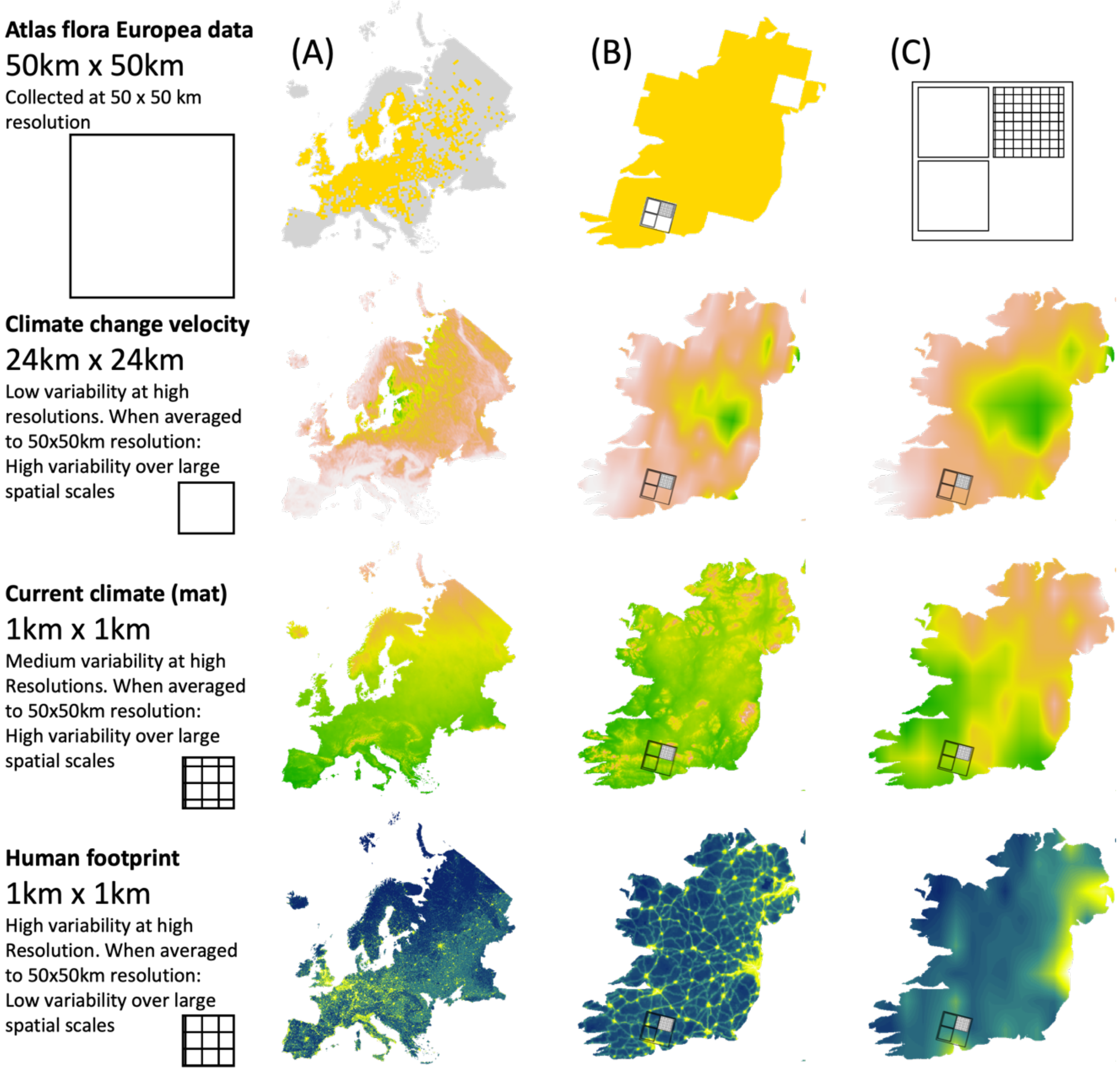


Figure 3.4. Illustration of how model covariates vary over small and large spatial scales in comparison to resolution of response data.
Row one shows species occurrence data on which response variables (metrics of spatial pattern) are based, and an illustration of cell sizes from data at resolutions of 50 x 50 km (largest square), 24 x 24 km (mid-sized empty squares) and 1 km^2 (grid of smallest squares within top right hand corner). Rows two to four show covariates past climate change velocity, climate (here mean annual temperature) and human footprint respectively. (A) Column showing covariates at the highest available resolution. (B) Column shows Ireland as an example of how covariates vary at their highest resolutions. (C) Column showing covariate variation through space once data has been aggregated to the resolution of the response data (50 x 50 km). Quartered square image in columns (B) and (C) illustrate relative cell size for data at resolutions 50 x 50 km, 24 x 24 km and $1km^2$.

3.5.5 Limitations

For mean annual temperature variation in particular, using the range of the covariates in the analysis would have been informative (i.e. range of temperature variability rather than average temperature variability experience by each species). However, we chose to use covariate means rather than ranges as while means were informative (with some interpretation) for all variables, range would have been completely uninformative for some variables i.e. human footprint, due to the spatial scale over which it varies.

Both climate and human footprint are likely to be highly relevant to the spread of non-native species (Kelly, Leach, et al., 2014; Lembrechts et al., 2016), with invasive species a key threat to biodiversity (IPBES, 2019). However, we consider only with European endemics, as such, our results do not reflect the potential relationships between contemporary climate, human footprint and spatial patterns of non-native species.

There are relationships between range metrics and between explanatory variables. Total area and range size are expected to be correlated, as they represent related but distinct dimensions of species spatial pattern (Gaston & Fuller, 2009). It may be that some of the relationships between range metrics are correlations and some are causal. Patch size distribution may drive higher occupied area through species-fragmented area population dynamics or stochastic extension (Hanski et al., 2013), but the processes enabling large patch size may not contribute to dispersal/niche breadth that may be more relevant to geographic range size, meaning the relationship between range size and patch size may be an artifact of the correlation that range size and patch size both have with occupied area. The complex and incomplete correlations between these range metrics indicate that different factors may be of different relative importance to these dimensions of spatial structure.

Our results provide evidence for the correlations between climate, human footprint and metrics of spatial patterns for European plant species. However they do not provide insight into the ecological mechanisms behind these relationships. Explicit investigation into the relationships between these spatial patterns and species' functional or life history traits is needed to understand why these variables - in particular human footprint - relate to spatial patterns. Our study investigates whether including modern human footprint along with past climate change velocity and contemporary climate improves our understanding of species spatial patterning; we do not account for past human land use. Further study investigating the interaction between past climate change velocity and contemporary human influences would give a fuller picture of the relative importance of forces driving broad scale spatial patterns.

3.6 Conclusion

Explicitly considering contemporary human footprint along with phylogeny, contemporary climate and past climate change velocity improves our understanding of some dimensions of species' spatial patterning in endemic European plant species. Range size was well explained by models of phylogeny, past climate change velocity, contemporary climate and human footprint. Range division was less well explained, and patch shape were not explained by our models. As a main effect, past climate change velocity was the most important variable for two metrics of range size and one of range division. Though adding human footprint improved most models, the signal was not as strong as expected. We suggest that the relatively low strength of the human footprint signal relates to the resolution at which species occurrence data was obtained, and the spatial extent over which past climate change, contemporary climate and human footprint vary. We conclude that higher resolution occurrence data is needed in order to quantify the relative influence of human footprint compared to climate variables. Species' spatial patterns are a physical manifestation of their realised niche. If human footprint is affecting broad scale spatial patterns in addition to climate, then this adds a further factor constraining or expanding available niche space. In trying to untangle the multifaceted drivers of ecological patterns, terrestrial human activities should be considered as a force acting on species' ecology. As the primary driver of global biodiversity loss, human footprint should be considered in addition to both contemporary climate and future climate change in assessing species' vulnerability to global change.

Chapter 4 Relationship between fishing pressure and community life history traits is scale dependant

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Author contribution: Research was conceived and designed by CMM and RK. Data was obtained from DATRAS and cleaned by CMM and RK. CMM obtained further data and conducted the analysis with input from RK and YB.

4.1 Abstract

Human influence in the oceans is pervasive and is affecting marine life. Understanding species' differing responses to human influence, and how human influence compares to other environmental variables in reshaping marine communities is needed to facilitate the sustainable management of the seas. Despite previous evidence that fishing pressure affects marine life history strategies, several recent large scale studies have not shown strong relationships between fishing pressure and community composition. We test the hypothesis that the signal of the effect of fishing pressure on community weighted mean life history strategy depends on the scale at which community is defined. Using high resolution annual fishing pressure data, we show that fish community life history strategy is correlated with fishing pressure in the North East Atlantic, and that the relative importance of fishing pressure compared to sea surface temperature and depth increases with the scale at which a community is defined. We suggest that this scale dependence is a result of the spatial extent over which covariates vary, and how fish movement moderates communities' experience of this variability. We suggest that the most ecologically meaningful scale at which to define fish communities in the North East Atlantic may therefore be related to some measure of community weighted mean movement. Our findings highlight the importance of explicit consideration of scale in ecological research, supporting the idea that studying systems at ecologically relevant scales is necessary to detect and interpret the effects of global change.

4.2 Introduction

4.2.1 Anthropogenic influence

As in terrestrial biomes, human influence is pervasive throughout the marine environment (Halpern et al., 2008; Jones et al., 2018; Kroodsma et al., 2018; Sala & Knowlton, 2006). In the last century, human activities - overfishing foremost amongst them - have increasingly impacted marine life, precipitating acute declines in biomass and diversity (Díaz et al., 2019; Cardinale et al., 2012; Di Minin et al., 2019; Jackson et al., 2001). In addition to increased pressure from overfishing and habitat loss, the marine environment is experiencing the ongoing effects of anthropogenic climate change (Simpson et al., 2011), from which marine ecosystems and the services they provide are increasingly under threat (Asch et al., 2018; Rocha et al., 2015).

Recognition of the importance of biodiversity to human society (Díaz et al., 2006; Folke et al., 2021), and the ability of marine ecosystems to provide protein for human consumption (Béné et al., 2015; Costello et al., 2020; Weindl et al., 2020), has led to an increased interest in sustainable harvesting of marine life (Bentley et al., 2019; Howell et al., 2021; Kroodsma et al., 2018; Ward et al., 2022), and the protection of marine ecosystems through the establishment of marine protected areas (Halpern et al., 2015; Probst et al., 2021). However, the response of fish stocks to these efforts is uncertain (Britten et al., 2021), and detailed knowledge of species' differential responses to and recovery from changes in environmental and anthropogenic pressures is still needed to facilitate the sustainable management of the seas (Greenstreet et al., 2011; Thompson et al., 2020). In terrestrial systems, human influence is being shown as comparable to other environmental factors driving ecological patterns (Ellis et al, 2008; McKeon et al, *in prep.*). We are still developing an understanding of the relative importance of human vs non-human environmental factors on marine biodiversity (Fu et al., 2012), how species differ in their responses to these factors (Beukhof et al., 2019) and the spatial scales at which the effects of these factors are most relevant (de Castro et al., 2015).

4.2.2 Traits, community and ecological scales

To understand species' differential responses to human influence, it is helpful to characterise them by their intrinsic traits. Intrinsic traits, such as functional traits (Thuiller *et al.* 2006; Garnier *et al.* 2018), life history strategy (Doak & Morris, 2010; Harrison et al., 2018; Ramula et al., 2008; Shryock et al., 2014; Stearns, 1992) and life form (Smith 1909; Broennimann *et al.* 2011), mediate species' responses to their environment. Characterising species by their intrinsic traits can help reduce the complexity of ecological systems (König et al., 2019; Lavorel et al., 2002; Mouquet et al., 2015), allowing the study of how suites of species differ in their ecological patterns and responses to global change (Carmona et al., 2021; Leung et al., 2020; Newbold et al., 2018). In particular, viewing species through their intrinsic traits can help us understand how human influence produces shifts in community composition (Murgier et al., 2021; Allan et al., 2015; Comte et al., 2021; Danneyrolles et al., 2019; Eriksson & Hillebrand, 2019; Frelat et al., 2022; Garnier et al., 2007, 2018; Hillebrand et al., 2018).

One characterisation of species intrinsic traits is life history strategy. As a characterisation of ecological complexity, life history strategy (LHS) represents how species deal with the fundamental challenges of evolution – survival, growth, and reproduction (Stearns, 1992). Life history can be broadly described by the shape and pace of life with regards to aging (Baudisch, 2011; Healy et al., 2019), and fertility (Baudisch & Stott, 2019; Healy et al., 2019). Life history strategy can be further simplified by models relating trade-offs in species' life history to their environments. These trade-offs have been described by complimentary frameworks such as r-K selection (Pianka, 1970), and the fast-slow continuum (Franco & Silvertown, 1996), which has been used to describe how life history covaries with temperature in marine communities (Beukhof et al., 2019). In terrestrial environments, trade-offs between strategies dealing with competition, disturbance and physiological extremes have been described for plants by the Grime's triangle (Grime, 1997, 1974), where the relative abundance of those strategies in communities reflects heterogeneity in the productivity, stability and tolerability of the environment. In the marine realm, the equilibrium–periodic–opportunistic (EPO) triangle put forward by Winemiller and Rose (1992) describes fish life history strategy in relation to the stability and predictability of the environment, and has been found to align with life history strategy variation in marine communities (Pecuchet et al., 2017). Equilibrium strategy is characterised by species with high juvenile survivorship and slow pace of life (i.e. long generation time) and is expected to be best suited to more stable, less variable environments. Periodic species are expected to be suited to predictably variable environments (i.e. environments with strong seasonality) and are characterised by high fecundity. Opportunistic species are characterised by short generation time and fast growth rates (i.e. fast pace of life), strategies suited to take advantage of suitable conditions in unpredictable, variable environments (Winemiller & Rose, 1992).

Life history strategies in fish communities co-vary with the environment. Equilibrium strategy is expected to increase in deeper, colder waters with less variable temperature (Pecuchet et al., 2017), whereas opportunistic strategies are expected to increase in warmer, more variable waters (Pecuchet et al., 2017), i.e. deep, cold, invariable waters favour slow-lived species, warm, shallow waters with high temperature variation favour fast lived species (Beukhof et al., 2019). Human influence is expected to result in changes in life history strategies in marine communities. Fishing effort is expected to cause a shift in community life history strategy, away from equilibrium strategies (Pecuchet et al., 2017) towards faster lived, more productive, species (de Juan et al., 2007; Jennings et al., 1999; Sguotti et al., 2016). High resolution, long term data on fish abundance and distribution (ICES, 2022) and life history data (Froese & Pauly, 2022) are available for investigating how community life history strategy is structured by the constraints of the environment, and how the relative effects of environmental factors compare. However, recent work using DATRAS has found mixed evidence for the relative importance of fishing pressure in structuring fish community life history strategy: fishing pressure was found to be a weak predictor of fish abundance (Rutterford et al., 2015) and community structure (Beukhof et al., 2019) and important only to one (equilibrium) life history strategy (Pecuchet et al., 2017). Here, we investigate the hypothesis that these discrepancies between theoretical expectations and empirical findings arise from the spatial resolution at which community is defined.

Multiple forces affect marine biodiversity, including climate, trophic interactions and human activities (Fu et al., 2012), but the strength of the signal between variables and ecological patterns is scale dependant (Beukhof et al., 2019; Carl et al., 2016; Chase, 2014; Levin, 1992; Sandel & Smith, 2009). Knowledge of the scale at which ecological units – be that individuals, species, communities or ecosystems - experience variation in the factors that affect them is relevant to how they are studied and how they are managed. In the marine environment, the degree of environmental variability experienced by species is moderated by species' movement (Green et al., 2015; Kramer & Chapman, 1999; Weeks et al., 2017). Therefore fish movement across space and time, and the scale at which to consider marine communities is a key area of marine research (de Castro et al., 2015; Neat et al., 2014; Probst et al., 2021), as fish movement is expected to be relevant to how populations are effected by human pressure (Claudet et al., 2008; Kramer & Chapman, 1999; Shephard et al., 2011). For example in the Celtic Sea, Shepard et al (2011) found a strong relationship between fishing pressure and fish community size structure using Large Fish Index (LFI) at a resolution of approx. 70 x 70 km, a weak relationship at resolutions of approx. 35 x 35 km, and no relationship at resolutions of approx. 17 x 17 km. Similarly, De Castro et al. (2015) find that resolutions of approx. 62 x 62 km best explain the signal of fishing pressure on community size structure in 18 abundant ground fish. We investigate a potential explanation for limited evidence supporting the effects of fishing pressure in structuring fish community life history in recent large scale studies is the scale of investigation.

4.2.3 Aims

Using 12 years of high resolution scientific survey data we compare the influence of non-human environmental factors (temperature, temperature variation and depth) and fishing pressure on the community composition of fish life history strategy in the North East Atlantic ocean. We test the hypothesis that current weak evidence for the impact of fishing pressure on fish community composition in this dataset is a result of a mismatch between the spatial scales at which community is defined and the scales at which communities are experiencing environmental variability.

Our study had two aims:

1) To test how extrinsic factors sea surface temperature, depth and fishing pressure relate to community weighted means of three dimensions of fish life history strategy;
2) To assess how the effects of these extrinsic factors depend on the spatial resolution at which communities are defined

Our data comes from the Celtic-Biscay Shelf Large Marine Ecosystems, which is currently and historically some of the among the most heavily exploited in the world (Halpern et al., 2008). We therefore expect that fishing pressure will effect fish community life history. We expect fishing pressure to correlate with higher mean community fecundity, faster pace of life, and lower tropic level (Jennings & Blanchard, 2004). Based on the EPO model, this would mean increases in opportunistic and periodic, rather than episodic species, i.e. species adapted to unstable and predictable, or unstable and unpredictable environments. We expect temperature and temperature variation to correlate positively with faster lived species (Beukhof et al., 2019), and depth to correlate with slower lived, lower fecundity species with higher trophic level (Pecuchet et al., 2017). We hypothesise that our ability to detect these relationships, in particular relationships between community composition and fishing pressure, will depend on the spatial scale at which ecological communities are defined.

4.3 Methods

We modelled how community weighted means of fish life history traits responded to the environmental covariates: sea surface temperature (SST); depth; and fishing pressure. We obtained life history trait data from Beukhof et al. (2019), species identity and abundance data from DATRAS (https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx, date downloaded: 04/21/2022), and SST, depth and fishing pressure data from MODIS-Aqua (NASA/JPL, 2020), NOAA (Amante, 2009) and OSPAR (ICES, 2021) respectively. Data were cleaned and merged prior to analysis (see https://github.com/cmmckeon/fishies). Analyses were carried out on a subset of 208 fish species (including all Chordata but excluding tunicates and sea birds) for which trait data were available, using frequentist general linear mixed models in R version 3.6.3 (R Core Team, 2020).

4.3.1 Biodiversity data

We obtained fish identity and abundance data from co-ordinated international scientific survey effort DATRAS (ICES, 2022). Two steps of quality control and standardisation were required: cleaning “haul” data – (data relating to the sampling efforts themselves), and cleaning biodiversity data collected by the hauls. Moriarty et al., (Greenstreet & Moriarty, 2017a, 2017b; Moriarty et al., 2017, 2019) created reproducible scripts to clean and standardise the haul and biodiversity data from 1996 to 2016. Sampling protocol could differ by country, ship and gear type, and so, once cleaned, the haul data were standardised to produce a final product with comparable fishing effort and catch data. We downloaded data from DATRAS in March 2022 and updated this workflow to clean and standardise data up to 2021. From all available DATRAS data, we downloaded surveys targeting the whole fish community, with more than 10 years of data available. We excluded surveys that were of the deep sea, short time frame, had known issues with data quality or were not contiguous with other data. Cleaning and standardisation for haul data included merging data from different surveys, checking for and correcting outliers, imputing/filling in missing values, i.e. depth data obtained from NOAA (Amante, 2009) at a 1 minute resolution was used to validate the recorded depths from the haul data, and to fill in missing values. Cleaning for biodiversity data involved obtaining a phylogeny from WoRMS (WoRMS Editorial Board, 2022) and checking for outliers in max length, abundance and catch weight. We constrained our study to the North East Atlantic Celtic-Biscay Shelf (**Figure 4.1.**) and so DATRAS surveys ultimately included in this study were EVHOE, FR-CGFS, IE-IGFS, NIGFS, ROCKALL, SCOROC, SCOWCGFS, SWC-IBTS. Our cleaned dataset contained 250 unique species. For more details of data cleaning workflow see https://github.com/cmmckeon/fishies.

4.3.2 Covariates

Sea surface temperature was obtained from MODIS-Aqua (NASA/JPL, 2020) (https://oceancolor.gsfc.nasa.gov/l3/order/) as seasonal (three month) daytime averages at a 5 minute resolution (approx. 5 x 5 km at European latitudes) for 2009 – 2021 inclusive (**Figure 4.1.**). SST for spring and for winter, as well as annual SST variability (difference between summer and winter averages) were included in our models. Fishing pressure was obtained from OSPAR (ICES, 2021) (https://ices-library.figshare.com/articles/dataset/Data_for_OSPAR_request_on_the_production_of_spatial_data_layers_of_fishing_intensity_pressure/18601508) as total annual kilowatt fishing hours in 3 minute grid cells for 2009 – 2020 inclusive (**Figure 4.1.**). Covariate data were extracted seasonally (SST), annually (fishing pressure) or as a fixed value (depth) for the location of each haul.

4.3.3 Trait data

We obtained Celtic-Biscay Shelf ecosystem specific values for seven continuous fish life history traits for each species from Beukhof et al. (2019): trophic level, offspring size, age at maturity, fecundity (total offspring produced per female per year), von Bertalanffy growth coefficient (estimating individual growth rate per year) maximum length, and maximum age. Trait data were available for 208 species, meaning that over 83% of species in the community from our cleaned dataset were included in our analysis. Trait data and covariates were log transformed and scaled to a mean of zero and a standard deviation of one.

4.3.4 Principal Component Analysis

We compiled a dataset of unique transformed trait values, i.e. one trait value per species. We reduced the dimensionality of this life history trait data using Principle Component Analysis, resulting in three principle components (PC's) that best explained life history variation in our species. For each haul, we then obtained community weighted means for PC1, PC2 and PC3 based on raw abundance data using the vegan package (Oksanen et al., 2020). PC1, PC2 and PC3 were then scaled and added to our modelling dataset.

4.3.5 Analysis

To test how environmental factors affected community weighted life history strategy, we ran null models to establish appropriate random effect structures (see Chapter 1). We then ran three models testing whether SST, depth and fishing pressure related to the community weighted mean of the three principle components which we interpret as broadly representing the pace of life axis, the reproductive axis and trophic level. We used mixed effects models (Brooks et al., 2017) with Gaussian error structures to test the community weighted mean of each principal component against spring SST, winter SST, SST variation, depth and fishing pressure, and all two way interactions between these terms. The season in which the sample had been collected (spring or winter) and the year of collection were included in the models as main effects (not in interaction with other terms). Fishing gear, ship and haul location were included as nested random effects to account for non-independence in the data. We evaluated all models for goodness of fit using QQnorm and residual vs predicted plots using the DHARMa model diagnostics package (Hartig, 2018), and used model AICs to determine whether our main models accounted for more of the variance and were more parsimonious than our null models. All models converged and produced satisfactory residuals, and all main models improved on respective null model AICs.

To investigate how the spatial extent at which a community is defined affected these relationships, we then applied the same modelling workflow to datasets where community was defined at a series of decreasing spatial resolutions. We achieved this by aggregating 5 minute SST rasters by a factor of 5, 10, 20 and 50, ultimately producing 250 x 250 minute (or approx. 250 x

250 km in Europe) grid cells, i.e. at minimum resolution, community was defined by all hauls in grid cells about 4.17 degrees wide (**Figure 4.1**). Using our existing principle components, we then recalculated community weighted mean abundance for communities at each resolution.

4.3.6 Scale at which community experiences the environment

To inform our discussion of fish movement and ecologically meaningful community scale, we obtained data on consistent core areas for 48 demersal species in our dataset (Appendix Table C.2) from Probst et al. (2021), who studied population distributions of mobile fish species in the North Sea over a 21 year period, assessing whether their use of space overlapped with marine protected areas. Probst et al. define core areas as “grid cells containing 50% of cumulative population biomass in any given year and season”, with grid cells containing at least 50% of all core areas for the whole study duration considered consistent core areas.

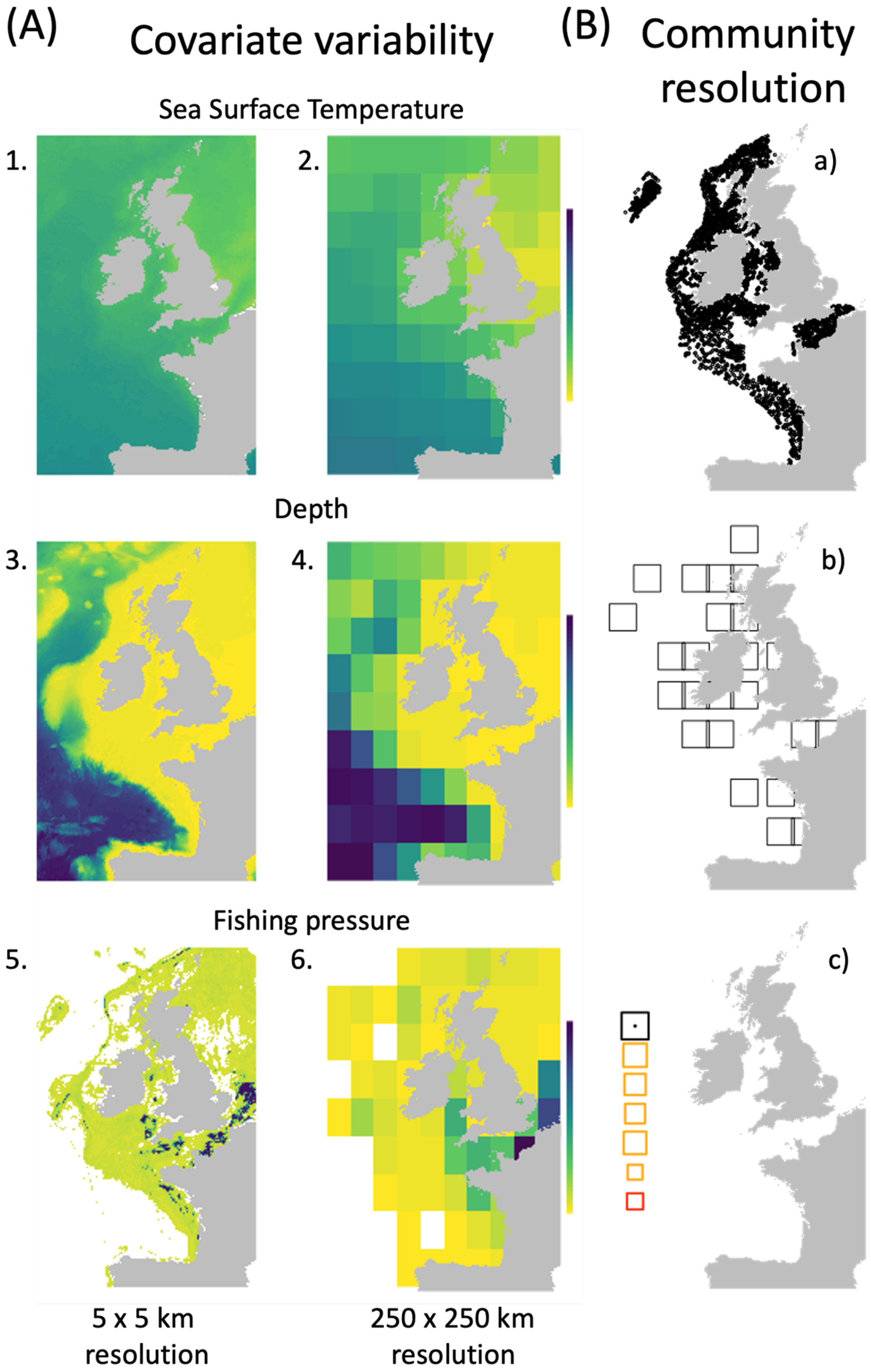

Figure 4.1. Covariate variability, and community resolutions.

(A) Schematic showing data on which model covariates are based at the highest resolution (1, 3, 5) (approx. 5 minutes or 5 x 5 km grid cells) and the lowest resolution used in our models (2, 4, 6) (approx. 4.16 minutes or 250 x 250 km grid cells). (B) Maps of study area showing (a) locations of hauls (highest resolution definition of community); (b) illustration of communities at the lowest resolution used in our models (all hauls in a 4.16 minute grid cell) and (c) illustration of our lowest resolution community size (top black box) compared to communities at the level of haul (dot inside top black box) and size of average winter consistent core areas for 48 species in our dataset after Probst et al (2021) (bottom red box, size = approx. 150 x 150 km) and sizes of consistent core areas for five most abundant species in our dataset (from top orange box to bottom): *Merlangius merlangus* = 218 x 218 km; *Trisopterus esmarkii* = 197 x 197 km; *Melanogrammus aeglefinus* = 183 x 183 km; *Pleuronectes platessa* = 210 x 210 km; *Scyliorhinus canicular* = 138 x 138 km. Average and example consistent core areas are shown to illustrate size in comparison to finest and coarsest resolutions at which we define communities – consistent core areas data comes from North Sea populations and so are not depicted here in the correct spatial locations.

4.4 Results

4.4.1 Principal Component Analysis

Three principle components explained a cumulative 84% of variance across the traits (**Figure 4.1., Table 4.1.**) - PC1 (51.52%), PC2 (20.94 %) and PC3 (11.97%). PC1 had a positive correlation with age at maturity (0.44), maximum length (0.44), maximum age (0.43) and offspring size (0.40) and a negative relationship with growth coefficient (-0.42). PC1 can be considered to represent a pace of life Life history axis (Baudisch, 2011; Healy et al., 2019). PC2 had a strong positive relationship with fecundity (0.76) and a negative relationship with offspring size (-0.50), representing the reproductive life history axis (Healy et al., 2014). PC3 represented trophic level, with a strong negative correlation of -0.89.

Table 4.1. Principle component analysis of life history trait variation.
Values in black highlight correlations of over 30%.

Life history trait	**PC1**	**PC2**	**PC3**
Trophic level	0.2620178	0.18684176	**-0.8915949**
Offspring size	**0.3950247**	**-0.5023745**	-0.0977324
Age at maturity	**0.4398705**	0.02730555	0.26597648
Fecundity	-0.1661993	**0.76322546**	0.02685936
Growth coefficient	**-0.41951**	-0.1957586	-0.2296948
Max length	**0.4376938**	0.17022719	-0.0997469
Max age	**0.4320063**	0.24930423	0.24765496
Importance of components			
Standard deviation	1.899	1.2107	0.9154
Proportion of variance	0.5152	0.2094	0.1197
Cumulative	0.5152	0.7246	0.8443

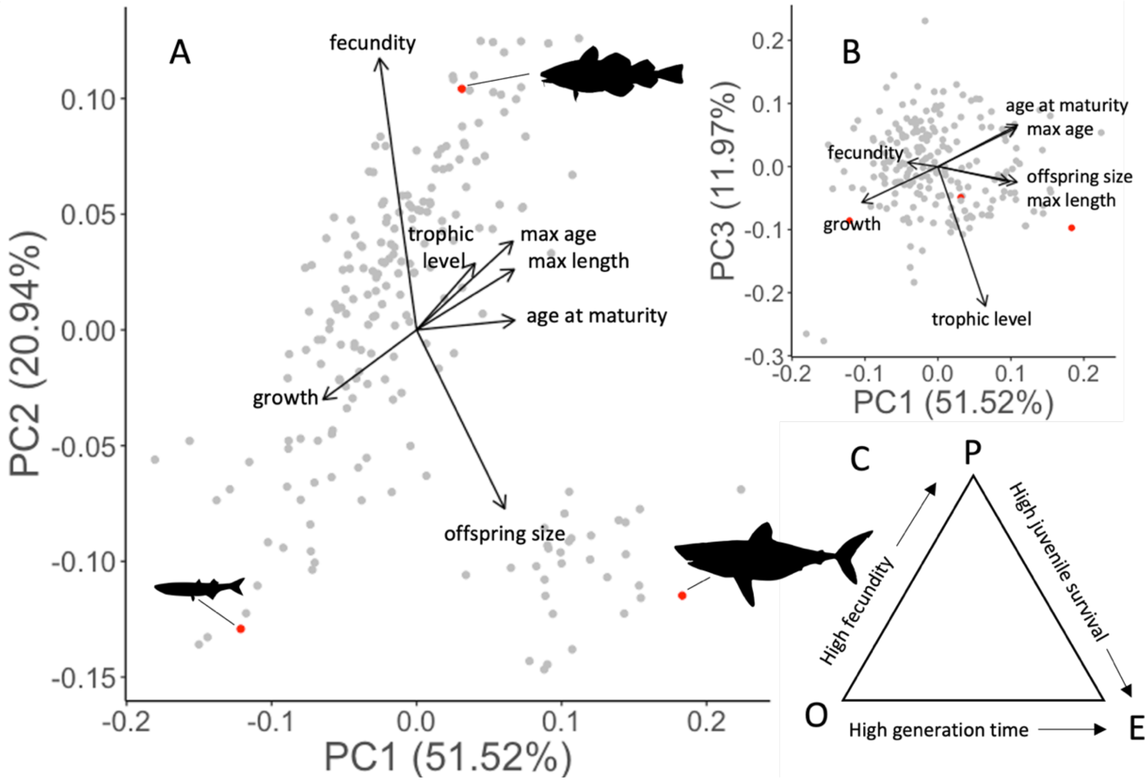

Figure 4.2. Principle component analysis of life history trait variation.
(A) Plot of PC1 (pace of life axis) against PC2 (reproductive investment axis), showing the loadings of the seven life history traits. X and Y axes display the variance explained by each principle component. Points in red highlight example species in our data to show how our PC axes align closely with the equilibrium-periodic-opportunistic (EPO) model of life history trade-offs. *Lamna nasus* (porbeagle) has a high value on PC1 and represents equilibrium LHS, with high offspring size, max age, max length and age at maturity. *Gadus morhua* (cod) has a high PC2 value and represents periodic LHS with high fecundity, and *Spinachia spinachia* (sea stickleback) has a low PC3 value, representing opportunistic LHS with high growth coefficient. (B) Plot of PC1 against PC3 (trophic level). (C) Schematic of the EPO triangle linking trade-offs in LHS to stability and predictability of the environment (see introduction).

4.4.2 Covariates

Sea surface temperature, depth, fishing pressure and interactions between these variables were significantly correlated with community weighted means of fish life history traits described by principle components relating to pace of life, reproductive investment and trophic level. The effects of the covariates differed across the community weighted means of the three principle components, and these relationships differed depending on the spatial extent at which communities were defined. When communities were defined at the level of an individual haul, terms involving depth and sea surface temperature had larger effects than terms involving fishing pressure. When community was defined by all hauls in approx. 25 x 25km, 50 x 50km, 100 x 100km and 250 x 250 km, the strength and direction of the effects differed from effects on communities based on individual hauls, with the interaction of fishing pressure increasing in importance in communities defined at the coarsest spatial resolution.

4.4.3 Communities at the level of haul

Here we highlight examples of the strongest correlations for each community weighted mean principle component (**Figure 4.3**). For full model summaries including p-values see Appendix Tables C.1.1, C.2.1 and C.3.1. SST variation has a negative effect on community weighted mean of PC1 (**Figure 4.3**). This means that with increased SST variation, there are lower community weighted mean values for pace of life, i.e. lower maximum age and length, lower age at maturity, and smaller offspring size. The effect of SST variation on pace of life gets more negative with higher spring SST and fishing pressure (**Figure 4.3**), i.e. the higher the spring SST and the more fishing pressure, the greater the correlation between SST variation and more faster living species in communities. Depth interacting with spring SST and winter SST correlates with slower community weighted mean pace of life (**Figure 4.3**). Winter SST interacts with SST variation to increase the community weighted mean of PC1, i.e. warmer winter SST where SST is more variable leads to slower mean pace of life in a community.

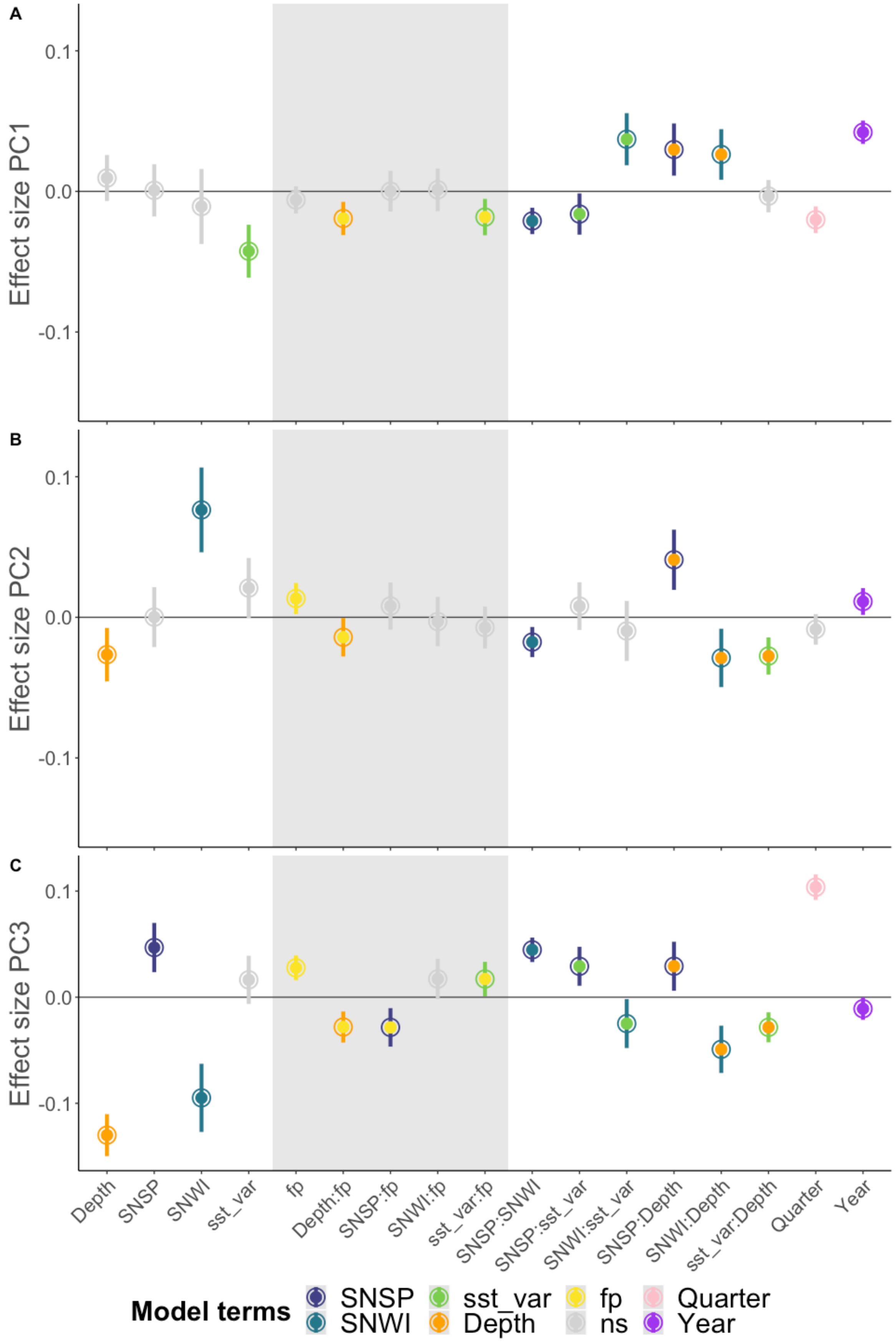

Figure 4.3. Community weighted means of life history principle components at the level of haul. (A) Effects of SST, depth and fishing pressure on community weighted mean of PC1 (representing pace of life Life history axis). (B) Effects of SST, depth and fishing pressure on community weighted mean of PC2 (representing reproductive investment life history axis). (C) Effects of SST, depth and fishing pressure on community weighted mean of PC3 (representing trophic level). In all panels, the

x axis represents change in community weighted mean value of PC associated with a one standard deviation change in each model term. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). The colour of points and vertical lines refers to the terms in the model. If a point and vertical line are the same colour, this represents a main effect. If point and vertical line are different colours, this represents the interaction between two main effects as per the legend. Non-significant model terms (p-value > 0.05) are shown in grey. Light grey vertical bar highlight terms associated with fishing pressure. Vertical lines represent 95% Confidence interval. CIs overlapping continuous horizontal lines indicate that the slope of the relationship is not significantly different from zero (no effect). Significant effects have been coloured for clarity. For graphic with colours corresponding to all effects regardless of significance see Appendix Figure C.1. Total number of observations (communities) in the models = 8160.

For PC2, greater depth leads to lower community weighted mean, i.e. lower mean fecundity and larger offspring values in the community (**Figure 4.3**). Higher winter SST correlates with higher fecundity, but this relationship gets less positive as depth increases. Fishing pressure has a positive effect on community weighted mean PC2 – higher fishing pressure correlates with higher community weighted mean fecundity (**Figure 4.3**). Higher spring SST at greater depths correlates with increased community weighted mean fecundity. Greater depth and warmer winter SST correlate with lower community weighted mean PC3 (**Figure 4.3**), i.e. higher mean trophic level. Warmer spring SST and higher fishing pressure correlate with lower trophic level (higher PC3).

Quarter has a negative relationship with PC1, but correlates positively with PC3 (**Figure 4.3**), i.e. hauls caught in spring have faster community weighted mean pace of life, and lower mean trophic level. Year is correlated with positively with PC1 and PC2, i.e. over time at average values of SST, depth and fishing pressure, communities are trending towards slower community weighted mean pace of life and higher fecundity.

4.4.4 Communities at larger spatial extents

How community was defined affected the strength and direction of relationship between the variables and the community weighted mean PC values (**Figure 4.4**). Fishing pressure in interaction with other variables gained in importance as community was defined at coarser resolutions. Here we contrast the above findings with results from models where community was defined at the largest spatial extent. We focus on results from this resolution by way of illustration as it is not yet clear which resolution is the most ecologically meaningful. For tables of all model summaries see Appendix Tables C.1, C.2 and C.3.

For communities defined at 250 x 250km extent, community weighted mean of PC1 was positively correlated with winter SST, SST variation and the interaction of spring SST with depth. Community weighted mean of PC1 was negatively correlated with the interaction of winter SST with fishing pressure (**Figure 4.4**) – warmer winter SST with more fishing pressure relates to faster lived communities, as does the interaction between warmer winter SST and spring SST. PC2 had similar direction and significance of relationships to PC1 in communities defined at the largest (coarsest) spatial resolution (**Figure 4.4**). The main difference was depth had a positive relationship with community weighted mean fecundity, and a negative effect in interaction with SST variation, and warmer spring SST in areas of higher fishing pressure relating to higher community fecundity (**Figure 4.4**).

At the largest spatial resolution, fishing pressure interacts with higher winter SST to correlate with faster lived communities with lower fecundity (**Figure 4.4**) – i.e. communities with greater proportions of opportunistic life history strategies. At this resolution, warmer spring SST at greater depths correlates with slower lived species with higher fecundity – more of the community having periodic and equilibrium strategies.

The strongest effects on PC3 in 250 x 250km communities were depth as a main effect and the interaction of fishing pressure with spring and winter SST and depth (**Figure 4.4**). More fishing pressure at greater depth or at higher spring SST correlates with higher community weighted mean trophic level, whereas more fishing pressure at higher winter SST correlates with lower community weighted mean trophic level. At the largest spatial scales, the effects of quarter and year are small or non-significant (**Figure 4.4**).

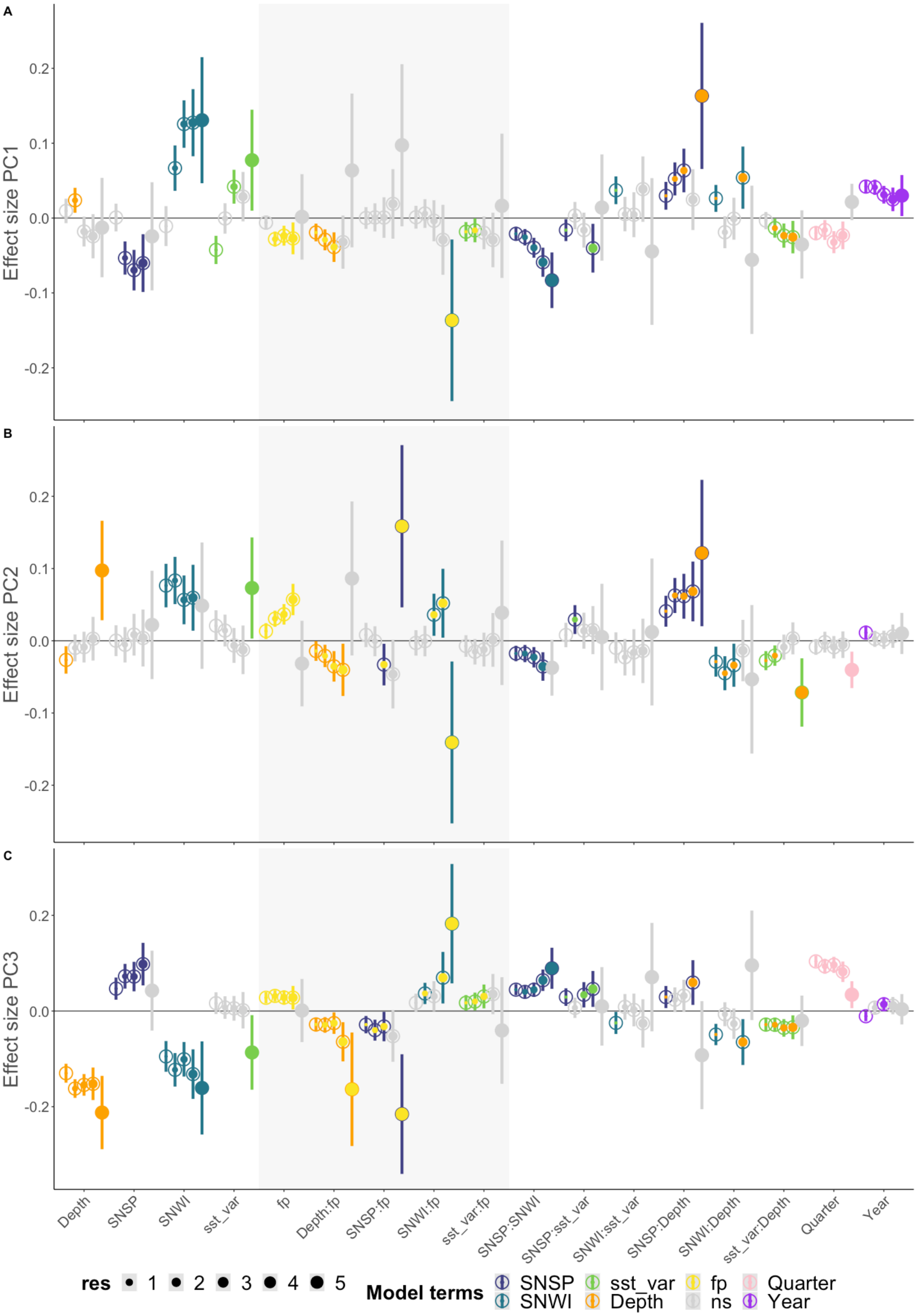

Figure 4.4. Comparison of relative importance of covariates across community resolutions. A) Effects of SST, depth and fishing pressure and their two-way interactions on community weighted mean of PC1 (representing pace of life Life history axis) at each community resolution. B) Effects of SST, depth and fishing pressure on community weighted mean of PC2 (representing reproductive investment life history axis) at each community resolution. C) Effects of SST, depth and fishing pressure on community weighted mean of PC3 (representing trophic level) at each community resolution. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea

surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure. All continuous covariates are average values at resolution of community. Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Communities were defined at the level of haul (1), or all hauls in grid cells aggregated by factors of 5, 10, 20 or 50 (see methods). Number of observations (communities) per model: res1 = 8160, res5 = 6030, res10 = 3945, res20 = 1963, res50 = 564. In all panels, x axis represents change in community weighted mean value of PC associated with a one standard deviation change in each model term. Vertical lines represent 95% Confidence interval. CIs overlapping continuous horizontal lines indicate that the slope of the relationship is not significantly different from zero (no effect). The colour of points and vertical lines refers to the terms in the model. If a point and vertical line are the same colour, this represents a main effect. If point and vertical line are different colours, this represents the interaction between two main effects as per the legend. Significant effects have been coloured for clarity. For graphic with colours corresponding to all effects regardless of significance see Appendix Figure C.2. The size of points refers to community resolution of the model as per the legend. Light grey vertical bar highlight terms associated with fishing pressure.

4.5 Discussion

Fishing pressure, the main driver of change in marine systems in recent human history (Sala & Knowlton, 2006), is expected to interact with species' inherent characteristics to affect community composition. Recent work using European datasets of large spatial and temporal extent has found fishing pressure to be of low relative importance to fish relative abundance and distribution (Rutterford et al., 2015), and community life history strategy (Beukhof et al., 2019; Pecuchet et al., 2017). We provide evidence for the correlation between fishing pressure and community life history strategy, highlight that our ability to detect this signal is dependent on the scale at which a community is defined, and show that the relative importance of fishing pressure increases as communities are defined at larger scales. We suggest this scale dependency arises from the relationship between fish movement and the environmental variability that communities experience.

4.5.1 Life history variation

The three principle components describing life history variation for the fish in our dataset closely aligned with the findings of other works describing marine life history variance (Beukhof et al., 2019; Pecuchet et al., 2017). Our first two PC's describe pace of life and reproductive investment – well established life history axes in other systems (Healy et al., 2019). Interestingly, our third PC described trophic level, a dimension of variation not applicable to plants and not traditionally included in terrestrial life history frameworks (Healy et al., 2019). This third principle component was where our characterisation of life history variation differed most from related studies. Trophic level was not found to covary with environmental variables by Beukhof et al. (2019) (whose life history trait dataset we use), whereas in our data the strongest correlations between environmental variables and community weighted means were with PC3 (trophic level) across all scales. Visually, the plot representing our first and second principle components aligns very closely with Pecuchet et al.'s PC plot, and our axes of pace of life and reproductive investment map onto their archetypal analysis of opportunistic (fast growing, low fecundity), periodic (high fecundity, low juvenile survival) and episodic (long generation time, high juvenile survival) life histories. Again, our main deviation from this characterisation of life history strategies is our third, orthogonal trophic level axis.

Of the 16 commercial species studied by de Castro et al. (2015) present on our dataset, 12 had higher than average trophic level. It may be that the surprising positive relationship between community mean weighted tropic level and fishing pressure at greater depths and warmer summer SST arises from fishing vessels seeking areas with high stocks of these fish, rather than the fishing pressure driving high community trophic level.

4.5.2 Scale at which community is defined

Factors contributing to community composition include all conditions that community members have experienced. When community is defined at the level of haul, we are associating community structure with fishing pressure in the 5 minute grid cell where the haul occurred (approx. 5 x 5 km). However, much of the community will move in an area greater than 5 minutes (Probst et al., 2021; Neat et al., 2014; de Castro et al., 2015; Shephard et al., 2011), and so community mean values will have been affected by environmental values outside of that cell. Defining community at the level of haul asks the model whether there is an association between community weighted mean traits in that haul, and fishing pressure in that 5 minute grid cell. Defining community at lower spatial resolutions allows us to ask whether there is an association between community composition and average fishing pressure at a larger spatial extent – and so is likely to capture a more realistic value of the fishing pressure experienced by much of the community.

Terms involving fishing pressure have some of the lowest relative importance in models at the smallest spatial scale. We suggest that increased relative importance of fishing pressure at greater spatial scales relates to the amount of variability in environmental variables experienced by the community. SST and depth exhibit low variability at small spatial extents, SST especially showing a gradient of values. This means SST values associated with a community in one area are likely to be similar to SST nearby, i.e. average temperature over a small area will be similar to average temperature over the larger surrounding area, and so even at fine scale community resolutions, temperature gives a good amount of information about the full range temperature experienced by the community in the broader area. This is not true of fishing pressure. Because fishing pressure has high variability over smaller spatial extents, fishing pressure values aggregated to larger spatial resolutions will be dissimilar to fine scale values. We suggest that this is why the relative importance of fishing pressure increases with scale in comparison to the other environmental variables.

Stronger signal between fishing pressure and community life history strategy at lower resolution may additionally relate to the movement of fish. How fish use space is a key consideration of human impacts on marine communities (Claudet et al., 2008; Kramer & Chapman, 1999). Considering the high relative importance of SST and depth at high resolutions, there may be a closer match between these variables values at the location of a haul and the rest of the values experienced by a community, as fish can actively respond to gradients of temperature and depth in a way that they cannot respond to fishing pressure.

It is not the case that the composition of communities defined at a high resolution is unaffected by fishing pressure, it is rather that the model is unlikely to associate high resolution fishing pressure with the observed community composition. This is evident in the methods of earlier studies finding relationships between fishing pressure and community life history. Jennings et al. (1999) found that fishing pressure corresponded to a decrease in the abundance of slower life history species. The community unit in this study was defined at approx. 300 x 300km resolution. Sguotti et al. (2016) linked fishing pressure to a shift towards faster lived, more productive species, measuring shark and ray occurrence per haul (high resolution definition of community). However, they did not explicitly include location specific fishing pressure in their model but instead compared the change in occurrence over a 112 year time period, where time represented an increase in fishing pressure. This corroborates the idea that rather than shifts in life history strategy not being evident in communities defined at a small scale, models can fail to correlate those shifts with fine scale data on fishing pressure. De Juan et al, (2007) also found fishing pressure to relate to shifts in community life history strategy. Again, the resolution of their study unit was less than 5 minutes, but they studied infaunal and epifaunal benthic communities where only four out of 38 species were fish (*Citharus linguatula, Lepidotrigla cavillone, Arnoglossus laterna, and Lesuerogobius suerii)* – i.e. communities whose constituents have small home ranges matching the resolution at which fishing pressure was included in the model. This supports the idea that the average home range of constituent species is an ecologically meaningful spatial scale at which to define a community.

Probst et al (2021) assessed fish population use of space to determine whether MPAs provide relief from human pressure. For 48 species from Probst et al. (2021), the average width of a consistent core area was 150km, i.e. on average 50% of populations of species in our dataset could were found in areas of approx. 150 x 150km. Their data come from populations in the North Sea, and populations in the North East Atlantic can differ in ranging and spatial patterning (de Castro et al., 2015; Neat et al., 2014). However, the size of these consistent core areas imply that grid cells of around 150 x 150km may be an ecologically meaningful resolution at which to define community. Additionally de Castro et al find approx. 60 x 60 km to be the scale that best explains the effects of fishing pressure on fish length, and Neat et al (2014) find the home range of Atlantic cod (*Gadus morhua*) is similar to our lowest resolution definition of community (all hauls in approx. 250 x 250km). These studies suggest fish movement for species with high abundance in our dataset to be closer to our maximum sizes (250 250km) than our minimum (5 x 5km) community resolution. However, the home range of one of our less abundant species shorthorn sculpin (*Myoxocephalus scorpius*) is estimated to be less than our highest resolution definition of community (approx. 5 x 5 km) (Ivanova et al., 2018). We therefore suggest the use of community weighted mean home range for further study – average (or median) annual or ecosystem specific seasonal range of all species in a study (i.e. all DATRAS species, or all species in a LME) weighted by abundance, as a potential metric for deciding the resolution at which to define a community.

Our study is similar to, and in many ways corroborates findings from both Beukhof et al. (2019) and Pecuchet et al. (2017). However, there are important methodological differences, in part due to the greater availability of data, which allow us to build on and expand findings from both works. Considering communities at a lower resolutions, and including annual fishing pressure data allowed us to find support for the high relative importance of fishing pressure in explaining community life history. This evidence of scale dependency in the observed relationships between environmental variables and life history community composition is extremely important, in particular, the increased signal of anthropogenic effects at larger scales. Our findings may explain why studies carried out at small spatial extents, or studies at large extents defining community at a high resolution may find weak evidence for the relationship between fishing pressure and life history strategies in fish communities. Studying systems at ecologically meaningful scales best enables us to detect signals of the variables affecting those systems. This is crucial for our ability to make informed decisions about sustainable management in light of global change.

4.5.3 Limitations

We defined communities as all hauls in grid cells aggregated by a factors of 5, 10, 20 and 50, showing the relationships between our covariates and community life history to change with scale. However, these communities are not necessarily spatially co-located with actual ecosystem boundaries. Additionally, the average width of consistent core area grid cells for 48 species after

Probst et al (2021) falls between the width of our second lowest and lowest resolution communities. Though our traits values are ecosystem specific (Beukhof et al., 2019), we are still limited to one value per species. Other studies investigating the scale dependence of fishing pressure impacts on fish communities (de Castro et al., 2015; Shephard et al., 2011) have used the LFI, an OSPAR metric for good ecosystem health. LFI does not capture the breadth of information present in life history data, but by assuming one value for each life history trait per species, we are relating fishing pressure to changes in relative abundance of species with certain life history trait values, but we are not capturing whether fishing pressure is associated with any change in life history trait values within species. Further work should aim to incorporate both of these elements; how abundance of species with certain life history strategies changes with the environment, but also whether species show changes in life history in response to the environment – particularly fishing pressure, as has been shown in cod (*Gadus morhua*) (Andersen et al., 2007; Jørgensen et al., 2009) and other commercial species (Sharpe & Hendry, 2009).

Though DATRAS marine survey data exists for most European waters from 1985 onwards, the temporal extent of available fishing pressure data constrained our study to the last 12 years. Given the potential effects of the North Atlantic Oscillation (NAO) (Báez et al., 2021; de Eyto et al., 2016; Stige et al., 2006), and the potential temporal mismatch between the action of environmental variables i.e., temperature anomalies and community life history structure, a longer time series would be ideal for disentangling fish community responses to environmental conditions. Due to available computing resources, we constrained the spatial extent of this study to the Celtic-Biscay Shelf ecosystem. Including a larger subset of the DATRAS data in our study (especially data from the well-studied North sea), would be useful as a follow up to other works, in particular the works of Beukhof et al (2019) and Pecuchet et al. (2017) which we have built on, in order to see how results from our updated methods compare to findings in the same areas. Larger standard errors in the coarsest resolution models is likely due to the smaller sample size of the model datasets – larger sample sizes would increase the power of these models. We did not include information on salinity, chlorophyll concentration or sea bottom temperature in our analyses. These variables are expected to be relevant to fish occurrence and abundance, though findings of their importance have been inconsistent in recent studies (Beukhof et al., 2019; Pecuchet et al., 2017; Rutterford et al., 2015). As we used GLMMs in our analysis, we do not explicitly account for spatial autocorrelation in the data. We find that community life history traits are related to fishing pressure, and that the signal of this relationship varies with scale. We suggest that some measure of the average movement of fish in a community could be a good way to decide the most ecologically meaningful scale to investigate this relationship, but we do not have the data to explicitly test that in this study.

4.6 Conclusion

Fishing pressure correlates with community weighted mean life history strategies in marine communities. How community composition correlates with fishing pressure depends on the scale at which community is defined and the movement of species within the community. In order to understand the drivers of ecological patterns, and the divergent responses of species to global change, we must consider the spatial extent at which organisms and communities are experiencing the environment.

Chapter 5 Twin pressures of intensification and abandonment negatively impact grassland biodiversity in the Burren.

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Author contribution: Research was conceived and designed by CMM, AF, ID and YMB. Data were collected in the field by AF, CMM, MPL and YMB, and processed further in the lab by AF. CMM conducted the data analysis and wrote the first draft. YMB and ID provided advice on analyses. All authors provided feedback on the manuscript.

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5.1 Abstract

A major component of Earth’s dry surface is human-managed grassland, making the relationships among management actions, grassland biodiversity and ecosystem services of great ecological interest. Common management practises—fertiliser addition and large herbivore grazing—influence grassland diversity and productivity. The Nutrient Network, a distributed research effort, investigates these relationships across grasslands at a global scale. The Burren contains internationally important grasslands with high biodiversity maintained by traditional farming practices. Using six years of data from the Slieve Carran Nutrient Network site, we examine the effects of fertilisation and large mammal herbivory on plant diversity and biomass in a unique Irish context. We find 1) fertiliser addition and herbivore exclusion both decrease diversity and increase biomass, and 2) independent of our experimental treatments, biomass increased throughout the study. Our findings on treatment effects align with results from the wider Nutrient Network experiment. Additionally, the increase in biomass during the study is consistent with an abandonment effect. This research shows twin pressures of agricultural intensification and abandonment of traditional management practises detrimentally impact Burren grassland biodiversity. This is relevant to future management decisions, as biodiversity provides key ecosystem services in the Burren, including supporting tourism contributing to local communities.

5.2 Introduction

Grasslands are the primary terrestrial land use globally, encompassing over 20% of the world's dry surface (Ramankutty et al., 2008). They cover a wide range of habitats and vary greatly in terms of management, productivity, cultural value, and conservation status, providing multiple benefits to people (Binder et al., 2018; Millennium Ecosystem Assessment, 2005). Productive grasslands support livestock and, at the same time, diverse grasslands provide a myriad of regulating, cultural and provisioning ecosystem services (Haughey et al., 2018; Allan et al., 2015; Balvanera et al., 2013). Historically, and through ongoing agricultural changes in the last century, human management affects grassland ecology. Through land use changes, such as intensification or abandonment, fertilisation and grazing regimes influence the productivity and diversity of grasslands. It is, therefore, important to have both general and site-specific understanding of how management affects the ecological processes that maintain biodiversity, productivity and species composition within grasslands.

5.2.1 Drivers of grassland productivity and diversity

Two key human influences on grassland ecosystems are nutrient addition and large mammal herbivory. Human activities have greatly increased the availability of nutrients in terrestrial systems (Foley et al., 2007), raising primary productivity and reducing species diversity (Crawley et al., 2005; Harpole & Tilman, 2007). Human alteration of grazing regimes also influences both productivity and biodiversity (Millennium Ecosystem Assessment, 2005; Foley et al., 2011). Plant species face a trade-off between coping with low nutrient environments and competing for light (Dybzinski & Tilman, 2007). When nutrient availability in grassland systems is increased, nutrient-limited species can outcompete their low nutrient-competent neighbours (Hautier et al., 2009). At the same time, a trade-off also exists between competing for light and investing in herbivore defences (Lind et al., 2013; Grime & Pierce, 2012). As a result, even in high nutrient systems, herbivores are expected to “rescue” (maintain) species diversity by a) creating light availability through disturbance and biomass removal and b) selectively grazing on species with lower herbivory defence (Borer, Seabloom, et al., 2014). Though there is clear evidence of the relationship between nutrient addition and diversity loss, the underlying mechanism behind this relationship is not always clear (Adler et al., 2011; Grace et al., 2014). Soil, climate, grazing regime and species identity all influence these relationships (Bakker et al., 2006; Dwyer & Laughlin, 2017; Faucon et al., 2017). While some general ecological patterns have been found in grassland systems, some relationships can be context-specific.

5.2.2 The Nutrient Network

The Nutrient Network (NutNet) is a globally-distributed collaborative research network established to investigate how nutrient addition and herbivory affect grassland productivity, diversity and composition at the global scale (Borer, Harpole, et al., 2014). NutNet uses consistent methodology across environmental gradients with realistic levels of complexity to directly compare the relationship between, and the mechanisms underpinning, productivity and diversity across the globe. When investigating the effects of nutrient addition and herbivory on productivity and diversity, a multi-site study by Borer and Seabloom et al. (2014) showed rescue effects of herbivory on grassland diversity in nutrient enhanced systems. In 2015, we established a NutNet site at Slieve Carran to test whether the relationships established in Borer and Seabloom et al. (2014) are borne out in the unique context of a highly diverse calcareous Irish grassland. Though the NutNet study sites were designed to be analysed in the context of a globally-distributed experiment, it is nonetheless informative to report the striking evidence of how human management alters the grassland ecology in the context of the Burren.

5.2.3 Unique Irish context

The Burren is one of the most unique ecological systems in Europe due to the co-occurrence of artic-alpine and Mediterranean flora which are otherwise geographically and climatically distinct (Webb & Scannell, 1983). Covering an area of approximately 350 km^2, it is characterised by its landscape of exposed limestone rock and deposited boulder clay, containing low intensity livestock farmland and semi natural grasslands supporting high floral diversity. Some 70% of Ireland's native plant species are found in a land area equating to approximately 1% of the total land area of the island of Ireland (Webb & Scannell, 1983).

The Burren's unique hydrology (Drew, 1990; Osborne et al., 2003), geology (Jeffrey, 2003) and cultivation (Dunford & Feehan, 2001) history all contribute to its highly diverse flora. Historically, the Burren comprised a rich soil supporting extensive pine woodlands, which were cleared for cultivation by early farmers, resulting in soil erosion (Feeser & O'Connell, 2010, 2009). By the 17th century, most of the remaining hazel woodlands were cleared, converting the landscape into a mostly open farmed landscape (Feeser & O'Connell, 2009). Permeable limestone rock and shallow soil lead to low water availability during summer months (Drew, 1990). Combined with warming characteristics of the exposed rock, relativity high soil temperature is maintained well into the winter months, extending the growing season. These features lead to the locally adapted practice of transhumance or 'winterage', where livestock forage in the lowlands in summer before being moved to the uplands in winter (Dunford & Feehan, 2001). Winter grazing prevents dominant plants from monopolising resources, reducing competition for nutrients, light and space (Borer, Seabloom, et al., 2014; Parr et al., 2009). The absence of summer grazers allows flowering plants to thrive, flower and reproduce while physical disturbance and biomass removal through grazing during winter foraging allows for an increase in potential seedling establishment (Jutila & Grace, 2002).

In light of agricultural intensification and reduction in traditional land management across Europe (Quintas-Soriano et al., 2016; Zabel et al., 2019), a mechanistic and context-specific understanding of the drivers of grassland diversity is relevant to navigating environmental and agricultural sustainability issues. Here, we describe the effects of globally important agricultural managements—nutrient addition and large herbivore grazing—on biodiversity and productivity in a species diverse grassland in the Burren.

5.2.4 Other Burren studies

Large herbivore exclosures have been used previously to investigate the relationship between traditional management (grazing) and diversity and productivity in the Burren. Moles et al. (2005) found a steep decline in overall plant diversity in a fenced exclosure, with grass species increasing in abundance, concluding that the disturbance provided by grazing animals is integral to the conservation of Burren grassland biodiversity. Deenihan et al. (2009),in a follow-up study at the same exclosure, found increased heather and scrub cover and decreased grassland and pavement cover during the 15-year exclosure experiment, also concluding that there was a loss of diversity as a result. Notably, a similar (though smaller in scale) shift towards heather and scrub was observed in unfenced plots, suggesting that the traditional management regime within the National Park may not be effective in prevent scrub encroachment. Additionally, over a three-year exclosure experiment, Long (2011) found significant decreases in both plant species richness and Simpson's Diversity Index across four grassland exclosure sites. Long (2011) noted the complete loss of certain species such as *Euphrasia* agg*, Linum catharticum, Odontites vernus* and *Rhinanthus minor* from some or all fenced plots, as well as decreases in *Prunella vulgaris* and both *Trifolium pratense* and *T. repens*. In contrast, a minority of species were found to increase in cover in response to the fencing, including *Potentilla erecta* and *Pteridium aquilinum*, though the most consistent increases were in grass species cover (all species combined). Long (2011) also found significant increases in litter in fenced and, to a lesser extent, unfenced (control) plots.

5.2.5 Aims

Here, we examine the effects of nutrient addition and exclusion of large herbivores on the productivity and biodiversity in traditionally managed high nature value grassland in the Burren National Park, Co Clare. We quantified changes in grassland productivity (biomass) and diversity (species richness, Shannon diversity, inverse Simpsons index and species evenness) across treatments over six years to assess the individual and combined effects of fertilisation and grazing. We aim to provide quantitative evidence for the interacting effects of these management actions, and to assess whether general relationships between biodiversity and management actions found in other grassland systems are borne out in the floristically unique grasslands of the Burren.

5.3 Methods

5.3.1 Study site

The experiment was conducted on calcareous grassland at Slieve Carran (N53.07202, W-8.992624) in the Burren National Park, Co. Clare. The site has been traditionally managed with annual winter cattle grazing, which has been reduced in recent years. The site at the top of a small hillock at an elevation of 112 m above sea level, with a mean annual temperature of 9.8 degrees Celsius and 1320 mm of mean annual precipitation. We found 85 vascular plant species during the experiment (Appendix **Table D.3**.), putting Slieve Carran in the 81st percentile for species richness out of 128 NutNet sites globally. There are two forms of human activity at the study site. "Management" refers to the National Parks and Wildlife Service (NPWS) traditional winter grazing, and "treatment" refers to the experimental manipulations (that is, fencing and nutrient addition) carried out within the context of this grassland study. In addition to the intended experimental treatments, there were unanticipated changes in the management at the site with a reduction in grazing over the course of the experiment.

5.3.2 Experimental treatments

The experiment was arranged in three blocks, each containing ten 5 x 5 m plots. Within each block there is one unfenced control plot, and seven plots each receiving annual addition of a fully-factorial fertilizer treatment of Nitrogen (N), Phosphorus (P) and Potassium (K) in single, double and three-way combinations. Each block also has a herbivore exclosure (fenced plot) with NPK addition, and a fenced plot with no added nutrients. Fenced plots were constructed with aviary wire mesh extending 2 m in height. Fertiliser was added annually in April as described in Appendix **Table D.1.** Permanent plots were established during year one when initial measurements and soil cores (**Table D.2.**) were taken prior to treatments being established. Field data were collected in late July and early August and dry weight of biomass obtained. For full details of treatment and data collection, see https://nutnet.org/exp_protocol and https://nutnet.org/nutrients.

5.3.3 Data collection and analyses

Data were collected for one pre-treatment year (2015), and for five subsequent years of experimental manipulation (2016-2020). Every year in each plot, we conducted relevés, determining species identity and percent cover in 1 x 1m permanent quadrats, and collected 10 cm x 2 m biomass strips from successive positions from which we obtained dry weight. We used

General Linear Mixed Models (GLMMs) (Bates et al., 2015) to determine whether four key treatments—control (that is, unfenced plots with no nutrient addition), fencing, NPK and NKP + fencing—were associated with changes in biomass, species richness, Shannon diversity, inverse Simpsons index and species evenness over the course of the experiment. We addressed non-independence in the data arising from repeated sampling by including the experimental blocks as random effects in our models, and assessing models with multiple optimizers to account for the low number of replicates (three) of the blocks. We also used the "vegan" community ecology package (Oksanen et al., 2020) to apply Permutational Multivariate Analysis of Variance to a Jaccard dissimilarity matrix (Jaccard, 1912) to assess whether the treatments and management actions at the site were driving changes in species identity among plots. We concentrate our formal analysis here on the NPK and fence treatments and do not analyse the one-way and two-way nutrient addition treatments here due to lack of power in the site-level experimental design to detect relatively small changes in biomass and diversity. Analyses were done in R Studio version 3.6.3 (R Core Team, 2020). All code used in this study is available at DOI: 10.5281/zenodo.6967631.

5.4 Results

We found that both productivity and diversity changed at our experimental grassland site over the course of the experiment, with biomass generally increasing and measures of diversity generally decreasing over time (**Figure 5.1**). On control plots with no added nutrients, plant biomass increased, species richness showed no significant change, and Shannon diversity and the inverse Simpsons index decreased (**Figure 5.2**). In unfenced NPK+ and fenced NPK+, species richness and Shannon diversity decreased significantly over the course of the experiment (**Figure 5.2**). For the fenced control with no added nutrients, species richness decreased significantly, while neither biomass, Shannon diversity nor inverse Simpsons index showed significant change (**Figure 5.2**). Permutational MANOVA (**Figure 5.3**) indicates that fencing and nutrient addition treatments (Pseudo-$F = 6.3036$, $R^2 = 0.218$, $p < 0.001$), year (Pseudo-$F = 7.4012$, $R^2 = 0.096$, $p < 0.001$), and the interaction between them (treatment*year: Pseudo-$F = 2.5599$, $R^2 = 0.074$, $p < 0.001$) account for over 36% of the variance in species identity among plots (see **Figure 5.4** for snapshot of changes in species identity).

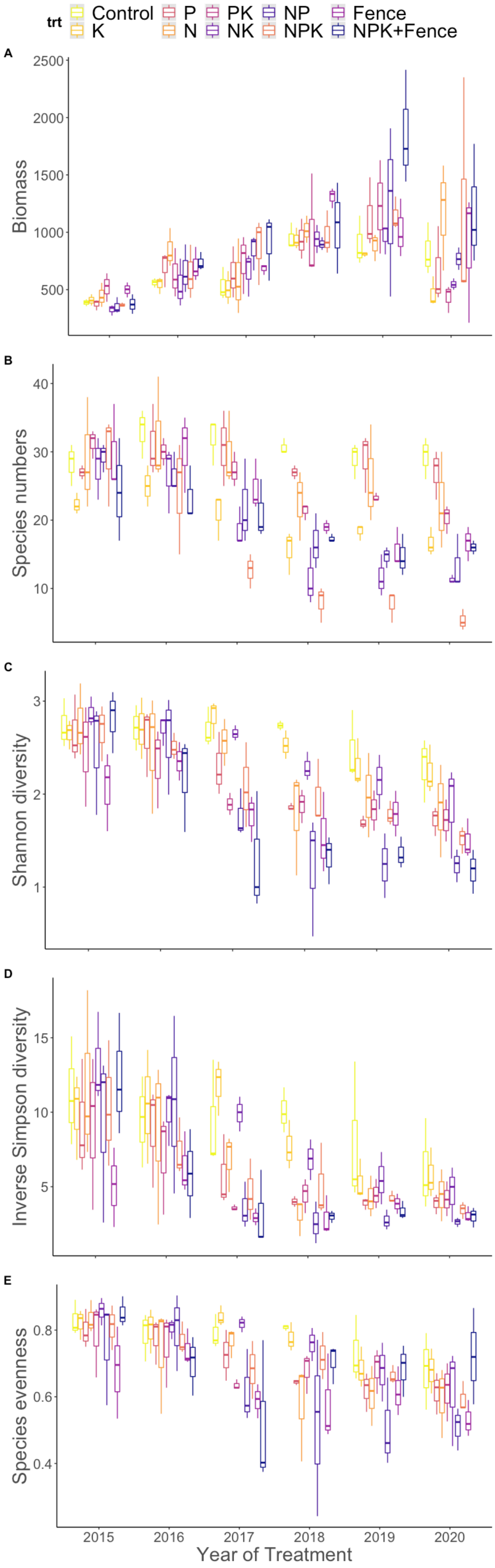
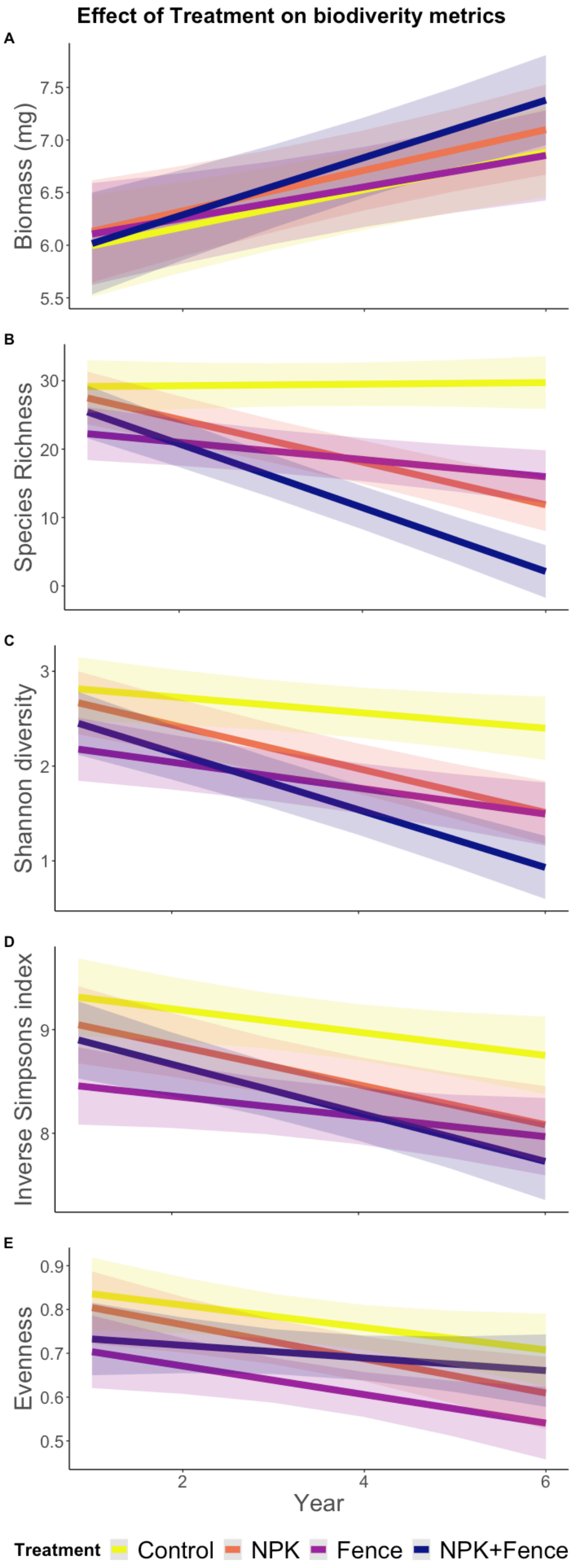


Figure 5.1. Grassland biodiversity in experimental plots belonging to the various experimental treatments. Plots based on values for each treatment over three blocks. Boxes show interquartile range. Central line shows median. Whiskers show 1.5 times the interquartile range. Colours correspond to treatments as described in legend.



	Biomass (mg)		
Indepentant variable	Estimate	Std. Error	t_value
(Intercept)	**5.817 ***	**0.275**	**21.120**
trtNPK	0.122	0.390	0.314
trtFence	0.14	0.390	0.360
trtNPK+Fence	-0.073	0.390	-0.188
year	**0.178 ***	**0.049**	**3.605**
trtNPK:year	0.015	0.070	0.220
trtFence:year	-0.029	0.070	-0.409
trtNPK+Fence:year	0.095	0.070	1.356

	Species Richness		
Indepentant variable	Estimate	Std. Error	t_value
(Intercept)	**29.044 ***	**2.219**	**13.090**
trtNPK	1.556	3.138	0.496
trtFence	-5.533	3.138	-1.763
trtNPK+Fence	1.067	3.138	0.340
year	0.114	0.449	0.255
trtNPK:year	**-3.238 ***	**0.635**	**-5.100**
trtFence:year	**-1.371 ***	**0.635**	**-2.160**
trtNPK+Fence:year	**-4.781 ***	**0.635**	**-7.529**

	Shannon diversity		
Indepentant variable	Estimate	Std. Error	t_value
(Intercept)	**2.897 ***	**0.195**	**14.880**
trtNPK	0.002	0.275	0.007
trtFence	**-0.582 ***	**0.275**	**-2.113**
trtNPK+Fence	-0.142	0.275	-0.516
year	**-0.083 ***	**0.041**	**-2.010**
trtNPK:year	**-0.149 ***	**0.058**	**-2.545**
trtFence:year	-0.054	0.058	-0.923
trtNPK+Fence:year	**-0.221 ***	**0.058**	**-3.789**

	Inverse Simpsons index		
Indepentant variable	Estimate	Std. Error	t_value
(Intercept)	**9.426 ***	**0.227**	**41.485**
trtNPK	-0.186	0.321	-0.578
trtFence	**-0.871 ***	**0.321**	**-2.711**
trtNPK+Fence	-0.291	0.321	-0.904
year	**-0.112 ***	**0.053**	**-2.127**
trtNPK:year	-0.081	0.075	-1.078
trtFence:year	0.014	0.075	0.194
trtNPK+Fence:year	-0.122	0.075	-1.634

	Evenness		
Indepentant variable	Estimate	Std. Error	t_value
(Intercept)	**0.861 ***	**0.053**	**16.338**
trtNPK	-0.018	0.075	-0.240
trtFence	-0.125	0.075	-1.676
trtNPK+Fence	-0.114	0.075	-1.530
year	-0.026	0.013	-1.924
trtNPK:year	-0.013	0.019	-0.713
trtFence:year	-0.007	0.019	-0.374
trtNPK+Fence:year	0.011	0.019	0.593

Figure 5.2. Effects of treatments on biomass and diversity.
Model estimates of the changes in A. biomass, B. species richness, C. Shannon diversity, D. inverse Simpsons index and E. species evenness in plots with no added nutrients, fenced, NPK and NPK + fenced plots over the course of the experiment. Coloured lines show model estimates for the mean. Coloured bands show 95% confidence intervals. Colours correspond to treatments as described in legend. Adjacent tables show model outputs. Model terms with statistically significant increases are highlighted in blue, and model terms with statistically significant decreases are highlighted in red.

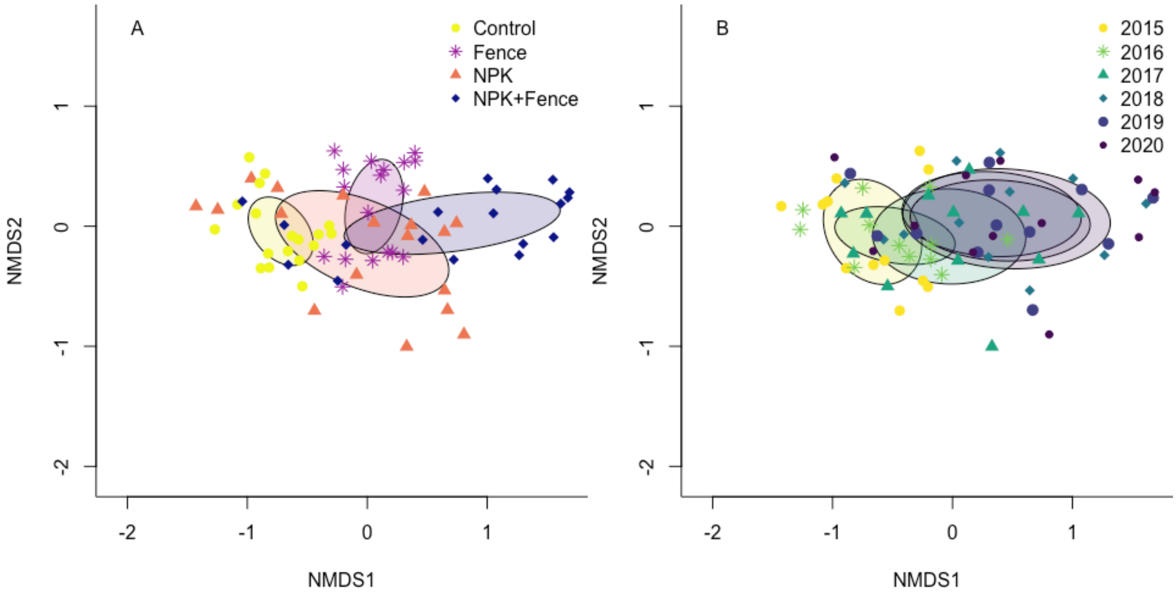


Figure 5.3. Nonmetric Multidimensional Scaling of compositional dissimilarity by A) treatment and B) year.

Two dimensional ordination of Jaccard's dissimilarity in species' identity among plots. Each point corresponds to an individual experimental plot in a single year. The shapes and colours of points correspond to unfenced and fenced plots with no added nutrients, unfenced NPK+ and fenced NPK+, and years 2015-2020.

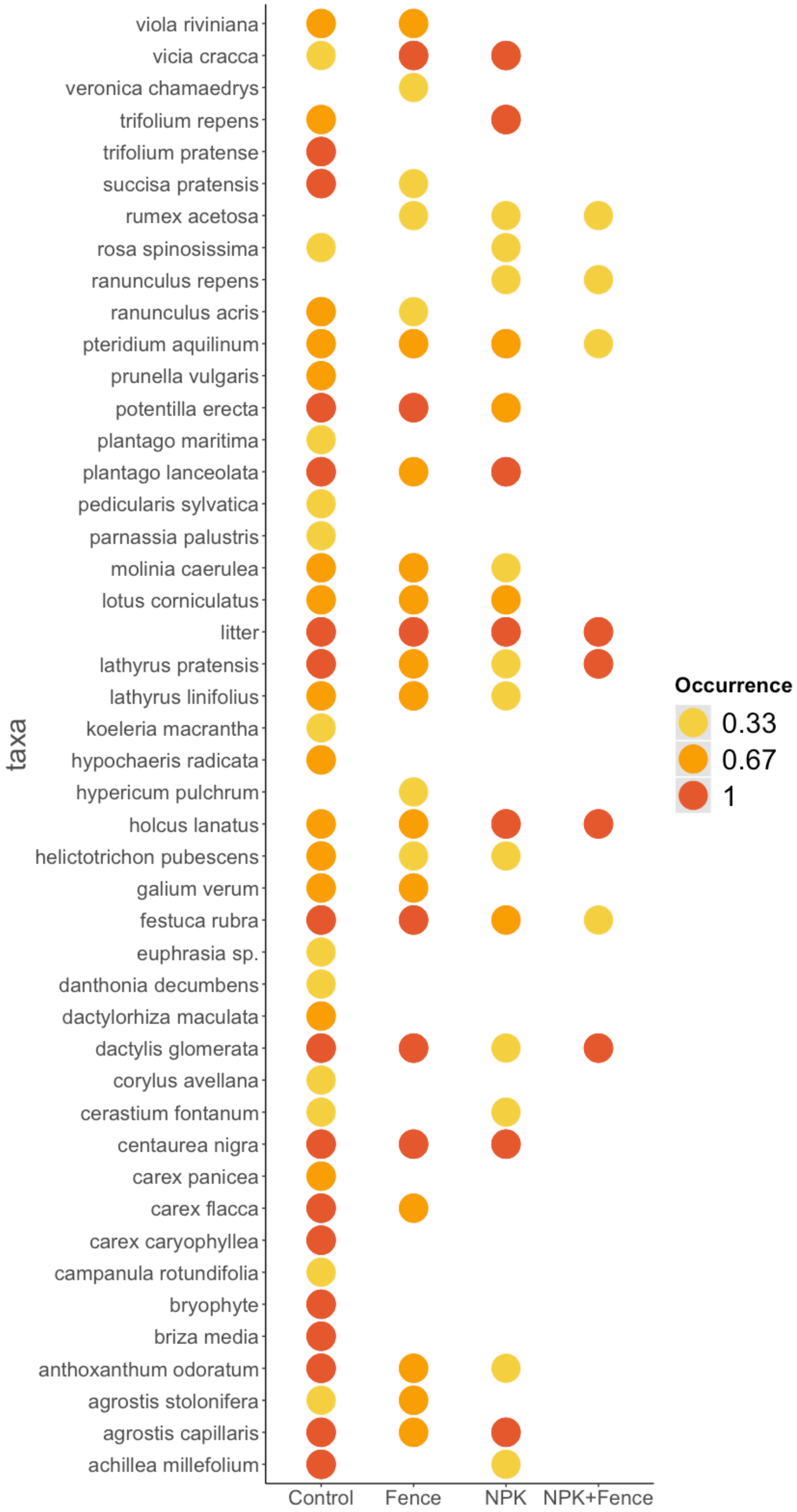


Figure 5.4. Species occurrence in final year of treatment (2020).
Occurrence of the 44 species recorded in the final year of the experiment across the four main treatments. Dots are coloured by whether a species occurred in 1/3 plots (yellow), 2/3 plots (orange) or 3/3 plots (red). White/blank spaces represent no occurrence of a species in any plots of a particular treatment in 2020.

5.5 Discussion

There was a clear effect of fertiliser addition and herbivore exclusion on both productivity and biodiversity at Slieve Carran, with the effects of the treatments increasing over time. Metrics of productivity and diversity responded differently to the treatments, but the combination of fencing and nutrient addition was consistently important, decreasing diversity and increasing biomass production. As evidenced by significant increases in unfenced control plot biomass, changes in the site management regime appear to have been affecting the plant community since the beginning of the experiment, highlighting the importance of continued management in maintaining this unique and diverse ecosystem.

Theory predicts that, in grassland ecosystems, nutrient addition will increase productivity by shifting the balance to favour species that have invested in light competition over nutrient capture, leading to decreased diversity (Hautier et al., 2009). Theory also predicts that large herbivores will maintain diversity by increasing light availability (Borer, Seabloom, et al., 2014). Both these predictions are borne out at Slieve Carran, as highlighted by the differences in response to the treatments. The combined fertiliser and fencing treatment had the most immediate, the largest, and the most consistent influence across diversity and productivity metrics. In the final year of experimental manipulation (Year 6), unfenced plots with no added nutrients had a median of 30 species, while fenced NPK+ plots had a median of just five species. The fenced and fertilised treatment prevents herbivory, and the consequent build-up of biomass reduces light availability under the canopy, while simultaneously increasing soil nutrient availability. These results are consistent with findings from grasslands around the globe (Borer, Seabloom, et al., 2014) but are particularly notable because of the high biodiversity previously maintained at this site by the traditional winter grazing. The findings are also consistent with other exclosure studies from the Burren (e.g. (Long, 2011; Deenihan et al., 2009; Moles et al., 2005), which, though limited to grazing exclusion (that is, the study did not examine the effects of nutrient addition), demonstrated both significant decreases in plant richness and diversity and shifts in species composition. It is as yet unclear whether these effects plateau, or whether continued treatment would continue to increase biomass and decrease diversity. Recent work suggests, however, that low intensity herbivory is unlikely to be able keep pace with increasing biomass arising from sustained nutrient addition, particularly in low nutrient systems (Borer et al., 2020).

5.5.1 Biomass

Though biomass increased across all treatments, with the largest increases in fenced NPK+ treatments, this increase was not significantly different to the increase across unfenced plots with no added nutrients. The increase in biomass across control plots indicates an abandonment effect, consistent with, albeit not as extreme as, the complete experimental exclusion of large herbivores. Traditional winter grazing has been responsible for maintaining high diversity by increasing light availability through physical disturbance and removal of biomass **(i.e. Figure 5.4).** Anecdotal evidence of reduction in this management is consistent with the significant increase in biomass across all plots, including unfenced control plots, throughout the experiment. This experiment has not been running sufficiently long to show succession from grassland to woodland in the non-grazed plots. However, hazel saplings and brambles are emerging across the site, suggesting the potential for the transition to hazel woodland with the long-term decrease in traditional management. As the conservation objective for this site includes restoring "favourable conservation condition of semi-natural dry grasslands" (NPWS, 2022), increased intensity of conservation grazing may be needed. If monitoring of the site is maintained as conservation grazing is intensified, it may be possible to investigate whether grazing can provide "rescue" from the effects of fertilisation on diversity.

5.5.2 Diversity

Overall, diversity decreased in response to fertiliser addition and herbivore exclusion. Different diversity metrics—species richness, Shannon diversity, inverse Simpson's index and species evenness—describe diversity in different ways, and so responded differently to the treatments. Inverse Simpsons index decreased through time, possibly in response to the reduction in traditional management, but did not show additional decreases in fertilised plots in comparison to the unfenced controls. While species richness did not decrease in response to the reduction in traditional management (that is, unfenced control plots did not change significantly), richness and Shannon's diversity decreased in response to the fertiliser treatments. These differences reflect the ability of the metrics to describe different dimensions of diversity (Jost, 2006). Richness—purely the sum of number of species—most readily detects the loss of species from a plot, Shannon diversity measures proportional change in relative abundance, while inverse Simpsons index gives even more weight to changes in abundance, and so is less affected by the loss of rare species. These differences indicate that the reduction in winter grazing caused shifts in relative abundance, while the most immediate effect of nutrient addition was the loss of rare species, followed to a lesser extent by changes in ratios of abundance. This may imply that while nutrient addition and herbivory may appear to counterbalance one another, they work through different mechanisms and so affect aspects of grassland diversity in different ways.

Analysis of Jaccard dissimilarity indicates that treatment, management and their interaction account for over 36% of differences in species identity between plots, implying these actions are contributing to species turnover. Given the link between species identity, function and service (Luck et al. 2009; Byrnes et al. 2014), particularly in the context of agricultural land managed for its biodiversity and cultural benefits (Binder et al. 2018), this provides further evidence for the negative effects of both intensification and abandonment on grasslands in the Burren.

5.5.3 Limitations

The three-replicate design of the experiment is not ideally suited to answering questions about an individual study site. Our models had relatively low statistical power as a consequence. While this did not constrain our ability to detect large changes, it could have hampered our ability to detect smaller effects. For example, stochastic differences in initial plot biomass would be expected to average out over high numbers of replicate blocks. Initially low Shannon diversity and inverse Simpsons index values in fenced control plots may have obscured the effects of complete herbivore exclusion without the influence of fertiliser. Visually, Shannon diversity in fenced control plots showed a downward trend, but our models did not have sufficient power to detect statistical significance. We use statistical analysis to provide evidence of a correlation between variables measured in our experiment - response variables (biomass and diversity), and nutrient addition and year. We consider available information about the system (unquantified reduction in winter grazing) to inform our interpretation of these results. However, the reduction in winter grazing was not part of the original experimental design and this leads to limitations. Including experimental Burren sites from more than one location may have shown differences in management, providing a contrast to the effects of relaxation of traditional management at the Slieve Carran site. While nutrient addition appears to have had a larger impact on diversity than fencing, we cannot compare the effects of fencing to a true control due to the reduction in winter grazing. Including other sites at which grazing was not reduced would allow us to explicitly test the effects of grazing reduction in addition to the effects of nutrient addition and grazing exclusion tested at our site. However, despite these limitations, our experiment demonstrates clearly the detrimental combined effects of nutrient addition and herbivore exclusion to this highly biodiverse grassland system.

5.6 Conclusion

We provide quantitative evidence that nutrient addition and herbivore exclusion together decreased biodiversity and increased productivity (plant biomass) at Slieve Carran. Loss of rare species is the most immediate response to nutrient addition, while change in relative abundance is the more immediate result of the reduction in grazing. Our results are consistent with findings from a global network of manipulative grassland experiments, as well as a suite of smaller-scale local exclusion studies, showing that nutrient addition and large mammal herbivory can respectively decrease and rescue grassland diversity. Our findings strengthen the case for the maintenance of winter grazing and no nutrient addition as strategies for managers seeking to promote high grassland biodiversity. Additionally, our findings support winter grazing as a management strategy to help reduce the loss of biodiversity in systems under low levels of nutrient addition.

Chapter 6 General discussion

6.1 Human influence is an ecological force

There is a tendency to investigate ecological patterns outside of human influence; what would have happened, or what would be happening, if human activity was not a dominant physical pressure on the surface of the earth. If we are interested in sustaining and evening enhancing life on earth, then we must understand ecological dynamics, patterns, and processes in light of human pressure (Ellis, 2015, 2019; Liu et al., 2007). If we are interested in knowledge for knowledge's sake, then it remains the case that species are reacting in their complex, intrinsic and emergent ways to the fact of human influence as though it was (and it is) just another external force affecting ecology and evolution. Though we may try to be impartial and objective scientists studying ecology and evolution, we are ultimately social mammals, acting as scientists, steeped in cultural context and subject to those very forces which we are trying to study. Whether it's the legacy of a belief in dominion over the creatures of the earth (Holland, 2019; Stafford, 2002) or denial over the extent to which our lives, disproportionally the lives of those in the global north (Steffen et al., 2015), are affecting all other lives on the planet, we are too often blind to our own presence as a unignorable part of the "natural" world (Mace, 2014). If we include our own influence in our investigations of life on earth, we will better understand and protect it.

Considering human influence as an ecological force allows for more holistic ecological investigations. Human impacts are currently pervasive throughout the biologically suitable terrestrial surface of the earth (Ellis et al., 2010; Ellis & Ramankutty, 2008) and the most productive marine habitats (Jones et al., 2018). Our influence has increased dramatically in the last century (Almond et al., 2020; Ellis, 2019; Sguotti et al., 2016; Steffen et al., 2015) and this increase is most pronounced in some of the most biologically suitable areas (Kennedy et al., 2019; Venter et al., 2016). In spite of this, and the evidence that human pressure is the main driver of biodiversity loss and ecosystem change (Díaz et al., 2019; Newbold et al., 2015), human influence is not always considered as an ecological variable (Ellis, 2015, 2019). In chapter two I investigate species' divergent responses to human pressure, building on work updating classic climate-based biogeographic paradigms of global vegetation patterns to include human impact (Ellis & Ramankutty, 2008; Olson et al., 2001). I find global vegetation patterns are shaped by both climate and human land use, and that human land use is comparable to some dimensions of climate in affecting plant occurrence across life forms. This adds to a better understanding of which forces are shaping contemporary global ecological patterns. I find that including human pressure as a model component improves our understanding of species spatial patterns (Chapter

3) and patterns of life history strategy in marine communities (Chapter 4), and that contemporary and traditional human land management practises interact to affect biodiversity (Chapter 5). In summary, this thesis shows how human activity is relevant to our fundamental ecological understanding, and our ability to assess and mitigate the ecological impacts of global change.

Human's ecological impacts, e.g. lower probability of occurrence for trees in a grassland (Chapter 2) are in some cases intuitive. There is abundant evidence for the negative ecological impacts of human pressure (Almond et al., 2020; Brondizio et al., 2019; Díaz et al., 2019; Foley et al., 2005; Grooten, Almond, & (Eds), 2018), and increasingly detailed maps of how humans use the land (Ellis & Ramankutty, 2008; Kennedy et al., 2019; Ramankutty et al., 2008; Ramankutty & Foley, 1999; Venter et al., 2018; Venter & Sydenham, 2021) and sea (ICES, 2021; Kroodsma et al., 2018). In spite of this, chapter two provides novel empirical evidence for how human land use and climate drive life form occurrence at a global scale, highlighting how there can be a disconnect between the study of ecology and reality of human activity.

6.2 Scale matters

In the ecological literature, discrepancies in our findings about the natural world arise from the metrics used to describe patterns, but also from the scale at which those patterns are measured (Chase & Knight, 2013; Eriksson & Hillebrand, 2019b; Gonzalez et al., 2016b; Hautier et al., 2018; Suggitt et al., 2019). Spatial scale is often explicitly considered in the meta-community and community ecology literature (Chase et al., 2019; Sandel & Smith, 2009), where species-area relationships may be relevant to responses (i.e. species richness), but are sometimes considered only implicitly in the study of other patterns – e.g. in observational studies or studies of individual species or suites of species (Estes et al., 2018; Teng et al., 2020). Matching the scale at which a pattern is studied to the scale at which a factor is affecting the pattern is key to our ability to understand the relationship between the two (Chase, 2014; Craven et al., 2020; Sandel & Smith, 2009; Windsor et al., 2022) and therefore integral to our ability to understand the drivers and consequences of global change (Chase et al., 2019; de Castro et al., 2015; Estes et al., 2018; Levin, 1992; Santini et al., 2021; Shephard et al., 2011; Teng et al., 2020).

The impacts of scale on ecological patterns is mediated by the variance in environmental factors experienced by the ecological unit under study, and how the ecological unit experiences variance is in turn mediated by the extent and resolution at which the pattern is investigated (chapters 3 and 4), and the ecological behaviour of organisms (chapter 4) (movement, dormancy, dispersal) (Levin, 1992; Sandel & Smith, 2009). In terrestrial plant systems studied at short temporal time scales, experienced variability is mediated by scale of investigation. The impacts of human pressure were most clearly comparable to the impacts of non-human environmental factors (climate) in chapter two. Though this was the study with the largest spatial extent, the resolution of the response data was quite high – occurrence and abundance of species in quadrats/transects < 1km^2. This chapter may therefore have constituted the most ecologically realistic scale of investigation, as the large spatial extent allowed for high variability in the climate data, but at the same time, the high resolution response data could capture the signal of human land use, expected to relate to ecological patterns at a finer scale than climate (Bruelheide et al., 2018; Carl et al., 2016). In chapter 3, our low resolution occurrence data prevented us from adequately interrogating the effect of human footprint on species' patterns, as species experience variability in human footprint at resolutions finer than 50 x 50km (Carl et al., 2016). Interestingly, the variables acting over the largest temporal scales (phylogeny and past climate change velocity) had the strongest signals, indicating a potential match between the scale of patterns and processes in space and time.

In marine systems, when considering ecological communities comprised of mobile fish species, experienced variability is mediated by scale of the investigation and by fish movement. This is important for how fish communities relate to fishing pressure vs other non-human environmental variables. Through movement, fish control how they experience variability in temperature and depth, but not how they experience fishing pressure, again positioning human pressure as an additional force acting to shape species' realised niche. Finally, the high spatial resolution and low extent in Chapter 5 illustrates the importance of scale by contrast to the other chapters. The extent is so small that the influences of climate and human influence cannot be compared, due to the invariability of climate at the spatial and temporal scale of the study.

6.3 Future research

In this thesis, while studying relationships between ecological patterns and their potential drivers, I have tried to integrate human influence, multiple scales of study and a consideration of species intrinsic traits. In future work, I would like to incorporate more variation in, and comparison between, traits and scales within studies, and focus on ecologically meaningful scales.

6.3.1 Ecologically meaningful scales

One of the draw backs of observational/macroecological studies is that they can be constrained by available data. In Chapter 2, our response variables are occurrence and abundance (local abundance when present), though more ideally I would investigate landscape scale abundance i.e. commonness, in line with Raunkiaer's original analyses (Smith, 1909). Additionally, an extension of Chapter 3 would be to compare the effect sizes of human footprint and past and contemporary climate variables over multiple resolutions of response data (based on species occurrence), similar to Carl et al. (2016) who compare the signal of contemporary climate and land cover on spring vegetation greening in central Europe over a range of spatial grains. Empirical data on endemic European species (Atlas Flora Europea) is not available at resolutions higher than 50 x 50 km, but a potential alternative would be using GBIF (GBIF, 2022) data with a some correction of recorder bias (i.e. (Baudraz, 2022, Chapter 4)). Fundamentally the finding from chapter 4 is that human pressure – community trait relationships vary with scale. Though I make an argument for what scale may best capture how communities experience fishing pressure, I do not have the data needed to support this. Obtaining data to calculate a community weighted mean home range/core area would give us more confidence interpreting the direction and relative importance of effects on community life history traits, allowing us to ask how species are differentially affected by their current environment.

6.3.2 Response to human influence is mediated by species intrinsic traits

Intrinsic traits have been shown to relate to range size (Estrada et al., 2015; Sporbert et al., 2021) and range filling (Estrada et al., 2018), and I originally intended to study how intrinsic traits related to metrics of spatial pattern, with a particular interest in how traits related to different processes (e.g. dispersal vs persistence/disturbance tolerance) might be expected to relate to range size compared to range structure (Sporbert et al., 2021), but was limited by data availability. This could potentially be studied with more open source trait data, and higher resolution plant occurrence. Further, comparing relationships between high and low resolution traits i.e. functional trait data (seed mass, SLA, plant height, dispersal vector) and life form, and high and low resolution occurrence data across metrics of spatial pattern could be an avenue for disentangling the mechanisms feeding into spatial pattern e.g. dispersal vs disturbance tolerance vs thermal niche.

A further expansion on this work would be to compare or integrate information from intrinsic trait data for different resolutions. Low resolution traits (Life Form) were most available, and showed findings (Chapter 2) in line with other work – slow lived large species respond most negatively to human pressure (Beukhof et al., 2019; Carmona et al., 2021; Jennings & Blanchard, 2004; Leung et al., 2020; Pecuchet et al., 2017), while fast lived, generalist disturbance tolerant species show the most positive response to human pressure. I am hesitant to interpret specific findings from our investigation of how fish life history traits relate to fishing pressure, due to uncertainty around the most meaningful ecological scale. However, it is clear that community weighted mean life history traits show differing relationships with fishing pressure. The direction of the relationships between trophic level and fishing pressure is particularly interesting, as fishing is expected to negatively affect trophic level, but is not independent from fish community attributes, i.e. fishing is deliberately carried out where communities have high desirability, which can relate to size or trophic level (Essington et al., 2006; Pauly et al., 1998). In Chapter 5, different diversity metrics are sensitive to different dimensions of community change. Similarly, it may be that intrinsic traits of different resolutions are suited to capturing patterns at different scales. For example, how does fishing pressure relate to Large Fish Index (LFI) vs community life history traits? Do these different measures of community traits show the signal of human footprint at different scales? It may that be that shifts in size distribution are detected at smaller scales (de Castro et al., 2015; Shephard et al., 2011), whereas shifts in community weighted life history strategies is evident at larger scales, i.e. local scale changes in attributes of individuals occurs before the extirpation of local populations (Csergő et al., 2017).

Though chapter 5 touches on biotic interactions, missing from this thesis is a study of how biotic interactions compare to climate, human influence, phylogenetic legacy as determinants of ecological patterns. Chapter five again provides the only manipulation experiment – all other chapters rely on correlations between observations. The use of natural experiments could provide an avenue to combine the benefits of broad scale observational data with the opportunity to investigate processes behind the patterns.

6.4 Conclusion

In investigating human land use and plant life form, human footprint and species spatial pattern, and fishing pressure and community traits, I find that including human pressure along with non-human ecological variables explains variation in ecological patterns, and that how species response to human pressures is mediated by their intrinsic traits. The relationship between human pressure and ecological patterns depends on the scale at which the pattern is studied - at some scales, the effects of human pressure on ecological patterns are comparable in magnitude to the effects of non-human environmental variables like climate or depth. Both the study of ecology and creating a sustainable future for living things on the planet require a realistic understanding of how species are affected by their environment. This necessitates considering all elements of the environment that species are experiencing in ecological studies – including human pressure (Ellis, 2015, 2019; Liu et al., 2007). Human activity is currently the most pressing cause of ecological change, and has been a force affecting ecological systems for thousands of years. Ignoring human influence in ecological investigations hampers our ability to understand

and protect life on earth (Folke et al., 2021). To understand the impacts of human pressure on natural systems, and how its impacts compare in importance to environmental variables (e.g. climate and climate change), it is essential to consider the scales at which these forces are acting (Chase et al., 2019; Estes et al., 2018; Levin, 1992; Santini et al., 2021; Teng et al., 2020). To make sense of the varied or divergent responses to ecological factors across the complexity of life, it is helpful to view species by the characteristics mediating their response to the environment – their intrinsic traits (Funk et al., 2017; Lavorel et al., 2002).

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Appendix A | Supplementary information for Chapter 2

Table A.1. Data sources.

Data source	Variable role	Variable type	Variable
PREDICTS (Hudson et al., 2016b)	Response variables	Occurrence, Abundance	Presence/absence, Percent cover
	Explanatory variables	Land use	Ten land use types: Primary forest, unknown Secondary vegetation, Mature secondary vegetation, Intermediate secondary vegetation, Young secondary vegetation, Plantation forest, Primary non-forest, Pasture, Cropland, Urban
		Site level total species richness	Species richness
		Random effects	Class, Order, Family, Genus, Species, Source, Study, Site, Block
BIOCLIM (Fick & Hijmans, 2017)		Climate	Mean annual temperature (MAT), Temperature seasonality (SD) (MAT_var), Mean annual precipitation (MAP), Mean annual precipitation seasonality (coefficient of variation) (MAP_var)
TRY & BIEN (Kattge et al., 2011) & (Maitner et al., 2018)		Life form	Raunkiærian life form: Phanerophytes, Chamaephytes, Hemicryptophytes, Cryptophytes, Therophytes

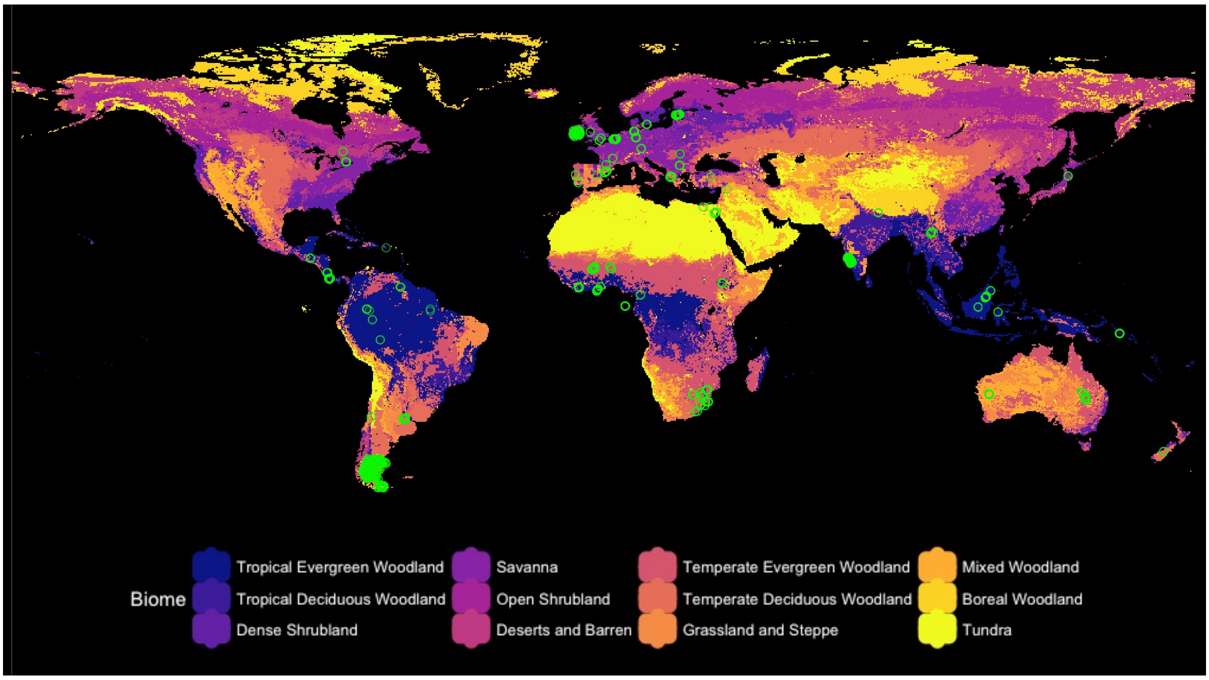

Figure A.1. Map of data origins. Site locations are shown with green empty circles. Colours refer to biomes after Ramankutty & Foley (1999) from Ellis et al. (2010).

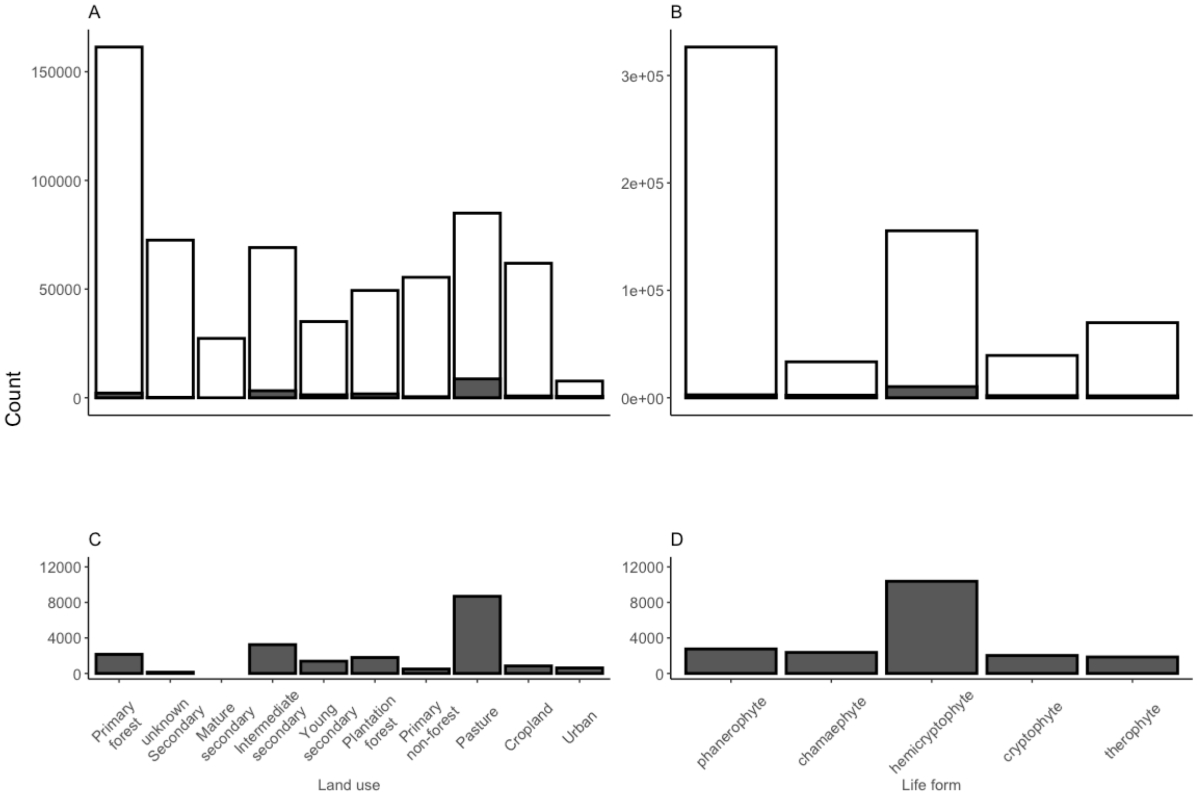

Figure A.2. Relative proportions of model data. White bars represent occurrence data, solid grey bars represent abundance data. Panels. A-D represent relative proportions of occurrence data in land use categories, occurrence data in life form categories, abundance data in land use categories and abundance data in life form categories respectively.

Supplementary information A.1. Data validation extended methods.
Data from 73 studies were included our analysis. All papers where checked for sampling target - whether authors surveyed the “entire community” (or else all vascular plants), and for whether sampling method and sampling effort respectively were uniform within studies. Sampling target, method and effort were deemed suitable for 52 studies based on information available within the PREDICTS database. Source papers were read to validated the sampling target (20 studies) and sampling effort (one study) of remaining studies. After validation, six studies remained outstanding (**Table A.2.**), five whose target was not “entire community” and one with inconsistent sampling effort. Of studies which did not survey “entire community”, two surveyed only herbaceous species, two only woody species, and one only palms, all in forest habitats. The details of the vegetation sampling for the study with inconsistent sampling effort could not be verified. These studies represent less than 6% of the data used in our models.

Table A.2. Studies not targeting “entire community” or with non-uniform sampling effort.

Source_ID (paper)	**Study_name**	**SS (Study)**	**Issue**
DL1_2009__Barquero	Small Palms	DL1_2009__Barquero 1	Sampling target not “entire community”
DL1_2009__Barquero	Medium Palms	DL1_2009__Barquero 2	
DL1_2009__Barquero	Large Palms	DL1_2009__Barquero 3	
DL1_2012__Hernandez	Large Plants	DL1_2012__Hernandez 1	
SC1_2004__Kolb	Herbaceous plants Germany	SC1_2004__Kolb 1	
SC1_2010__Baeten	Ancient and post agricultural forests_Belgium	SC1_2010__Baeten 1	
SC1_2012__ GendreauBerthiaume	Boreal mixedwoods	SC1_2012__ GendreauBerthiaume 1	
SC2_2011__LucasBorja	Vegetation Sampling	SC2_2011__LucasBorja 1	Sampling effort not uniform within study

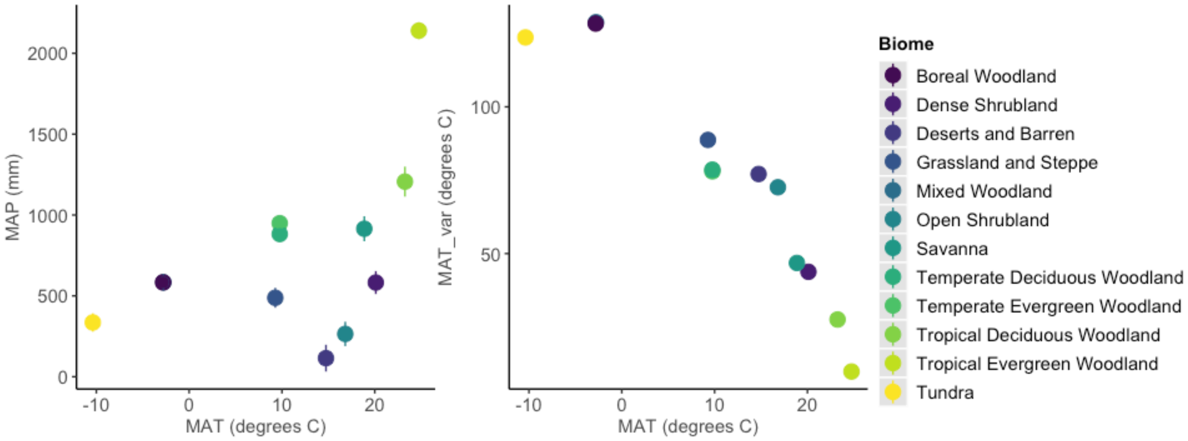

Figure A.3. Biome averages for climatic variables. MAT = Mean annual temperature, MAT_var = Mean annual temperature variation, MAP = Mean annual precipitation.

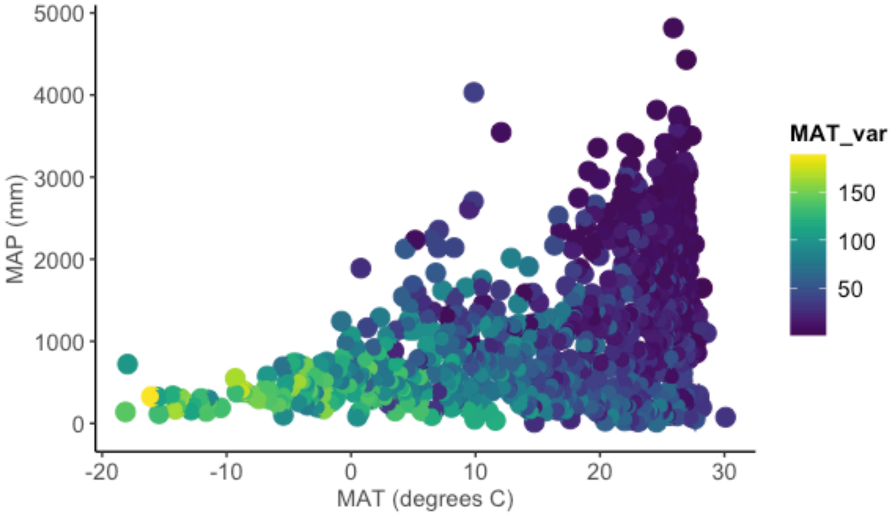

Figure A.4. Ecoregion averages for climatic variables. MAT = Mean annual temperature, MAT_var = Mean annual temperature variation, MAP = Mean annual precipitation.

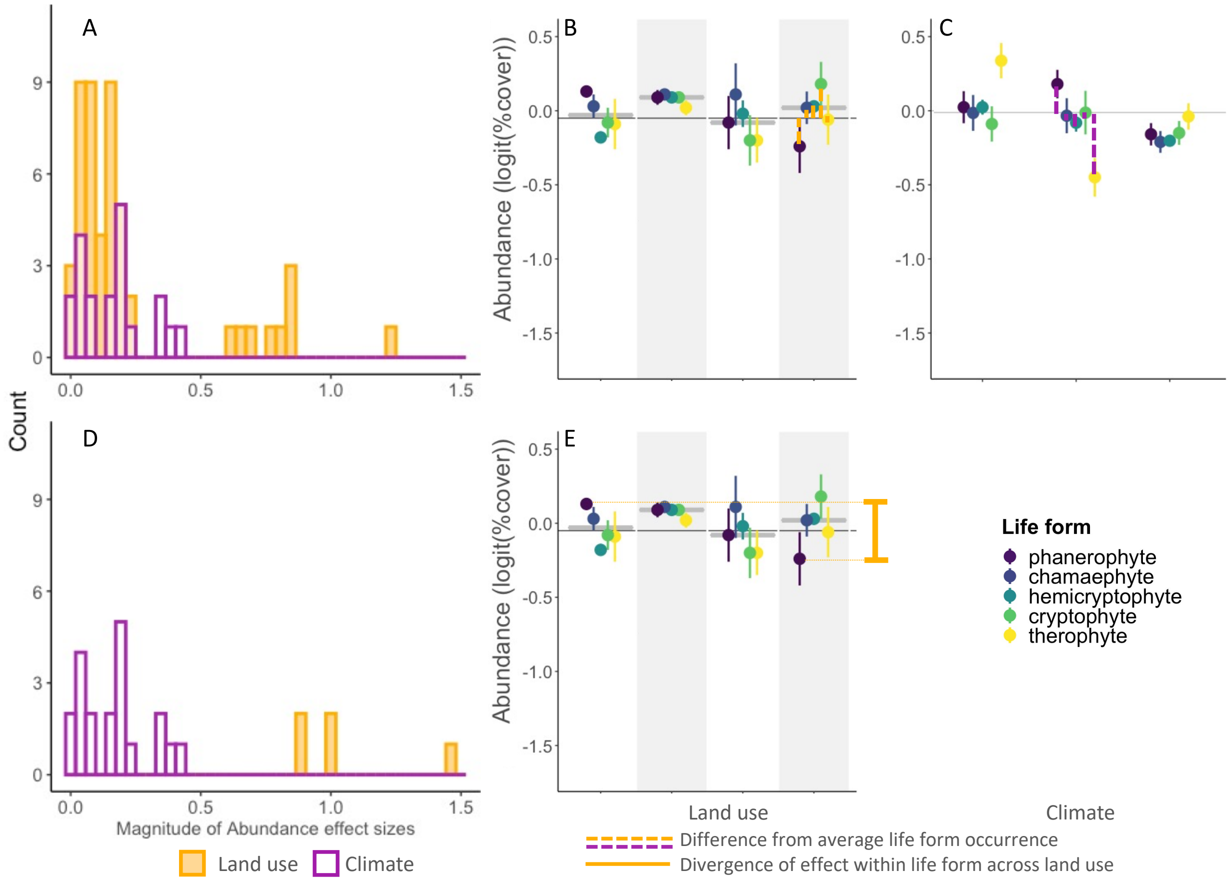

Figure A.5. Comparison of Climate and Land use Abundance effects. In histograms A and D orange bars represent magnitude of land use effects, purple bars represent magnitude of climate effects. Panels B, E and C show illustrative effect sizes of land use (for primary forest, pasture and cropland and urban land uses), and climate (for MAP var, MAT and MAT var) to enable interpretation of A and D. A - the distribution of effect sizes for life form by land use (dashed orange lines in B), compared to effect of 1 SD change in climate variables (dashed purple lines in C). D - the distribution of effect size range within life form across land uses (solid orange line in E), compared to effect on life form abundance of a 1 SD change in climate variables (dashed purple lines in C).

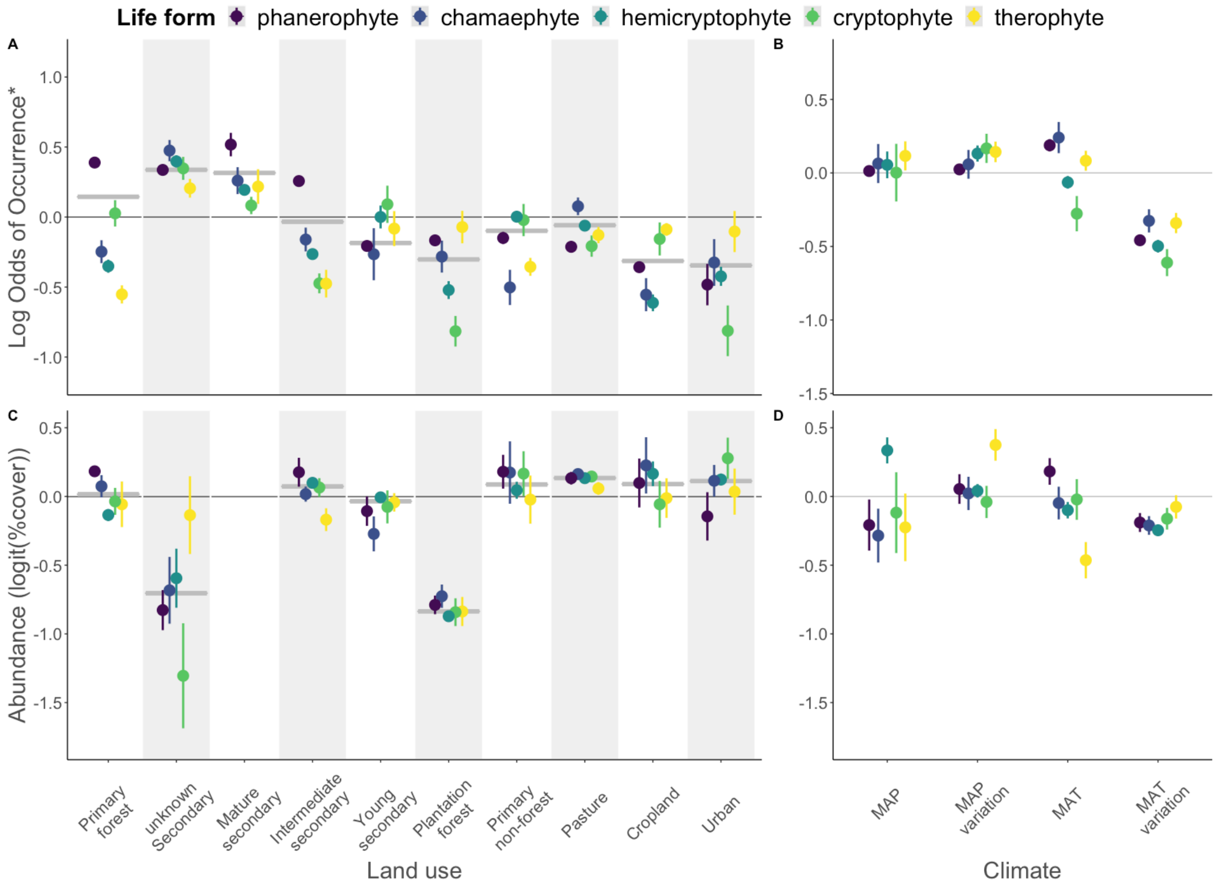

Figure A.6. Species occurrence and abundance by land use and life form for models with no species richness. A) Effects of land use and life form on occurrence. B) Effects of climate and life form on occurrence. C) Effects of land use and life form on abundance. D) Effects of climate and life form on abundance. In A) and B) Y axis represents log-odds ratio (probability of occurrence) (y axis in panel A represents the log odds minus the grand mean). In A) continuous horizontal line shows the centred weighted mean log-odds ratio, i.e. average probability of occurrence when at mean values of continuous variables, in B) the horizontal line represents zero (no relationship between continuous variable and response). In C) and D) Abundance data describes species' local dominance when present. Y axis represents scaled and logit transformed non-zero %cover data. In C) Horizontal line shows the weighted mean of this response, i.e. average (transformed) %cover when continuous variables are zero, in D) the horizontal line represents zero (no relationship between continuous variable and response). In A) and C) Horizontal line segments show land use means (across all life forms). Circular (coloured) points show "population" means, as estimated by the model, of the response variable within land uses for each life form. Points lower/higher than the horizontal line indicate that the mean probability of occurrence or abundance estimate of that particular land use*life form combination is lower/higher than the data average. In B and D) Circular (coloured) points represent the slope of relationship (change in log-odds ratio or abundance estimate), associated with 1 SD change in climate for each life form. In A-D) vertical lines represent 95% Confidence interval. CIs overlapping horizontal lines indicate that the probability of occurrence or abundance estimate is not significantly different from average. Total number of observations in occurrence model = 624,696 for 4804 species, and abundance model = 19,384 for 883 species. Note, abundance data for mature secondary forest were not available.

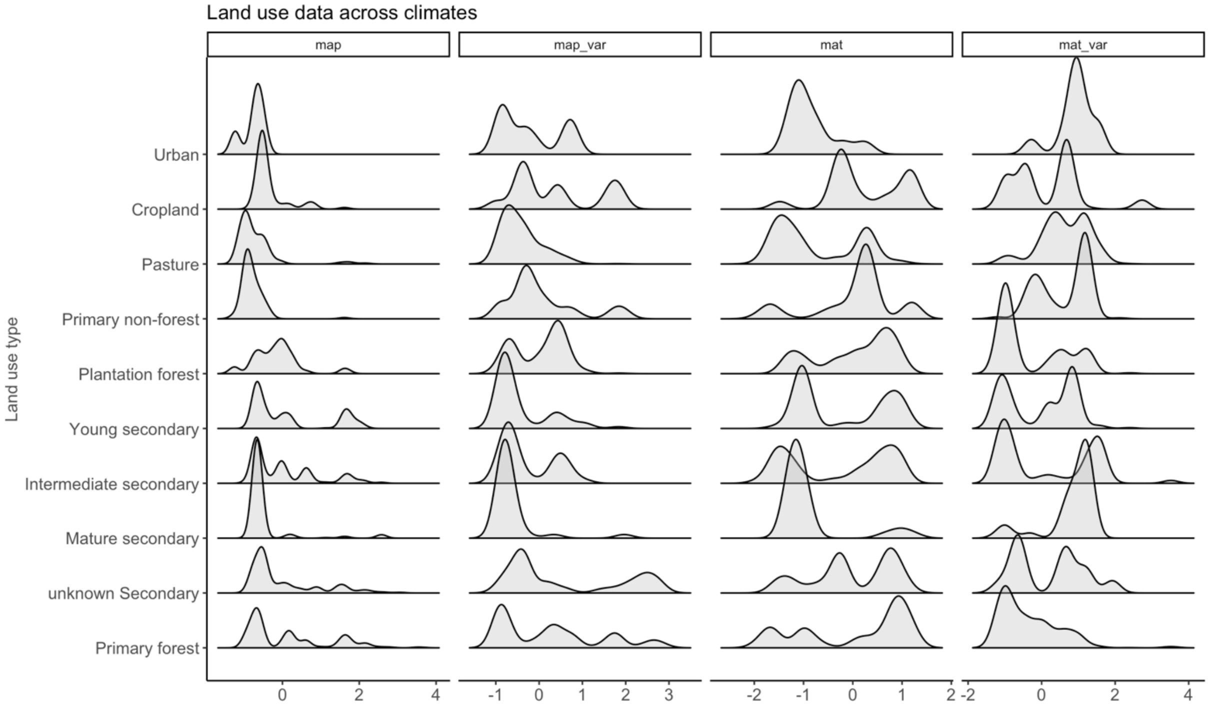

Figure A.7. Plot of climate values by land use type. Map(_var) = mean annual precipitation (variation), mat(_var) = mean annual temperature (variation). Plot based on sites included in occurrence models.

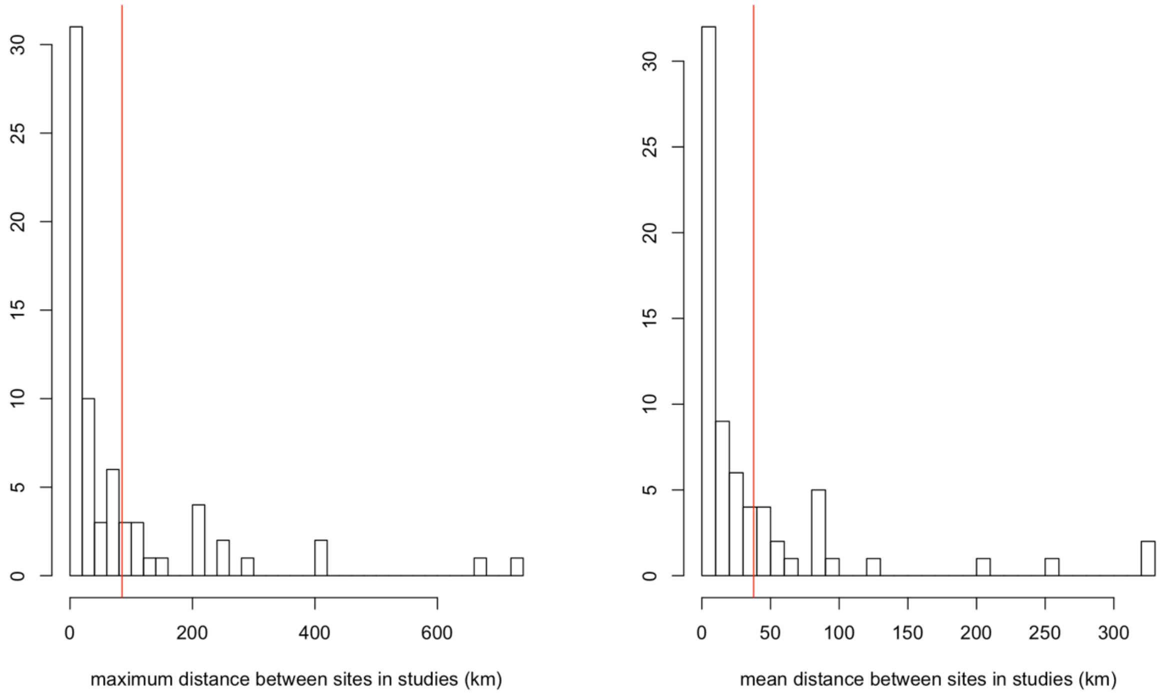

Figure A.8. Maximum and mean distances between sites within studies which contributed data to this work. Red line represents mean values (i.e. average maximum study extent (left hand panel), and average distance between sites within a study (right hand panel)).

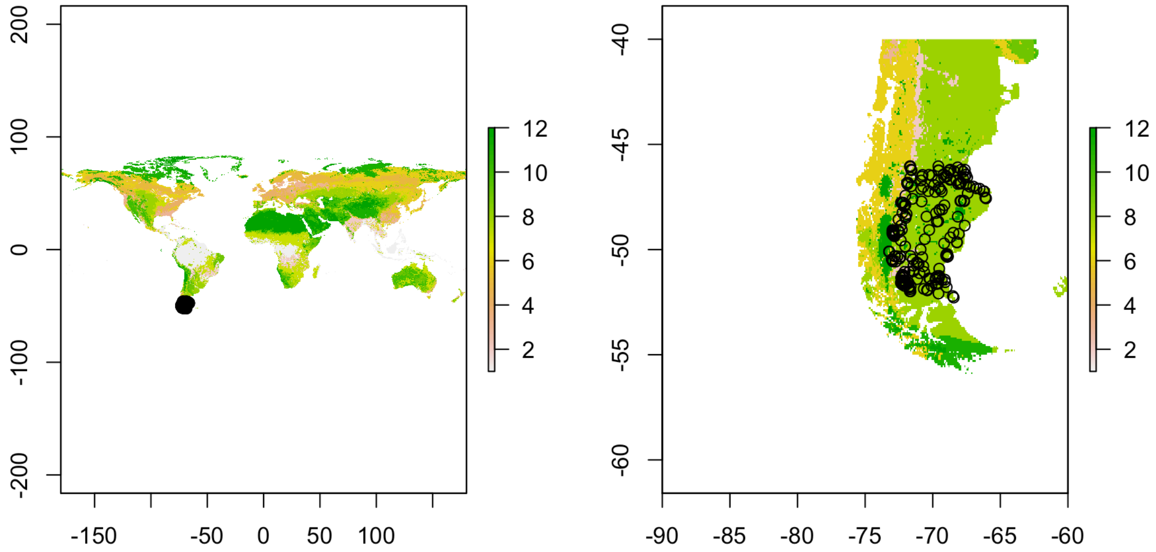

Figure A.9. Map of sites within the study with the largest extent. The maximum distance between sites within this study was 733km.

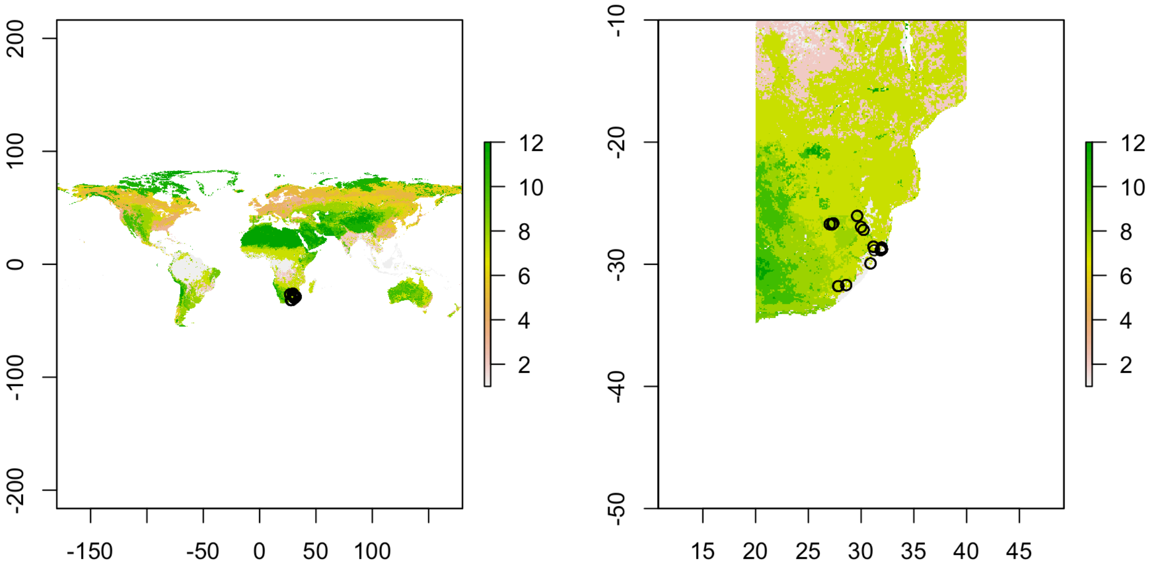

Figure A.10. Map of sites within the study with the second largest extent. The second largest distance between sites within a study was 664km.

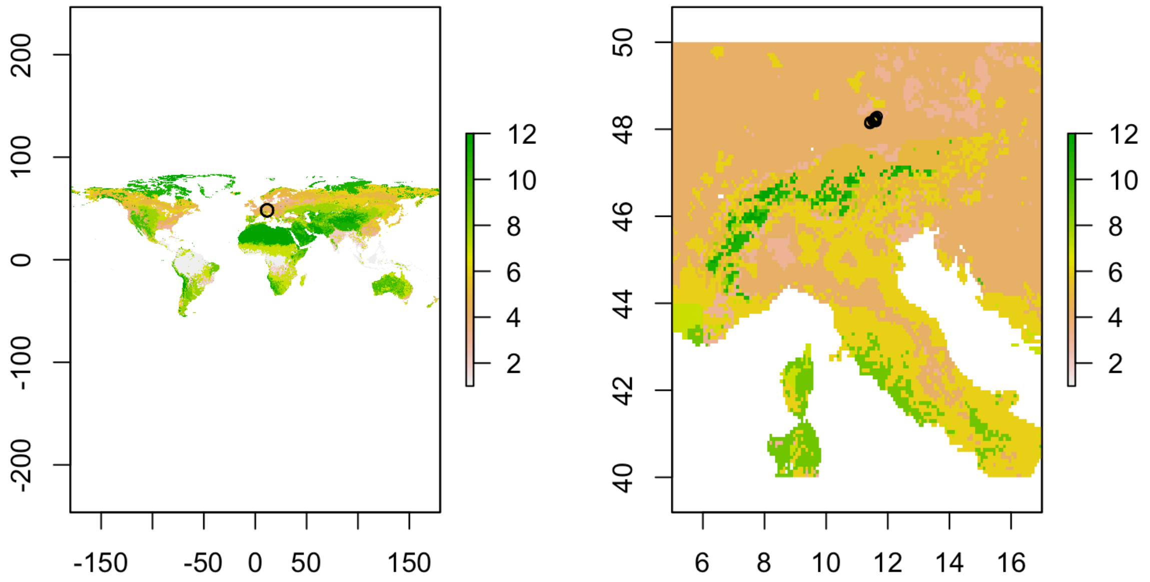

Figure A.11. Map of sites within the study with the median maximum extent (24km).

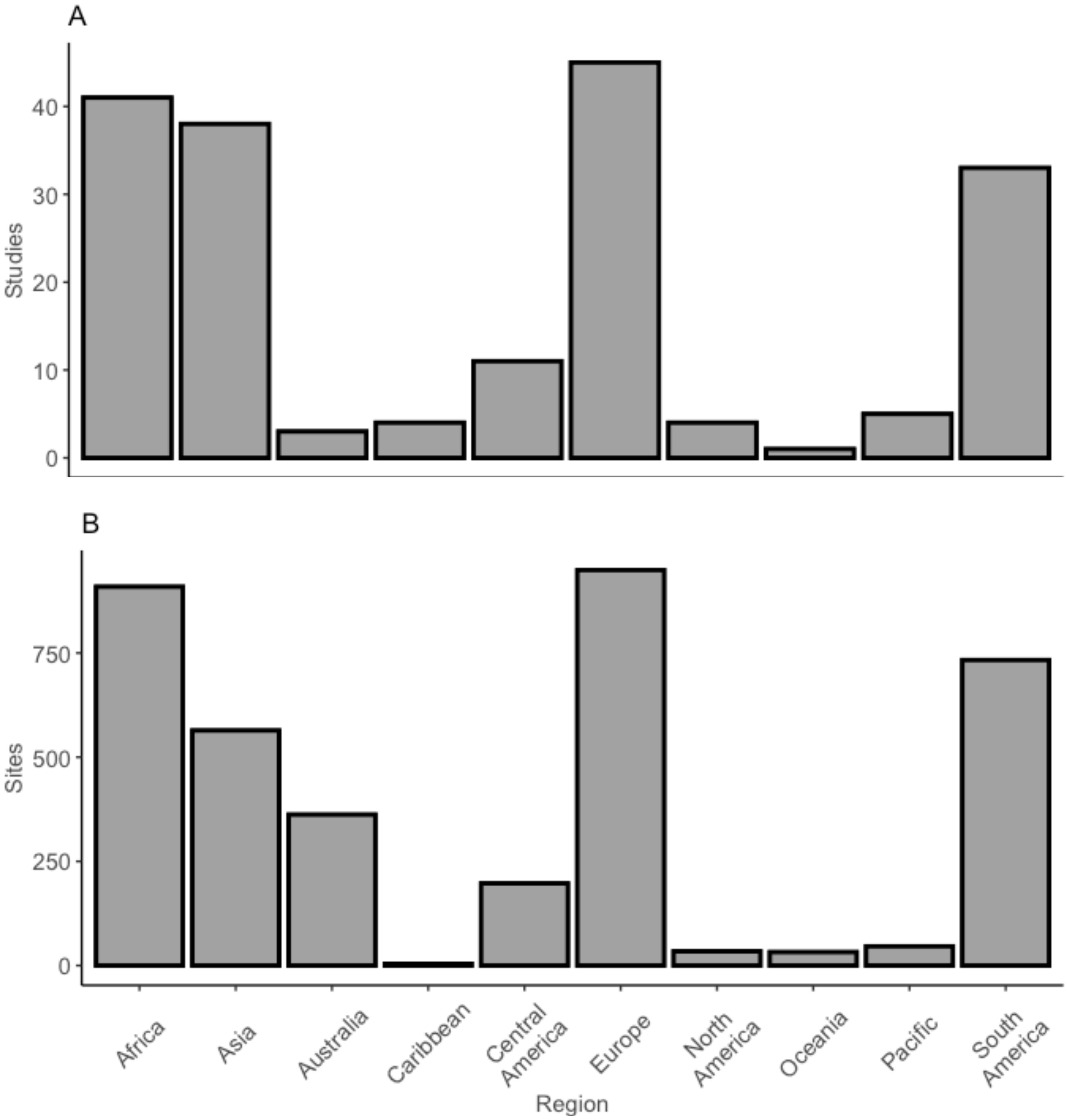

Figure A.12. Histogram of data per region. (A) Number of Studies per region, (B) number of sites per region.

Table A.3. Occurrence model output. Estimate refers to the Log Odds of occurrence. Colon indicates interaction between main effects. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects. Reference level is the weighted grand mean of the data (average log odds of occurrence across all land uses and life forms when continuous variables are zero). Model outputs have been rounded to three decimal place, and averages of values that differed at the third decimal place where obtained in order to recombine weighted effects coding outputs.

Model terms	Estimate	Std.Error	z value	Pr(>|z|)
Primary forest : therophyte	-0.4820000	0.041	-11.8310000	0.0000
Primary non-forest : therophyte	-0.0720000	0.040	-1.7965000	0.0720
Young secondary : therophyte	0.0860000	0.079	1.0885000	0.2760
Intermediate secondary : therophyte	-0.1910000	0.062	-3.0700000	0.0020
Mature secondary : therophyte	0.0450000	0.080	0.5570000	0.5770
unknown Secondary : therophyte	-0.0730000	0.045	-1.6480000	0.0990
Plantation forest : therophyte	0.3250000	0.074	4.4220000	0.0000
Cropland : therophyte	0.3700000	0.028	13.0705000	0.0000
Urban : therophyte	0.4030000	0.092	4.3580000	0.0000
therophyte	-0.1910000	0.032	-5.9030000	0.0000
therophyte : species richness	0.1530000	0.026	5.9360000	0.0000
therophyte : map	0.0690000	0.063	1.0870000	0.2770
therophyte : map_var	0.1360000	0.044	3.0875000	0.0020
therophyte : mat	-0.0450000	0.043	-1.0630000	0.2880
therophyte : mat_var	0.0920000	0.044	2.0970000	0.0360
Primary forest : hemicryptophyte	-0.3320000	0.030	-11.1500000	0.0000
Primary non-forest : hemicryptophyte	0.2230000	0.026	8.5990000	0.0000
Young secondary : hemicryptophyte	0.2480000	0.052	4.7495000	0.0000
Intermediate secondary : hemicryptophyte	-0.0720000	0.022	-3.3215000	0.0010
Mature secondary : hemicryptophyte	-0.0540000	0.020	-2.7310000	0.0060
unknown Secondary : hemicryptophyte	0.0030000	0.030	0.1140000	0.9095
Plantation forest : hemicryptophyte	-0.1145000	0.041	-2.8220000	0.0050
Cropland : hemicryptophyte	-0.1070000	0.038	-2.8170000	0.0050
Urban : hemicryptophyte	0.0650000	0.043	1.5085000	0.1310

Table A.3. Occurrence model output. Estimate refers to the Log Odds of occurrence. Colon indicates interaction between main effects. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects. Reference level is the weighted grand mean of the data (average log odds of occurrence across all land uses and life forms when continuous variables are zero). Model outputs have been rounded to three decimal place, and averages of values that differed at the third decimal place where obtained in order to recombine weighted effects coding outputs.

Model terms	Estimate	Std.Error	z value	Pr(>|z|)
hemicryptophyte	-0.1500000	0.022	-6.8975000	0.0000
hemicryptophyte : species richness	0.2740000	0.015	18.3500000	0.0000
hemicryptophyte : map	-0.1090000	0.060	-1.8130000	0.0700
hemicryptophyte : map_var	0.1200000	0.034	3.5045000	0.0000
hemicryptophyte : mat	-0.2020000	0.027	-7.4340000	0.0000
hemicryptophyte : mat_var	-0.1070000	0.028	-3.8455000	0.0000
Primary forest : chamaephyte	-0.2420000	0.052	-4.6845000	0.0000
Primary non-forest : chamaephyte	-0.2750000	0.079	-3.4770000	0.0010
Young secondary : chamaephyte	-0.1060000	0.118	-0.9025000	0.3670
Intermediate secondary : chamaephyte	-0.0300000	0.054	-0.5535000	0.5800
Mature secondary : chamaephyte	0.0190000	0.061	0.3080000	0.7580
unknown Secondary : chamaephyte	0.1950000	0.053	3.6530000	0.0000
Plantation forest : chamaephyte	0.1000000	0.072	1.3810000	0.1670
Cropland : chamaephyte	-0.1330000	0.075	-1.7670000	0.0770
Urban : chamaephyte	0.1080000	0.107	1.0080000	0.3130
chamaephyte	-0.1320000	0.031	-4.2185000	0.0000
chamaephyte : species richness	0.1500000	0.027	5.6330000	0.0000
chamaephyte : map	0.0186667	0.087	0.2133333	0.8310
chamaephyte : map_var	0.0630000	0.062	1.0240000	0.3060
chamaephyte : mat	0.1190000	0.066	1.7945000	0.0730
chamaephyte : mat_var	0.1390000	0.051	2.7350000	0.0060
Primary forest : phanerophyte	0.1130000	0.007	16.8270000	0.0000
Primary non-forest : phanerophyte	-0.1580000	0.028	-5.6755000	0.0000
Young secondary : phanerophyte	-0.0950000	0.021	-4.6420000	0.0000

Table A.3. Occurrence model output. Estimate refers to the Log Odds of occurrence. Colon indicates interaction between main effects. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects. Reference level is the weighted grand mean of the data (average log odds of occurrence across all land uses and life forms when continuous variables are zero). Model outputs have been rounded to three decimal place, and averages of values that differed at the third decimal place where obtained in order to recombine weighted effects coding outputs.

Model terms	Estimate	Std.Error	z value	Pr(>|z|)
Intermediate secondary : phanerophyte	0.1160000	0.018	6.4320000	0.0000
Mature secondary : phanerophyte	0.3080000	0.054	5.7255000	0.0000
unknown Secondary : phanerophyte	-0.0150000	0.017	-0.8600000	0.3900
Plantation forest : phanerophyte	0.0330000	0.015	2.2100000	0.0270
Cropland : phanerophyte	-0.2090000	0.022	-9.6050000	0.0000
Urban : phanerophyte	-0.3450000	0.092	-3.7290000	0.0000
phanerophyte	0.1460000	0.017	8.6845000	0.0000
phanerophyte : species richness	-0.0950000	0.005	-20.7295000	0.0000
phanerophyte : map	0.0050000	0.006	0.9540000	0.3400
phanerophyte : map_var	-0.0540000	0.011	-4.7300000	0.0000
phanerophyte : mat	0.2200000	0.026	8.4580000	0.0000
phanerophyte : mat_var	0.0440000	0.020	2.1740000	0.0300
Primary forest	0.0200000	0.012	1.5860000	0.1130
Primary non-forest	-0.1793333	0.023	-7.6456667	0.0000
Young secondary	0.0870000	0.034	2.5430000	0.0110
Intermediate secondary	0.0440000	0.018	2.4820000	0.0130
Mature secondary	0.0630000	0.032	1.9620000	0.0500
unknown Secondary	0.2830000	0.025	11.3060000	0.0000
Plantation forest	-0.1480000	0.028	-5.3525000	0.0000
Cropland	-0.2350000	0.023	-10.3420000	0.0000
Urban	0.1850000	0.060	3.0835000	0.0020
Grand Mean	-1.5790000	0.216	-7.3085000	0.0000
species richness	0.8350000	0.012	68.2205000	0.0000
map	-0.1240000	0.022	-5.7075000	0.0000

Table A.3. Occurrence model output. Estimate refers to the Log Odds of occurrence. Colon indicates interaction between main effects. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects. Reference level is the weighted grand mean of the data (average log odds of occurrence across all land uses and life forms when continuous variables are zero). Model outputs have been rounded to three decimal place, and averages of values that differed at the third decimal place where obtained in order to recombine weighted effects coding outputs.

Model terms	Estimate	Std.Error	z value	Pr(>|z|)
map_var	-0.0710000	0.039	-1.8100000	0.0700
mat	-0.1490000	0.043	-3.4570000	0.0010
mat_var	-0.7370000	0.074	-9.9550000	0.0000
Pasture : therophyte	0.0560000	0.037	1.5160000	0.1300
Primary non-forest : cryptophyte	0.0830000	0.074	1.1310000	0.2580
Young secondary : cryptophyte	0.3640000	0.086	4.2560000	0.0000
Intermediate secondary : cryptophyte	-0.2050000	0.046	-4.4910000	0.0000
Mature secondary : cryptophyte	-0.1180000	0.040	-2.9250000	0.0030
unknown Secondary : cryptophyte	0.0490000	0.058	0.8470000	0.3970
Plantation forest : cryptophyte	-0.4150000	0.069	-6.0090000	0.0000
Pasture : cryptophyte	0.0530000	0.048	1.0995000	0.2715
Cropland : cryptophyte	0.4770000	0.076	6.2780000	0.0000
Urban : cryptophyte	-0.2740000	0.114	-2.4050000	0.0160
cryptophyte	-0.1690000	0.036	-4.7375000	0.0000
cryptophyte : species richness	0.2670000	0.027	9.9670000	0.0000
cryptophyte : map	-0.3400000	0.135	-2.5210000	0.0120
cryptophyte : map_var	0.1750000	0.063	2.7910000	0.0050
cryptophyte : mat	-0.4470000	0.076	-5.8960000	0.0000
cryptophyte : mat_var	-0.3000000	0.059	-5.0645000	0.0000
Pasture : hemicryptophyte	0.1300000	0.015	8.8045000	0.0000
Pasture : chamaephyte	0.2550000	0.040	6.3785000	0.0000
Pasture	-0.0130000	0.019	-0.6955000	0.4870
Primary forest : cryptophyte	0.0520000	0.059	0.8750000	0.3810
Pasture : phanerophyte	-0.3010000	0.025	-12.0210000	0.0000

Table A.4. Abundance model output. Estimate refers to the scaled and logit transformed non-zero percent cover data. Colon indicates interaction between main effects. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects. Reference level is the weighted grand mean of the data (average (transformed) percent cover when continuous variables are zero). Model outputs have been rounded to three decimal place, and averages of values that differed at the third decimal place where obtained in order to recombine weighted effects coding outputs.

Model terms	Estimate	Std.Error	t value
Cropland : therophyte	-0.0410	0.089	-0.4650
Intermediate secondary : therophyte	-0.1820	0.051	-3.5480
Mature secondary : therophyte : species richness	0.0090	0.040	0.2300
Pasture : therophyte	0.0020	0.029	0.0670
Plantation forest : therophyte	0.0690	0.065	1.0660
Primary forest : therophyte	0.0100	0.101	0.0950
Primary non-forest : therophyte	-0.0360	0.107	-0.3370
unknown Secondary : therophyte	0.6520	0.174	3.7540
Urban : therophyte	-0.0070	0.102	-0.0730
Young secondary : therophyte	0.0760	0.041	1.8510
therophyte	-0.0730	0.027	-2.7380
therophyte : map	-0.2610	0.151	-1.7280
therophyte : map_var	0.2710	0.073	3.7080
therophyte : mat	-0.3610	0.080	-4.4840
therophyte : mat_var	0.1290	0.055	2.3620
Cropland : cryptophyte	-0.1090	0.104	-1.0460
Intermediate secondary : cryptophyte	0.0100	0.041	0.2480
Mature secondary : cryptophyte : species richness	0.0580	0.035	1.6640
Pasture : cryptophyte	0.0100	0.024	0.4000
Plantation forest : cryptophyte	0.0070	0.061	0.1170
Primary forest : cryptophyte	-0.0470	0.060	-0.7830
Primary non-forest : cryptophyte	0.0730	0.099	0.7320
unknown Secondary : cryptophyte	-0.5300	0.237	-2.2330
Urban : cryptophyte	0.1680	0.091	1.8440

Table A.4. Abundance model output. Estimate refers to the scaled and logit transformed non-zero percent cover data. Colon indicates interaction between main effects. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects. Reference level is the weighted grand mean of the data (average (transformed) percent cover when continuous variables are zero). Model outputs have been rounded to three decimal place, and averages of values that differed at the third decimal place where obtained in order to recombine weighted effects coding outputs.

Model terms	Estimate	Std.Error	t value
Young secondary : cryptophyte	-0.0030	0.075	-0.0390
cryptophyte	-0.0080	0.022	-0.3460
cryptophyte : map	-0.2410	0.188	-1.2840
cryptophyte : map_var	-0.1590	0.073	-2.1870
cryptophyte : mat	0.0780	0.090	0.8650
cryptophyte : mat_var	0.0170	0.049	0.3510
Cropland : hemicryptophyte	0.0680	0.055	1.2220
Intermediate secondary : hemicryptophyte	0.0280	0.011	2.6120
Mature secondary : hemicryptophyte : species richness	-0.0290	0.012	-2.3920
Pasture : hemicryptophyte	0.0060	0.006	0.9910
Plantation forest : hemicryptophyte	-0.0320	0.022	-1.4680
Primary forest : hemicryptophyte	-0.1430	0.026	-5.4170
Primary non-forest : hemicryptophyte	-0.0270	0.038	-0.7150
unknown Secondary : hemicryptophyte	0.0550	0.132	0.4120
Urban : hemicryptophyte	0.0190	0.027	0.7230
Young secondary : hemicryptophyte	0.0180	0.021	0.8360
hemicryptophyte	-0.0040	0.008	-0.5950
hemicryptophyte : map	0.3410	0.060	5.7090
hemicryptophyte : map_var	-0.0450	0.031	-1.4610
hemicryptophyte : mat	0.0100	0.036	0.2610
hemicryptophyte : mat_var	-0.0360	0.019	-1.9130
Cropland : chamaephyte	0.1770	0.127	1.3930
Intermediate secondary : chamaephyte	-0.0580	0.034	-1.7120
Mature secondary : chamaephyte : species richness	0.0600	0.034	1.7840

Table A.4. Abundance model output. Estimate refers to the scaled and logit transformed non-zero percent cover data. Colon indicates interaction between main effects. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects. Reference level is the weighted grand mean of the data (average (transformed) percent cover when continuous variables are zero). Model outputs have been rounded to three decimal place, and averages of values that differed at the third decimal place where obtained in order to recombine weighted effects coding outputs.

Model terms	Estimate	Std.Error	t value
Pasture : chamaephyte	0.0050	0.019	0.2430
Plantation forest : chamaephyte	0.1050	0.052	2.0180
Primary forest : chamaephyte	0.0410	0.049	0.8390
Primary non-forest : chamaephyte	0.0550	0.138	0.4000
unknown Secondary : chamaephyte	0.0470	0.150	0.3140
Urban : chamaephyte	-0.0170	0.070	-0.2460
Young secondary : chamaephyte	-0.2240	0.078	-2.8570
chamaephyte	0.0150	0.020	0.7360
chamaephyte : map	-0.3860	0.126	-3.0700
chamaephyte : map_var	-0.0840	0.074	-1.1370
chamaephyte : mat	0.0570	0.072	0.7910
chamaephyte : mat_var	-0.0440	0.045	-0.9860
Cropland : phanerophyte	-0.0500	0.111	-0.4540
Intermediate secondary : phanerophyte	0.0380	0.064	0.5970
Mature secondary : phanerophyte : species richness	0.0070	0.037	0.2010
Pasture : phanerophyte	-0.0580	0.029	-2.0140
Plantation forest : phanerophyte	-0.0180	0.042	-0.4290
Primary forest : phanerophyte	0.1040	0.021	4.8350
Primary non-forest : phanerophyte	0.0220	0.075	0.2910
unknown Secondary : phanerophyte	-0.1870	0.090	-2.0820
Urban : phanerophyte	-0.3180	0.107	-2.9610
Young secondary : phanerophyte	-0.1240	0.067	-1.8600
phanerophyte	0.0590	0.026	2.3025
phanerophyte : map	-0.2280	0.115	-1.9835

Table A.4. Abundance model output. Estimate refers to the scaled and logit transformed non-zero percent cover data. Colon indicates interaction between main effects. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects. Reference level is the weighted grand mean of the data (average (transformed) percent cover when continuous variables are zero). Model outputs have been rounded to three decimal place, and averages of values that differed at the third decimal place where obtained in order to recombine weighted effects coding outputs.

Model terms	Estimate	Std.Error	t value
phanerophyte : map_var	-0.0450	0.066	-0.6860
phanerophyte : mat	0.2720	0.059	4.6120
phanerophyte : mat_var	0.0080	0.046	0.1730
Cropland	-0.0340	0.168	-0.2020
Intermediate secondary	0.0870	0.022	3.8710
Mature secondary : species richness	-0.1050	0.017	-6.0290
Pasture	0.1420	0.015	9.2880
Plantation forest	-0.8280	0.099	-8.3850
Primary forest	0.0200	0.032	0.6255
Primary non-forest	0.1070	0.040	2.6440
unknown Secondary	-0.6920	0.087	-7.9670
Urban	0.0700	0.045	1.5505
Young secondary	-0.0310	0.047	-0.6530
Grand Mean	-0.0135	0.238	-0.0570
map	0.0470	0.114	0.4160
map_var	0.0810	0.103	0.7860
mat	-0.0790	0.087	-0.9120
mat_var	-0.1560	0.124	-1.2585

Table A.5a. Effect size for Life form Occurrence by Land use. Effect size refers to the difference in Log Odds between the weighted grand mean of the data (average log odds of occurrence across all land uses and life forms when continuous variables are zero), and the estimate for particular life form in a particular land use.

Land use	Life form	Effect size
Plantation forest	cryptophyte	-0.732
Primary forest	therophyte	-0.654
Primary non-forest	chamaephyte	-0.586

Table A.5a. Effect size for Life form Occurrence by Land use. Effect size refers to the difference in Log Odds between the weighted grand mean of the data (average log odds of occurrence across all land uses and life forms when continuous variables are zero), and the estimate for particular life form in a particular land use.

Land use	Life form	Effect size
Cropland	chamaephyte	-0.500
Cropland	hemicryptophyte	-0.492
Primary forest	hemicryptophyte	-0.462
Primary non-forest	therophyte	-0.443
Plantation forest	hemicryptophyte	-0.412
Primary forest	chamaephyte	-0.355
Intermediate secondary	therophyte	-0.339
Intermediate secondary	cryptophyte	-0.329
Cropland	phanerophyte	-0.299
Primary non-forest	cryptophyte	-0.265
Urban	cryptophyte	-0.258
Mature secondary	cryptophyte	-0.224
Primary non-forest	phanerophyte	-0.192
Plantation forest	chamaephyte	-0.180
Intermediate secondary	hemicryptophyte	-0.177
Pasture	phanerophyte	-0.169
Young secondary	chamaephyte	-0.152
Pasture	therophyte	-0.149
Mature secondary	hemicryptophyte	-0.140
Pasture	cryptophyte	-0.129
Intermediate secondary	chamaephyte	-0.118
Primary non-forest	hemicryptophyte	-0.106
Primary forest	cryptophyte	-0.098
Mature secondary	therophyte	-0.083
Cropland	therophyte	-0.057
Mature secondary	chamaephyte	-0.050

Table A.5a. Effect size for Life form Occurrence by Land use. Effect size refers to the difference in Log Odds between the weighted grand mean of the data (average log odds of occurrence across all land uses and life forms when continuous variables are zero), and the estimate for particular life form in a particular land use.

Land use	Life form	Effect size
Pasture	hemicryptophyte	-0.033
Young secondary	therophyte	-0.019
Plantation forest	therophyte	-0.014
Urban	phanerophyte	-0.014
unknown Secondary	therophyte	0.018
Plantation forest	phanerophyte	0.031
Cropland	cryptophyte	0.072
Urban	hemicryptophyte	0.099
Pasture	chamaephyte	0.109
unknown Secondary	hemicryptophyte	0.137
Young secondary	phanerophyte	0.137
Urban	chamaephyte	0.160
unknown Secondary	cryptophyte	0.163
Young secondary	hemicryptophyte	0.185
Primary forest	phanerophyte	0.278
Young secondary	cryptophyte	0.282
Intermediate secondary	phanerophyte	0.306
unknown Secondary	chamaephyte	0.346
Urban	therophyte	0.396
unknown Secondary	phanerophyte	0.414
Mature secondary	phanerophyte	0.517

Table A.5b. Effect size for Life form Occurrence by Climate. Effect size refers to the change in Log Odds associated with a 1 SD change in a particular climate variable. See table 5 for climate variable summary statistics.

Life form	Climate	Effect size
cryptophyte	mat_var	-1.037

Table A.5b. Effect size for Life form Occurrence by Climate. Effect size refers to the change in Log Odds associated with a 1 SD change in a particular climate variable. See table 5 for climate variable summary statistics.

Life form	Climate	Effect size
hemicryptophyte	mat_var	-0.844
phanerophyte	mat_var	-0.693
therophyte	mat_var	-0.645
chamaephyte	mat_var	-0.598
cryptophyte	mat	-0.596
cryptophyte	map	-0.463
hemicryptophyte	mat	-0.351
hemicryptophyte	map	-0.233
therophyte	mat	-0.195
phanerophyte	map_var	-0.125
phanerophyte	map	-0.118
chamaephyte	map	-0.105
therophyte	map	-0.055
chamaephyte	mat	-0.030
chamaephyte	map_var	-0.008
hemicryptophyte	map_var	0.049
therophyte	map_var	0.065
phanerophyte	mat	0.070
cryptophyte	map_var	0.104

Table A.5c. Range in Effect sizes for Life form Occurrence across Land use. Range across land uses refers to the maximum difference in Log Odds of occurrence within a particular life form across all land uses.

Life form	Range across land uses
hemicryptophyte	0.677
phanerophyte	0.816
chamaephyte	0.932
cryptophyte	1.014

Table A.5c. Range in Effect sizes for Life form Occurrence across Land use. Range across land uses refers to the maximum difference in Log Odds of occurrence within a particular life form across all land uses.

Life form	Range across land uses
therophyte	1.050

Abundance effect sizes

Table A.6a. Effect size for Life form Abundance by Land use. Effect size refers to the difference in between the weighted grand mean of the data (average (transformed) percent cover when continuous variables are zero), and the estimate for particular life form in a particular land use.

Land use	Life form	Effect size
unknown Secondary	cryptophyte	-1.2295
Plantation forest	hemicryptophyte	-0.8645
Plantation forest	therophyte	-0.8325
Plantation forest	cryptophyte	-0.8285
unknown Secondary	phanerophyte	-0.8205
Plantation forest	phanerophyte	-0.7865
Plantation forest	chamaephyte	-0.7075
unknown Secondary	hemicryptophyte	-0.6415
unknown Secondary	chamaephyte	-0.6305
Young secondary	chamaephyte	-0.2400
Urban	phanerophyte	-0.1895
Intermediate secondary	therophyte	-0.1695
Cropland	cryptophyte	-0.1505
Cropland	therophyte	-0.1485
Primary forest	hemicryptophyte	-0.1275
Mature secondary	hemicryptophyte	-0.1205
unknown Secondary	therophyte	-0.1135
Young secondary	phanerophyte	-0.0955
Mature secondary	phanerophyte	-0.0845
Mature secondary	therophyte	-0.0825
Primary forest	therophyte	-0.0435

Table A.6a. Effect size for Life form Abundance by Land use. Effect size refers to the difference in between the weighted grand mean of the data (average (transformed) percent cover when continuous variables are zero), and the estimate for particular life form in a particular land use.

Land use	Life form	Effect size
Young secondary	cryptophyte	-0.0415
Primary forest	cryptophyte	-0.0345
Mature secondary	cryptophyte	-0.0335
Mature secondary	chamaephyte	-0.0315
Young secondary	therophyte	-0.0275
Cropland	phanerophyte	-0.0245
Young secondary	hemicryptophyte	-0.0175
Urban	therophyte	-0.0115
Primary non-forest	therophyte	-0.0025
Cropland	hemicryptophyte	0.0295
Intermediate secondary	chamaephyte	0.0425
Urban	chamaephyte	0.0665
Pasture	therophyte	0.0705
Primary non-forest	hemicryptophyte	0.0755
Primary forest	chamaephyte	0.0765
Urban	hemicryptophyte	0.0845
Intermediate secondary	cryptophyte	0.0895
Intermediate secondary	hemicryptophyte	0.1105
Pasture	phanerophyte	0.1435
Pasture	cryptophyte	0.1445
Pasture	hemicryptophyte	0.1445
Cropland	chamaephyte	0.1585
Pasture	chamaephyte	0.1615
Primary non-forest	cryptophyte	0.1725
Primary non-forest	chamaephyte	0.1775
Primary forest	phanerophyte	0.1835

Table A.6a. Effect size for Life form Abundance by Land use. Effect size refers to the difference in between the weighted grand mean of the data (average (transformed) percent cover when continuous variables are zero), and the estimate for particular life form in a particular land use.

Land use	Life form	Effect size
Intermediate secondary	phanerophyte	0.1845
Primary non-forest	phanerophyte	0.1885
Urban	cryptophyte	0.2295

Table A.6b. Effect size for Life form Abundance by Climate. Effect size refers to the change in Abundance associated with a 1 SD change in a particular climate variable. See table 5 for climate variable summary statistics.

raunk_lf	clim	Magnitude
therophyte	mat	-0.440
chamaephyte	map	-0.338
therophyte	map	-0.214
chamaephyte	mat_var	-0.200
cryptophyte	map	-0.194
hemicryptophyte	mat_var	-0.192
phanerophyte	map	-0.181
phanerophyte	mat_var	-0.148
cryptophyte	mat_var	-0.139
cryptophyte	map_var	-0.078
hemicryptophyte	mat	-0.070
therophyte	mat_var	-0.027
chamaephyte	mat	-0.022
chamaephyte	map_var	-0.003
cryptophyte	mat	-0.001
hemicryptophyte	map_var	0.036
phanerophyte	map_var	0.036
phanerophyte	mat	0.193
therophyte	map_var	0.352

Table A.6b. Effect size for Life form Abundance by Climate. Effect size refers to the change in Abundance associated with a 1 SD change in a particular climate variable. See table 5 for climate variable summary statistics.

raunk_lf	clim	Magnitude
hemicryptophyte	map	0.389

Table A.6c. Range in Effect sizes for Life form Abundance across Land use. Range across land uses refers to the maximum difference in Abundance within a particular life form across all land uses.

Life form	Range across land uses
chamaephyte	0.885
therophyte	0.903
hemicryptophyte	1.009
phanerophyte	1.009
cryptophyte	1.459

Climate summary statistics

Table A.7. Summary statistics for climatic variables. Climate variable effect size in real world terms. Summary statistics for a) site level climate data used in model, and differences between climate variable averages for b) biomes (source: (Ellis et al., 2010) and c) ecoregions (after (Oslon et al., 2001). Climate variable averages were calculated using bioClim values for all cells of a particular biome or ecoregion (see https://doi.org/10.5281/zenodo.6376554 for details). SD = Standard Deviation. MAP = Mean annual precipitation, MAT = Mean annual temperature, MAP_var = Mean annual precipitation variation, MAT_var = Mean annual temperature variation.

Statistic	map	mat	map_var	mat_var
Model data				
SD	1218.41	8.14	36.58	23.84
mean	1557.93	18.39	46.87	31.15
median	929.00	20.80	34.00	25.32
Biome				
SD	500.35	9.13	14.02	31.01
mean	577.00	12.96	21.95	45.52
median	383.78	11.45	19.36	45.05
Ecoregion				
SD	766.94	9.42	25.68	36.84

Table A.7. Summary statistics for climatic variables. Climate variable effect size in real world terms. Summary statistics for a) site level climate data used in model, and differences between climate variable averages for b) biomes (source: (Ellis et al., 2010) and c) ecoregions (after (Oslon et al., 2001). Climate variable averages were calculated using bioClim values for all cells of a particular biome or ecoregion (see https://doi.org/10.5281/zenodo.6376554 for details). SD = Standard Deviation. MAP = Mean annual precipitation, MAT = Mean annual temperature, MAP_var = Mean annual precipitation variation, MAT_var = Mean annual temperature variation.

Statistic	map	mat	map_var	mat_var
mean	965.81	11.39	34.55	44.93
median	786.91	9.08	29.55	35.99

Biome averages

Table A.8. Biome averages for climatic variables. MAP = Mean annual precipitation, MAT = Mean annual temperature, MAP_var = Mean annual precipitation variation, MAT_var = Mean annual temperature variation.

Biome	map	mat	map_var	mat_var
Tropical Evergreen Woodland	2139.86	24.75	52.26	9.81
Tropical Deciduous Woodland	1206.47	23.25	92.52	27.54
Dense Shrubland	582.31	20.11	70.78	43.79
Savanna	914.99	18.87	77.17	46.80
Open Shrubland	264.68	16.82	75.40	72.60
Deserts and Barren	114.81	14.74	82.77	77.11
Temperate Evergreen Woodland	949.08	9.76	40.03	78.04
Temperate Deciduous Woodland	882.38	9.76	32.80	78.60
Grassland and Steppe	488.12	9.28	61.49	88.73
Mixed Woodland	583.80	-2.78	51.52	128.83
Boreal Woodland	583.56	-2.81	44.71	128.35
Tundra	335.45	-10.38	56.75	123.65

No species richness model outputs

Table A.9a. Occurrence no species richness model output. Estimate refers to the Log Odds of occurrence. Colon indicates interaction between main effects. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects. Reference level is the weighted grand mean of the data (average log odds of occurrence across all land uses and life forms when continuous variables are zero). Model outputs have been rounded to three decimal place, and averages of values that differed at the third decimal place where obtained in order to recombine weighted effects coding outputs.

Model terms	Estimate	Std.Error	z value	Pr(>|z|)
Primary forest : cryptophyte	0.0280	0.057	0.4860000	0.6270000
Primary non-forest : cryptophyte	0.2230	0.070	3.1960000	0.0010000
Young secondary : cryptophyte	0.4220	0.081	5.2105000	0.0000000
Intermediate secondary : cryptophyte	-0.2940	0.043	-6.7995000	0.0000000
Mature secondary : cryptophyte	-0.0870	0.038	-2.2980000	0.0220000
unknown Secondary : cryptophyte	0.1560	0.050	3.1285000	0.0020000
Plantation forest : cryptophyte	-0.3670	0.066	-5.5330000	0.0000000
Pasture : cryptophyte	-0.0020	0.046	-0.0505000	0.9595000
Cropland : cryptophyte	0.3030	0.072	4.2275000	0.0000000
cryptophyte	-0.1460	0.034	-4.2405000	0.0000000
cryptophyte : map	-0.0180	0.119	-0.1530000	0.8785000
cryptophyte : map_var	0.1110	0.060	1.8445000	0.0650000
cryptophyte : mat	-0.3480	0.073	-4.7535000	0.0000000
cryptophyte : mat_var	-0.1560	0.056	-2.7975000	0.0050000
Primary forest : hemicryptophyte	-0.3810	0.029	-13.2915000	0.0000000
Primary non-forest : hemicryptophyte	0.2150	0.025	8.5800000	0.0000000
Young secondary : hemicryptophyte	0.3000	0.050	6.0035000	0.0000000
Intermediate secondary : hemicryptophyte	-0.1170	0.021	-5.6980000	0.0000000
Mature secondary : hemicryptophyte	-0.0070	0.018	-0.3846667	0.7003333
unknown Secondary : hemicryptophyte	0.1750	0.027	6.4765000	0.0000000
Plantation forest : hemicryptophyte	-0.1050	0.039	-2.7080000	0.0070000
Pasture : hemicryptophyte	0.1110	0.014	7.8580000	0.0000000
Cropland : hemicryptophyte	-0.1850	0.036	-5.1115000	0.0000000

Table A.9a. Occurrence no species richness model output. Estimate refers to the Log Odds of occurrence. Colon indicates interaction between main effects. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects. Reference level is the weighted grand mean of the data (average log odds of occurrence across all land uses and life forms when continuous variables are zero). Model outputs have been rounded to three decimal place, and averages of values that differed at the third decimal place where obtained in order to recombine weighted effects coding outputs.

Model terms	Estimate	Std.Error	z value	Pr(>|z|)
hemicryptophyte	-0.1140	0.021	-5.4160000	0.0000000
hemicryptophyte : map	0.0355	0.055	0.6450000	0.5190000
hemicryptophyte : map_var	0.0760	0.033	2.2885000	0.0220000
hemicryptophyte : mat	-0.1350	0.026	-5.1355000	0.0000000
hemicryptophyte : mat_var	-0.0450	0.026	-1.7015000	0.0890000
Primary forest : chamaephyte	-0.2880	0.050	-5.7660000	0.0000000
Primary non-forest : chamaephyte	-0.3000	0.077	-3.9165000	0.0000000
Young secondary : chamaephyte	0.0240	0.113	0.2090000	0.8350000
Intermediate secondary : chamaephyte	-0.0240	0.051	-0.4590000	0.6460000
Mature secondary : chamaephyte	0.0490	0.058	0.8353333	0.4033333
unknown Secondary : chamaephyte	0.2410	0.046	5.2200000	0.0000000
Plantation forest : chamaephyte	0.1240	0.069	1.7855000	0.0740000
Pasture : chamaephyte	0.2390	0.038	6.2825000	0.0000000
Cropland : chamaephyte	-0.1380	0.072	13.8165000	0.0540000
chamaephyte	-0.1040	0.030	-3.4360000	0.0010000
chamaephyte : map	0.0440	0.081	0.5425000	0.5875000
chamaephyte : map_var	0.0020	0.060	0.0410000	0.9670000
chamaephyte : mat	0.1700	0.064	2.6416667	0.0080000
chamaephyte : mat_var	0.1280	0.048	2.6765000	0.0070000
Primary forest : phanerophyte	0.1300	0.006	20.3145000	0.0000000
Primary non-forest : phanerophyte	-0.1650	0.027	-6.1105000	0.0000000
Young secondary : phanerophyte	-0.1350	0.020	-6.8295000	0.0000000
Intermediate secondary : phanerophyte	0.1760	0.017	10.2510000	0.0000000

Table A.9a. Occurrence no species richness model output. Estimate refers to the Log Odds of occurrence. Colon indicates interaction between main effects. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects. Reference level is the weighted grand mean of the data (average log odds of occurrence across all land uses and life forms when continuous variables are zero). Model outputs have been rounded to three decimal place, and averages of values that differed at the third decimal place where obtained in order to recombine weighted effects coding outputs.

Model terms	Estimate	Std.Error	z value	Pr(>|z|)
Mature secondary : phanerophyte	0.0880	0.051	1.7295000	0.0840000
unknown Secondary : phanerophyte	-0.1150	0.016	-7.2380000	0.0000000
Plantation forest : phanerophyte	0.0210	0.014	1.4825000	0.1380000
Pasture : phanerophyte	-0.2670	0.024	-11.1080000	0.0000000
Cropland : phanerophyte	-0.1590	0.021	-7.5545000	0.0000000
phanerophyte	0.1140	0.016	7.0130000	0.0000000
phanerophyte : map	-0.0070	0.005	-1.2965000	0.1950000
phanerophyte : map_var	-0.0320	0.011	-2.9170000	0.0040000
phanerophyte : mat	0.1180	0.025	4.6570000	0.0000000
phanerophyte : mat_var	-0.0040	0.019	-0.2110000	0.8330000
Primary forest	0.1440	0.012	12.1435000	0.0000000
Primary non-forest	-0.0990	0.022	-4.4470000	0.0000000
Young secondary	-0.1850	0.032	-5.7200000	0.0000000
Intermediate secondary	-0.0340	0.017	-1.9660000	0.0490000
Mature secondary	0.3150	0.031	10.3223333	0.0000000
unknown Secondary	0.3370	0.025	13.5460000	0.0000000
Plantation forest	-0.3020	0.026	-11.5190000	0.0000000
Pasture	-0.0590	0.018	-3.2000000	0.0010000
Cropland	-0.3130	0.022	-14.4470000	0.0000000
Grand Mean	-1.5975	0.205	-7.8115000	0.0000000
map	0.0200	0.021	0.9405000	0.3470000
map_var	0.0560	0.039	1.4523333	0.1463333
mat	0.0710	0.042	1.6710000	0.0950000

Table A.9a. Occurrence no species richness model output. Estimate refers to the Log Odds of occurrence. Colon indicates interaction between main effects. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects. Reference level is the weighted grand mean of the data (average log odds of occurrence across all land uses and life forms when continuous variables are zero). Model outputs have been rounded to three decimal place, and averages of values that differed at the third decimal place where obtained in order to recombine weighted effects coding outputs.

Model terms	Estimate	Std.Error	z value	Pr(>|z|)
mat_var	-0.4540	0.071	-6.3760000	0.0000000
Primary non-forest : therophyte	-0.1070	0.039	-2.7370000	0.0060000
Young secondary : therophyte	0.2520	0.076	3.3345000	0.0010000
Intermediate secondary : therophyte	-0.2920	0.060	-4.8420000	0.0000000
Mature secondary : therophyte	0.0520	0.075	0.6950000	0.4870000
unknown Secondary : therophyte	0.0180	0.041	0.4290000	0.6680000
Plantation forest : therophyte	0.3810	0.070	5.4030000	0.0000000
Pasture : therophyte	0.0800	0.035	2.2590000	0.0240000
Cropland : therophyte	0.3740	0.027	13.8165000	0.0000000
Urban : therophyte	0.3920	0.089	4.4010000	0.0000000
therophyte	-0.1500	0.031	-4.7875000	0.0000000
therophyte : map	0.0960	0.060	1.6040000	0.1090000
therophyte : map_var	0.0870	0.043	2.0315000	0.0420000
therophyte : mat	0.0130	0.041	0.3050000	0.7610000
therophyte : mat_var	0.1130	0.042	2.6840000	0.0070000
Urban : cryptophyte	-0.3210	0.110	-2.9230000	0.0030000
Urban : hemicryptophyte	0.0360	0.041	0.8835000	0.3770000
Urban : chamaephyte	0.1250	0.102	1.2305000	0.2185000
Urban	-0.3460	0.057	-6.1050000	0.0000000
Primary forest : therophyte	-0.5470	0.039	-13.8740000	0.0000000
Urban : phanerophyte	-0.2510	0.090	-2.7860000	0.0050000

Table A.9b. Abundance no species richness model output. Estimate refers to the scaled and logit transformed non-zero percent cover data. Colon indicates interaction between main effects. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects. Reference level is the weighted grand mean of the data (average (transformed) percent cover when continuous variables are zero). Model outputs have been rounded to three decimal place, and averages of values that differed at the third decimal place where obtained in order to recombine weighted effects coding outputs.

Model terms	**Estimate**	**Std.Error**	**t value**
Cropland : therophyte	-0.0280	0.088	-0.3130
Intermediate secondary : therophyte	-0.1680	0.051	-3.3200
Pasture : therophyte	-0.0020	0.028	-0.0700
Plantation forest : therophyte	0.0720	0.065	1.1180
Primary forest : therophyte	0.0010	0.101	0.0060
Primary non-forest : therophyte	-0.0360	0.107	-0.3410
unknown Secondary : therophyte	0.6410	0.172	3.7230
Urban : therophyte	-0.0030	0.102	-0.0260
Young secondary : therophyte	0.0660	0.041	1.6160
therophyte	-0.0740	0.027	-2.7500
therophyte : map	-0.2540	0.149	-1.7000
therophyte : map_var	0.2770	0.070	3.9750
therophyte : mat	-0.3610	0.080	-4.4855
therophyte : mat_var	0.1240	0.052	2.3850
Cropland : cryptophyte	-0.1380	0.104	-1.3320
Intermediate secondary : cryptophyte	0.0010	0.041	0.0300
Pasture : cryptophyte	0.0200	0.023	0.8610
Plantation forest : cryptophyte	0.0030	0.061	0.0510
Primary forest : cryptophyte	-0.0430	0.060	-0.7120
Primary non-forest : cryptophyte	0.0890	0.099	0.8960
unknown Secondary : cryptophyte	-0.5920	0.232	-2.5490
Urban : cryptophyte	0.1750	0.091	1.9230

Table A.9b. Abundance no species richness model output. Estimate refers to the scaled and logit transformed non-zero percent cover data. Colon indicates interaction between main effects. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects. Reference level is the weighted grand mean of the data (average (transformed) percent cover when continuous variables are zero). Model outputs have been rounded to three decimal place, and averages of values that differed at the third decimal place where obtained in order to recombine weighted effects coding outputs.

Model terms	**Estimate**	**Std.Error**	**t value**
Young secondary : cryptophyte	-0.0310	0.073	-0.4310
cryptophyte	-0.0090	0.022	-0.4205
cryptophyte : map	-0.1470	0.178	-0.8260
cryptophyte : map_var	-0.1380	0.071	-1.9420
cryptophyte : mat	0.0810	0.090	0.8950
cryptophyte : mat_var	0.0370	0.048	0.7810
Cropland : hemicryptophyte	0.0800	0.055	1.4680
Intermediate secondary : hemicryptophyte	0.0310	0.011	2.8510
Pasture : hemicryptophyte	0.0030	0.006	0.5450
Plantation forest : hemicryptophyte	-0.0310	0.022	-1.4135
Primary forest : hemicryptophyte	-0.1470	0.026	-5.5970
Primary non-forest : hemicryptophyte	-0.0370	0.038	-0.9950
unknown Secondary : hemicryptophyte	0.1130	0.131	0.8640
Urban : hemicryptophyte	0.0160	0.027	0.5850
Young secondary : hemicryptophyte	0.0330	0.021	1.5870
hemicryptophyte	-0.0040	0.008	-0.5880
hemicryptophyte : map	0.3060	0.058	5.2930
hemicryptophyte : map_var	-0.0570	0.030	-1.8990
hemicryptophyte : mat	0.0030	0.036	0.0770
hemicryptophyte : mat_var	-0.0460	0.018	-2.6330
Cropland : chamaephyte	0.1220	0.125	0.9820
Intermediate secondary : chamaephyte	-0.0690	0.034	-2.0600
Pasture : chamaephyte	0.0150	0.018	0.8450
Plantation forest : chamaephyte	0.0960	0.052	1.8460

Table A.9b. Abundance no species richness model output. Estimate refers to the scaled and logit transformed non-zero percent cover data. Colon indicates interaction between main effects. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects. Reference level is the weighted grand mean of the data (average (transformed) percent cover when continuous variables are zero). Model outputs have been rounded to three decimal place, and averages of values that differed at the third decimal place where obtained in order to recombine weighted effects coding outputs.

Model terms	Estimate	Std.Error	t value
Primary forest : chamaephyte	0.0440	0.049	0.8980
Primary non-forest : chamaephyte	0.0740	0.138	0.5340
unknown Secondary : chamaephyte	0.0070	0.148	0.0470
Urban : chamaephyte	-0.0120	0.070	-0.1690
Young secondary : chamaephyte	-0.2510	0.077	-3.2410
chamaephyte	0.0140	0.020	0.6940
chamaephyte : map	-0.3140	0.119	-2.6380
chamaephyte : map_var	-0.0760	0.074	-1.0270
chamaephyte : mat	0.0550	0.072	0.7610
chamaephyte : mat_var	-0.0120	0.041	-0.2850
Cropland : phanerophyte	-0.0530	0.108	-0.4890
Intermediate secondary : phanerophyte	0.0420	0.064	0.6540
Pasture : phanerophyte	-0.0620	0.028	-2.2340
Plantation forest : phanerophyte	-0.0150	0.041	-0.3540
Primary forest : phanerophyte	0.1060	0.021	4.9710
Primary non-forest : phanerophyte	0.0320	0.075	0.4270
unknown Secondary : phanerophyte	-0.1850	0.089	-2.0720
Urban : phanerophyte	-0.3180	0.107	-2.9650
Young secondary : phanerophyte	-0.1330	0.065	-2.0550
phanerophyte	0.0610	0.026	2.3780
phanerophyte : map	-0.2380	0.113	-2.0990
phanerophyte : map_var	-0.0430	0.065	-0.6620
phanerophyte : mat	0.2850	0.059	4.8270
phanerophyte : mat_var	0.0100	0.042	0.2380

Table A.9b. Abundance no species richness model output. Estimate refers to the scaled and logit transformed non-zero percent cover data. Colon indicates interaction between main effects. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects. Reference level is the weighted grand mean of the data (average (transformed) percent cover when continuous variables are zero). Model outputs have been rounded to three decimal place, and averages of values that differed at the third decimal place where obtained in order to recombine weighted effects coding outputs.

Model terms	Estimate	Std.Error	t value
Cropland	0.0910	0.167	0.5470
Intermediate secondary	0.0750	0.022	3.3435
Pasture	0.1350	0.015	8.8520
Plantation forest	-0.8340	0.099	-8.4520
Primary forest	0.0180	0.032	0.5490
Primary non-forest	0.0880	0.040	2.1880
unknown Secondary	-0.7020	0.087	-8.0860
Urban	0.1130	0.044	2.5510
Young secondary	-0.0340	0.047	-0.7130
Grand Mean	-0.0015	0.241	-0.0060
map	0.0290	0.114	0.2570
map_var	0.0980	0.103	0.9425
mat	-0.1030	0.087	-1.1840
mat_var	-0.1995	0.125	-1.5980

Table A.10. Model sample sizes. Table showing number of occurrence and abundance observations for each land use and life form combination.

Land use	Life form	Occurrence sample size	Abundance sample size
Primary forest	phanerophyte	119310	919
Primary forest	chamaephyte	5709	276
Primary forest	hemicryptophyte	18611	680
Primary forest	cryptophyte	5014	216
Primary forest	therophyte	12734	61
unknown Secondary	phanerophyte	40421	57
unknown Secondary	chamaephyte	4527	25

Table A.10. Model sample sizes. Table showing number of occurrence and abundance observations for each land use and life form combination.

Land use	Life form	Occurrence sample size	Abundance sample size
unknown Secondary	hemicryptophyte	16046	30
unknown Secondary	cryptophyte	4063	11
unknown Secondary	therophyte	7462	21
Mature secondary	phanerophyte	4048	0
Mature secondary	chamaephyte	2276	0
Mature secondary	hemicryptophyte	13710	0
Mature secondary	cryptophyte	5384	0
Mature secondary	therophyte	1899	0
Intermediate secondary	phanerophyte	32584	167
Intermediate secondary	chamaephyte	3992	477
Intermediate secondary	hemicryptophyte	22016	2043
Intermediate secondary	cryptophyte	5949	342
Intermediate secondary	therophyte	4557	218
Young secondary	phanerophyte	23884	133
Young secondary	chamaephyte	754	93
Young secondary	hemicryptophyte	5949	703
Young secondary	cryptophyte	1796	125
Young secondary	therophyte	2681	328
Plantation forest	phanerophyte	33439	381
Plantation forest	chamaephyte	2153	204
Plantation forest	hemicryptophyte	8514	834
Plantation forest	cryptophyte	2805	222
Plantation forest	therophyte	2469	157
Primary non-forest	phanerophyte	19282	93
Primary non-forest	chamaephyte	3205	29
Primary non-forest	hemicryptophyte	18723	248

Table A.10. Model sample sizes. Table showing number of occurrence and abundance observations for each land use and life form combination.

Land use	**Life form**	**Occurrence sample size**	**Abundance sample size**
Primary non-forest	cryptophyte	4946	72
Primary non-forest	therophyte	9273	60
Pasture	phanerophyte	24611	806
Pasture	chamaephyte	6655	1107
Pasture	hemicryptophyte	36782	5189
Pasture	cryptophyte	5418	856
Pasture	therophyte	11474	730
Cropland	phanerophyte	27479	154
Cropland	chamaephyte	3417	55
Cropland	hemicryptophyte	11692	297
Cropland	cryptophyte	3067	117
Cropland	therophyte	16230	225
Urban	phanerophyte	1471	48
Urban	chamaephyte	736	103
Urban	hemicryptophyte	3391	355
Urban	cryptophyte	933	63
Urban	therophyte	1155	54

Table A.11. Number of Studies and Sites per Region.

Region	Number of studies	Number of sites
Africa	11	909
Asia	14	564
Australia	2	362
Caribbean	1	4
Central America	3	197
Europe	25	949
North America	3	34
Oceania	1	32
Pacific	1	46
South America	12	733

Supplementary information A.2 References 1

Bibliography for citations in supplementary figure legends and for papers supplying data used in study.

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Appendix B | Supplementary information for Chapter 3

Table B.1.1. Occupied area maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
(Intercept)	0.3525184	-0.1589850	0.8961730	10389.153	0.1720
vel	0.5471102	0.3896560	0.7036136	10384.508	0.0001
hf	0.1803147	0.0418002	0.3196968	10000.000	0.0110
map	-0.0768148	-0.2427020	0.0960782	10000.000	0.3778
mat	-0.2486392	-0.4532904	-0.0593505	10000.000	0.0174
map_var	0.0926135	-0.0794699	0.2626542	10000.000	0.2958
mat_var	-0.2056737	-0.3798087	-0.0252105	10000.000	0.0230
vel:hf	0.0980821	-0.0402933	0.2400697	10000.000	0.1760
vel:map	0.0399130	-0.1634899	0.2420306	10000.000	0.7048
hf:map	-0.0810062	-0.2257266	0.0649022	10000.000	0.2770
vel:mat	-0.0122441	-0.1907142	0.1667061	9018.999	0.8896
hf:mat	-0.1704144	-0.3028721	-0.0304626	9677.081	0.0130
map:mat	0.0889257	-0.0632624	0.2304928	10422.859	0.2352
vel:map_var	0.0193702	-0.1825099	0.2047271	10000.000	0.8416
hf:map_var	0.0244392	-0.1759471	0.2234192	10000.000	0.8072
map:map_var	0.0623827	-0.1699377	0.2842470	10000.000	0.5966
mat:map_var	0.1645389	-0.0642650	0.3863844	10582.186	0.1438
vel:mat_var	-0.0253848	-0.2209006	0.1701239	10000.000	0.8062
hf:mat_var	-0.0325488	-0.2418866	0.1640134	10000.000	0.7550
map:mat_var	0.1306496	-0.0088776	0.2766090	10309.353	0.0732
mat:mat_var	0.2923933	0.0561212	0.5315782	9378.320	0.0142
map_var:mat_var	-0.0479277	-0.2807248	0.1813599	10650.777	0.6870
vel:hf:map	0.2066745	0.0282993	0.3870106	10000.000	0.0236

Table B.1.1. Occupied area maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
vel:hf:mat	0.1038116	-0.0478334	0.2604317	10000.000	0.1802
vel:map:mat	-0.0885295	-0.2741108	0.0853527	10000.000	0.3378
hf:map:mat	0.2145321	0.0810966	0.3543442	10000.000	0.0024
vel:hf:map_var	-0.1017372	-0.2790676	0.0761866	9660.728	0.2576
vel:map:map_var	0.0396536	-0.2351761	0.2918803	10000.000	0.7724
hf:map:map_var	-0.2110873	-0.4448830	0.0206560	10000.000	0.0750
vel:mat:map_var	0.1553800	-0.0369571	0.3632027	10000.000	0.1224
hf:mat:map_var	-0.0252821	-0.1855587	0.1358588	10000.000	0.7532
map:mat:map_var	0.1387748	-0.0249432	0.2975887	10000.000	0.0936
vel:hf:mat_var	0.1578596	0.0085421	0.3220434	10295.984	0.0484
vel:map:mat_var	0.0468097	-0.0571092	0.1584235	9068.130	0.3964
hf:map:mat_var	-0.0201390	-0.1629589	0.1116972	10000.000	0.7738
vel:mat:mat_var	-0.3418258	-0.5375509	-0.1520983	10000.000	0.0006
hf:mat:mat_var	0.1728976	0.0137222	0.3398590	10000.000	0.0398
map:mat:mat_var	0.1084418	-0.0773959	0.3078900	10000.000	0.2714
vel:map_var:mat_var	0.0415843	-0.2096884	0.2891480	10000.000	0.7444
hf:map_var:mat_var	-0.0286480	-0.2915841	0.2198831	10000.000	0.8304
map:map_var:mat_var	-0.1150039	-0.3229816	0.0849375	10000.000	0.2662
mat:map_var:mat_var	-0.0393292	-0.2158013	0.1429643	10000.000	0.6704
vel:hf:map:mat	-0.0599872	-0.2070709	0.0868088	10000.000	0.4100
vel:hf:map:map_var	0.0271785	-0.2056146	0.2705271	10896.808	0.8300
vel:hf:mat:map_var	-0.0818040	-0.2341568	0.0732927	10428.214	0.2978
vel:map:mat:map_var	0.1761566	-0.0160840	0.3722443	10000.000	0.0770
hf:map:mat:map_var	-0.0593667	-0.1846089	0.0648306	10000.000	0.3462

Table B.1.1. Occupied area maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
vel:hf:map:mat_var	0.0899048	-0.0307210	0.2125959	9709.451	0.1426
vel:hf:mat:mat_var	-0.0151971	-0.1298820	0.1003980	10000.000	0.7964
vel:map:mat:mat_var	-0.0605072	-0.1913756	0.0695751	10777.165	0.3682
hf:map:mat:mat_var	-0.0083896	-0.1242126	0.1071072	10000.000	0.8804
vel:hf:map_var:mat_var	0.0429776	-0.1321171	0.2204701	10000.000	0.6400
vel:map:map_var:mat_var	0.1053063	-0.0142276	0.2389030	10000.000	0.1028
hf:map:map_var:mat_var	-0.1252940	-0.3382669	0.0878317	9470.022	0.2430
vel:mat:map_var:mat_var	0.0151426	-0.1413198	0.1797760	10000.000	0.8432
hf:mat:map_var:mat_var	0.0048935	-0.1554628	0.1687000	10000.000	0.9492
map:mat:map_var:mat_var	0.0477999	-0.1011878	0.2009457	10000.000	0.5268
vel:hf:map:mat:map_var	-0.1370792	-0.2872394	0.0224197	10000.000	0.0848
vel:hf:map:mat:mat_var	0.0949489	0.0026198	0.1903267	10000.000	0.0486
vel:hf:map:map_var:mat_var	-0.0235750	-0.1392018	0.0934979	9430.434	0.6966
vel:hf:mat:map_var:mat_var	-0.0529037	-0.2001376	0.0916765	10000.000	0.4750
vel:map:mat:map_var:mat_var	-0.0283953	-0.1507714	0.0898696	10000.000	0.6528
hf:map:mat:map_var:mat_var	0.0442339	-0.0848265	0.1717600	9377.888	0.5000
vel:hf:map:mat:map_var:mat_var	-0.1149272	-0.2173125	-0.0096272	10310.912	0.0318

Table B.1.2. Geographic range size maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
(Intercept)	0.4329387	-0.1498795	1.0262619	10000.000	0.1492
vel	0.5466848	0.3894562	0.6935953	10000.000	0.0001

Table B.1.2. Geographic range size maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	**post.mean**	**l-95% CI**	**u-95% CI**	**eff.samp**	**pMCMC**
hf	0.1939563	0.0656023	0.3359243	10000.000	0.0062
map	-0.1014342	-0.2552334	0.0691132	10000.000	0.2280
mat	-0.3195503	-0.5087902	-0.1262531	10393.078	0.0006
map_var	0.1840736	0.0084468	0.3468573	10000.000	0.0324
mat_var	-0.2248886	-0.4011946	-0.0575941	10000.000	0.0124
vel:hf	0.0717744	-0.0633633	0.2123045	9911.390	0.3084
vel:map	0.1585037	-0.0296592	0.3671383	10000.000	0.1136
hf:map	-0.1424428	-0.2784748	-0.0013388	10000.000	0.0458
vel:mat	0.1749418	0.0042016	0.3535877	9632.622	0.0486
hf:mat	-0.1533010	-0.2845438	-0.0212703	10773.410	0.0226
map:mat	0.0826793	-0.0564378	0.2334351	10000.000	0.2664
vel:map_var	0.0573761	-0.1254143	0.2518226	10000.000	0.5512
hf:map_var	0.0139492	-0.1730852	0.2124104	10000.000	0.8810
map:map_var	0.1171052	-0.1016727	0.3370266	10000.000	0.2980
mat:map_var	0.3247644	0.1041341	0.5429430	10410.155	0.0044
vel:mat_var	0.1306712	-0.0620116	0.3205961	10000.000	0.1856
hf:mat_var	-0.1978158	-0.3952840	-0.0002299	10000.000	0.0472
map:mat_var	0.1440000	-0.0036704	0.2779207	10000.000	0.0452
mat:mat_var	0.4165580	0.1895174	0.6590787	10596.993	0.0006
map_var:mat_var	0.0394535	-0.1889445	0.2644462	10288.819	0.7430
vel:hf:map	0.2410451	0.0718217	0.4220621	10000.000	0.0092
vel:hf:mat	0.0409531	-0.1098089	0.1926201	9872.861	0.5974
vel:map:mat	-0.2730331	-0.4429992	-0.0892651	10000.000	0.0026
hf:map:mat	0.2572038	0.1213826	0.3869782	10000.000	0.0001

Table B.1.2. Geographic range size maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
vel:hf:map_var	0.0085820	-0.1620693	0.1878115	10708.037	0.9194
vel:map:map_var	0.2405482	-0.0340168	0.4858988	9444.300	0.0752
hf:map:map_var	-0.2569668	-0.4846623	-0.0365089	10000.000	0.0262
vel:mat:map_var	0.3116784	0.1276556	0.5160133	10000.000	0.0022
hf:mat:map_var	-0.0304789	-0.1857645	0.1272349	10000.000	0.6954
map:mat:map_var	0.1736751	0.0205794	0.3351416	10000.000	0.0328
vel:hf:mat_var	0.1350556	-0.0178549	0.2888039	10000.000	0.0842
vel:map:mat_var	-0.0252955	-0.1278789	0.0791467	10322.421	0.6366
hf:map:mat_var	0.0601434	-0.0803150	0.1865669	10000.000	0.3738
vel:mat:mat_var	-0.3378325	-0.5335318	-0.1625424	10000.000	0.0006
hf:mat:mat_var	0.2213873	0.0606843	0.3755849	10000.000	0.0068
map:mat:mat_var	0.0800832	-0.1101032	0.2667676	9174.698	0.4068
vel:map_var:mat_var	0.1566966	-0.0964465	0.3960212	10000.000	0.2134
hf:map_var:mat_var	-0.0744326	-0.3270056	0.1733270	10000.000	0.5648
map:map_var:mat_var	-0.1999633	-0.4023592	-0.0010998	10380.218	0.0494
mat:map_var:mat_var	0.0255952	-0.1604694	0.1904979	10000.000	0.7750
vel:hf:map:mat	-0.1341713	-0.2730128	0.0019861	10000.000	0.0564
vel:hf:map:map_var	0.1216219	-0.1024210	0.3534039	10000.000	0.3070
vel:hf:mat:map_var	-0.0830425	-0.2346443	0.0650972	10000.000	0.2858
vel:map:mat:map_var	0.2079538	0.0170349	0.3938101	9540.498	0.0316
hf:map:mat:map_var	-0.0594448	-0.1741069	0.0692420	10000.000	0.3352
vel:hf:map:mat_var	0.0457354	-0.0699902	0.1660061	10000.000	0.4560
vel:hf:mat:mat_var	-0.0128419	-0.1262404	0.0949646	10000.000	0.8172
vel:map:mat:mat_var	-0.0055576	-0.1364815	0.1219959	9222.781	0.9462

Table B.1.2. Geographic range size maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
hf:map:mat:mat_var	-0.0368312	-0.1504908	0.0743949	10342.161	0.5190
vel:hf:map_var:mat_var	0.0346653	-0.1368620	0.2133818	10000.000	0.7034
vel:map:map_var:mat_var	0.1014319	-0.0211330	0.2265967	10525.756	0.1090
hf:map:map_var:mat_var	-0.2079311	-0.4099678	0.0045365	10342.349	0.0516
vel:mat:map_var:mat_var	0.0878782	-0.0747136	0.2383161	9461.301	0.2752
hf:mat:map_var:mat_var	-0.0009347	-0.1621089	0.1532168	8908.911	0.9900
map:mat:map_var:mat_var	0.0993295	-0.0467580	0.2449857	11242.593	0.1822
vel:hf:map:mat:map_var	-0.1651817	-0.3230942	-0.0160912	10000.000	0.0362
vel:hf:map:mat:mat_var	0.1417388	0.0491907	0.2313315	10000.000	0.0022
vel:hf:map:map_var:mat_var	-0.0017654	-0.1149706	0.1159799	10000.000	0.9776
vel:hf:mat:map_var:mat_var	-0.0666520	-0.2190388	0.0732591	10000.000	0.3666
vel:map:mat:map_var:mat_var	-0.0349101	-0.1513557	0.0840044	9639.709	0.5704
hf:map:mat:map_var:mat_var	0.0592299	-0.0702156	0.1792535	10034.795	0.3476
vel:hf:map:mat:map_var:mat_var	-0.1446632	-0.2484102	-0.0479472	10000.000	0.0058

Table B.1.3. Patch size distribution maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
(Intercept)	-0.0217130	-0.3693351	0.3604670	10000.000	0.8302
vel	0.4297204	0.2245554	0.6181854	10000.000	0.0002
hf	0.0122223	-0.1645068	0.1885320	10000.000	0.8982
map	0.0836335	-0.1248808	0.3046448	9224.645	0.4434
mat	0.0592360	-0.1937802	0.3087066	9348.560	0.6394

Table B.1.3. Patch size distribution maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
map_var	-0.1019370	-0.3121409	0.1169288	10000.000	0.3732
mat_var	-0.1354662	-0.3582922	0.0888879	10000.000	0.2382
vel:hf	0.1828747	0.0084969	0.3584135	10000.000	0.0398
vel:map	-0.1719327	-0.4121471	0.1000228	10067.886	0.1830
hf:map	0.1457892	-0.0432008	0.3192420	10000.000	0.1152
vel:mat	-0.3733268	-0.6043909	-0.1476338	10000.000	0.0010
hf:mat	-0.1729495	-0.3350056	-0.0042820	10000.000	0.0434
map:mat	-0.0367010	-0.2265293	0.1550181	10000.000	0.6988
vel:map_var	0.0701135	-0.1812643	0.3065292	10000.000	0.5812
hf:map_var	-0.0512146	-0.2976391	0.2035054	10000.000	0.7004
map:map_var	-0.0454786	-0.3390402	0.2319565	10000.000	0.7570
mat:map_var	-0.2581470	-0.5431766	0.0263873	10000.000	0.0806
vel:mat_var	-0.2268010	-0.4847587	0.0068450	10000.000	0.0710
hf:mat_var	0.2765567	0.0221435	0.5330392	10000.000	0.0336
map:mat_var	0.0787300	-0.0978301	0.2682502	10000.000	0.3998
mat:mat_var	0.0060431	-0.3088458	0.2980993	10000.000	0.9654
map_var:mat_var	-0.2776844	-0.5740782	0.0269808	9654.647	0.0720
vel:hf:map	0.1625859	-0.0529910	0.3921248	10000.000	0.1532
vel:hf:mat	0.2309261	0.0402532	0.4239364	10000.000	0.0200
vel:map:mat	0.2647275	0.0396886	0.4973270	10000.000	0.0244
hf:map:mat	0.0341343	-0.1409875	0.2020599	10000.000	0.6928
vel:hf:map_var	-0.3541499	-0.5769613	-0.1377582	10795.978	0.0016
vel:map:map_var	-0.4473434	-0.7833274	-0.1054273	9627.816	0.0110
hf:map:map_var	0.0529035	-0.2483309	0.3376330	10000.000	0.7256

Table B.1.3. Patch size distribution maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
vel:mat:map_var	-0.3279835	-0.5897995	-0.0832236	10000.000	0.0130
hf:mat:map_var	0.0172139	-0.1915879	0.2172617	10000.000	0.8732
map:mat:map_var	0.0094853	-0.1961921	0.2164534	10000.000	0.9202
vel:hf:mat_var	0.2546104	0.0538247	0.4524093	10000.000	0.0122
vel:map:mat_var	0.2081629	0.0747912	0.3438407	10000.000	0.0026
hf:map:mat_var	-0.1573249	-0.3327787	0.0112439	10000.000	0.0726
vel:mat:mat_var	-0.3216405	-0.5592428	-0.0776007	10000.000	0.0070
hf:mat:mat_var	0.0453657	-0.1571789	0.2587241	10000.000	0.6636
map:mat:mat_var	0.1655087	-0.0889417	0.4082561	9612.414	0.1872
vel:map_var:mat_var	-0.1499563	-0.4525277	0.1804247	10000.000	0.3496
hf:map_var:mat_var	0.1129766	-0.2222662	0.4304830	10000.000	0.4972
map:map_var:mat_var	0.1028887	-0.1558646	0.3621174	9518.536	0.4444
mat:map_var:mat_var	-0.1025125	-0.3360321	0.1193731	10000.000	0.3868
vel:hf:map:mat	0.1604338	-0.0210691	0.3442093	9480.878	0.0844
vel:hf:map:map_var	-0.0941950	-0.3913286	0.1989348	10000.000	0.5352
vel:hf:mat:map_var	-0.0504412	-0.2514751	0.1399608	10000.000	0.6196
vel:map:mat:map_var	0.0653954	-0.1824609	0.3142600	10000.000	0.6068
hf:map:mat:map_var	-0.0995143	-0.2535202	0.0582534	10000.000	0.2182
vel:hf:map:mat_var	0.1268226	-0.0278496	0.2781558	9950.421	0.1090
vel:hf:mat:mat_var	-0.0280486	-0.1712934	0.1157690	10000.000	0.7048
vel:map:mat:mat_var	-0.1800948	-0.3433498	-0.0100437	8996.595	0.0360
hf:map:mat:mat_var	0.0554214	-0.0904824	0.1984221	10000.000	0.4546
vel:hf:map_var:mat_var	0.0667362	-0.1615271	0.2815089	10000.000	0.5598
vel:map:map_var:mat_var	0.1209582	-0.0362590	0.2857338	9282.197	0.1370

Table B.1.3. Patch size distribution maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
hf:map:map_var:mat_var	0.0716025	-0.1941217	0.3344718	10000.000	0.5994
vel:mat:map_var:mat_var	-0.1551791	-0.3565720	0.0501273	10000.000	0.1396
hf:mat:map_var:mat_var	-0.0546995	-0.2580629	0.1454834	10000.000	0.5968
map:mat:map_var:mat_var	-0.0843748	-0.2784400	0.0968091	10000.000	0.3732
vel:hf:map:mat:map_var	-0.0962743	-0.2909790	0.0918338	10000.000	0.3254
vel:hf:map:mat:mat_var	-0.0583938	-0.1820110	0.0542468	10000.000	0.3320
vel:hf:map:map_var:mat_var	-0.0592159	-0.2063181	0.0876743	10000.000	0.4402
vel:hf:mat:map_var:mat_var	-0.0553083	-0.2365901	0.1275289	10000.000	0.5508
vel:map:mat:map_var:mat_var	-0.0313700	-0.1892248	0.1186064	10165.279	0.6896
hf:map:mat:map_var:mat_var	-0.0113646	-0.1739214	0.1456082	10000.000	0.8936
vel:hf:map:mat:map_var:mat_var	-0.0068924	-0.1362950	0.1234249	10000.000	0.9176

Table B.1.4. Geographic range filling maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
(Intercept)	-0.4798255	-1.0700790	0.1235414	10443.801	0.1014
vel	-0.2259723	-0.4303686	-0.0346323	10000.000	0.0268
hf	-0.1866199	-0.3650706	-0.0055667	10000.000	0.0390
map	0.1949022	-0.0235233	0.4052944	10000.000	0.0756
mat	0.4705232	0.2169297	0.7201417	9576.621	0.0006
map_var	-0.2918623	-0.5147233	-0.0796247	10627.762	0.0088
mat_var	0.1743523	-0.0528516	0.4041416	10000.000	0.1368
vel:hf	0.0939057	-0.0841393	0.2742958	10000.000	0.3010

Table B.1.4. Geographic range filling maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	**post.mean**	**l-95% CI**	**u-95% CI**	**eff.samp**	**pMCMC**
vel:map	-0.2884777	-0.5374206	-0.0261771	10000.000	0.0284
hf:map	0.2732771	0.0942600	0.4556747	10000.000	0.0030
vel:mat	-0.4739276	-0.6912000	-0.2443626	10000.000	0.0001
hf:mat	0.0086981	-0.1589215	0.1855014	10000.000	0.9162
map:mat	-0.0893586	-0.2819853	0.0867018	10000.000	0.3582
vel:map_var	-0.0861629	-0.3380803	0.1530208	10000.000	0.5046
hf:map_var	0.0345281	-0.2238674	0.2856261	10000.000	0.7962
map:map_var	-0.1296544	-0.4181045	0.1478431	10000.000	0.3802
mat:map_var	-0.4899319	-0.7816148	-0.2117552	10000.000	0.0010
vel:mat_var	-0.3373110	-0.5760775	-0.0787637	10000.000	0.0070
hf:mat_var	0.4103663	0.1592600	0.6806067	10301.317	0.0022
map:mat_var	-0.0889733	-0.2662128	0.0970565	10000.000	0.3440
mat:mat_var	-0.5057754	-0.8187636	-0.2124829	10795.028	0.0004
map_var:mat_var	-0.0957696	-0.3933883	0.2000517	9965.628	0.5242
vel:hf:map	-0.1539703	-0.3778743	0.0684577	10383.216	0.1756
vel:hf:mat	0.1554027	-0.0359282	0.3534966	10000.000	0.1200
vel:map:mat	0.5699807	0.3373232	0.7887400	9673.387	0.0002
hf:map:mat	-0.2260061	-0.4024587	-0.0554553	10000.000	0.0114
vel:hf:map_var	-0.2786045	-0.4940981	-0.0585569	10000.000	0.0116
vel:map:map_var	-0.6416035	-0.9659101	-0.2958254	10000.000	0.0006
hf:map:map_var	0.2944341	0.0031775	0.5846155	10000.000	0.0470
vel:mat:map_var	-0.4987220	-0.7386467	-0.2402094	10259.396	0.0001
hf:mat:map_var	0.0061523	-0.2069108	0.2024949	10000.000	0.9580
map:mat:map_var	-0.1351531	-0.3415059	0.0705236	10289.847	0.1924

Table B.1.4. Geographic range filling maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
vel:hf:mat_var	0.0394006	-0.1590490	0.2325143	10000.000	0.7030
vel:map:mat_var	0.1715165	0.0327253	0.3042307	10000.000	0.0146
hf:map:mat_var	-0.1768838	-0.3553117	-0.0035904	10000.000	0.0484
vel:mat:mat_var	0.1576201	-0.0774034	0.4074286	10000.000	0.2060
hf:mat:mat_var	-0.1906255	-0.4084861	0.0085016	10000.000	0.0722
map:mat:mat_var	0.0200888	-0.2422258	0.2468529	9634.998	0.8730
vel:map_var:mat_var	-0.4020337	-0.7097524	-0.0845901	10000.000	0.0108
hf:map_var:mat_var	0.1777314	-0.1525327	0.4935975	10000.000	0.2876
map:map_var:mat_var	0.3247601	0.0593369	0.5835956	10000.000	0.0148
mat:map_var:mat_var	-0.1870573	-0.4256450	0.0316056	10000.000	0.1054
vel:hf:map:mat	0.2797926	0.1023780	0.4685249	10000.000	0.0036
vel:hf:map:map_var	-0.2504022	-0.5446719	0.0584735	10000.000	0.1108
vel:hf:mat:map_var	0.0179079	-0.1849102	0.2078183	10000.000	0.8610
vel:map:mat:map_var	-0.1174518	-0.3613418	0.1384413	10000.000	0.3540
hf:map:mat:map_var	-0.0151639	-0.1733057	0.1383056	10000.000	0.8520
vel:hf:map:mat_var	0.0813372	-0.0742814	0.2335699	10000.000	0.3094
vel:hf:mat:mat_var	0.0076361	-0.1484897	0.1443628	10000.000	0.9168
vel:map:mat:mat_var	-0.1241127	-0.2948116	0.0380907	10000.000	0.1496
hf:map:mat:mat_var	0.1116581	-0.0355772	0.2562337	10000.000	0.1336
vel:hf:map_var:mat_var	-0.0159733	-0.2352596	0.2180242	10636.214	0.8880
vel:map:map_var:mat_var	-0.0318745	-0.1878258	0.1279493	8698.289	0.7050
hf:map:map_var:mat_var	0.3244132	0.0566252	0.5828957	9679.013	0.0148
vel:mat:map_var:mat_var	-0.1399225	-0.3560761	0.0553465	9898.658	0.1798
hf:mat:map_var:mat_var	-0.0198222	-0.2177399	0.1864085	10000.000	0.8442

Table B.1.4. Geographic range filling maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
map:mat:map_var:mat_var	-0.1753262	-0.3672770	0.0106730	10000.000	0.0694
vel:hf:map:mat:map_var	0.1202308	-0.0706761	0.3185796	10000.000	0.2238
vel:hf:map:mat:mat_var	-0.1848873	-0.2994213	-0.0649334	9814.229	0.0020
vel:hf:map:map_var:mat_var	-0.0570173	-0.2008310	0.0946677	10356.239	0.4642
vel:hf:mat:map_var:mat_var	0.0698018	-0.1163529	0.2532963	10000.000	0.4582
vel:map:mat:map_var:mat_var	0.0620893	-0.0937789	0.2127348	10000.000	0.4290
hf:map:mat:map_var:mat_var	-0.0872146	-0.2488393	0.0695066	10430.829	0.2884
vel:hf:map:mat:map_var:mat_var	0.1609351	0.0317096	0.2924094	9113.234	0.0150

Table B.1.5. Patch shape complexity maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
(Intercept)	0.1689058	-0.1333509	0.5279487	10000.000	0.2556
vel	0.1979006	-0.0362241	0.4181518	10000.000	0.0900
hf	-0.0391084	-0.2484761	0.1697609	9624.637	0.7194
map	0.0972969	-0.1553030	0.3496721	10000.000	0.4460
mat	0.2020282	-0.0980962	0.4928779	10000.000	0.1760
map_var	0.0695984	-0.1810870	0.3330282	10000.000	0.5896
mat_var	0.0288593	-0.2318690	0.2959389	10000.000	0.8262
vel:hf	-0.0208793	-0.2446424	0.1740631	10000.000	0.8488
vel:map	0.0178303	-0.2712608	0.3202228	10000.000	0.9006
hf:map	0.1343088	-0.0799977	0.3461840	10000.000	0.2138
vel:mat	-0.0767943	-0.3401220	0.1920123	10000.000	0.5778

Table B.1.5. Patch shape complexity maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
hf:mat	-0.0554231	-0.2627053	0.1432990	10000.000	0.5954
map:mat	0.0765343	-0.1444222	0.2970007	10000.000	0.5020
vel:map_var	0.0729699	-0.2122471	0.3522989	10000.000	0.6148
hf:map_var	0.0969789	-0.1917389	0.4030276	10000.000	0.5278
map:map_var	-0.1904174	-0.5121543	0.1556730	10000.000	0.2694
mat:map_var	-0.3101987	-0.6466594	0.0168997	10000.000	0.0652
vel:mat_var	-0.2751886	-0.5659525	0.0043516	10348.410	0.0568
hf:mat_var	0.2750276	-0.0321484	0.5695420	10000.000	0.0734
map:mat_var	-0.0383459	-0.2480581	0.1749505	10000.000	0.7214
mat:mat_var	-0.0686043	-0.4068629	0.2936554	10000.000	0.7030
map_var:mat_var	-0.1525861	-0.5107887	0.1816024	10000.000	0.3834
vel:hf:map	0.2593073	-0.0018637	0.5251131	10000.000	0.0528
vel:hf:mat	0.1719600	-0.0553951	0.3955752	10351.739	0.1382
vel:map:mat	0.1062339	-0.1540106	0.3678384	9578.487	0.4316
hf:map:mat	0.0556207	-0.1491165	0.2600470	10396.801	0.5984
vel:hf:map_var	-0.2014290	-0.4754941	0.0457000	10000.000	0.1278
vel:map:map_var	-0.1370763	-0.5240680	0.2650240	10000.000	0.5014
hf:map:map_var	0.2217069	-0.1134470	0.5669148	9604.014	0.2016
vel:mat:map_var	-0.1683196	-0.4597628	0.1197338	10000.000	0.2564
hf:mat:map_var	0.0506347	-0.1842726	0.2960284	9096.814	0.6850
map:mat:map_var	-0.0042439	-0.2442150	0.2440845	9759.323	0.9682
vel:hf:mat_var	0.1711353	-0.0567908	0.4154257	10000.000	0.1478
vel:map:mat_var	0.0804620	-0.0732624	0.2432640	10000.000	0.3268
hf:map:mat_var	-0.0575564	-0.2607171	0.1414023	9439.077	0.5782

Table B.1.5. Patch shape complexity maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
vel:mat:mat_var	-0.0646422	-0.3556234	0.2128958	10000.000	0.6662
hf:mat:mat_var	-0.0610388	-0.3002276	0.1847870	10000.000	0.6224
map:mat:mat_var	0.3997057	0.1165800	0.6867931	10000.000	0.0070
vel:map_var:mat_var	-0.0400971	-0.4147435	0.3147516	10000.000	0.8376
hf:map_var:mat_var	0.4412853	0.0667529	0.8210962	10000.000	0.0218
map:map_var:mat_var	-0.1509328	-0.4531645	0.1437499	10000.000	0.3240
mat:map_var:mat_var	0.0660719	-0.1928809	0.3362446	9665.960	0.6234
vel:hf:map:mat	0.0217731	-0.1955986	0.2336839	10828.735	0.8458
vel:hf:map:map_var	0.3552775	0.0058253	0.7004962	10000.000	0.0446
vel:hf:mat:map_var	0.1938193	-0.0322897	0.4266932	10000.000	0.1038
vel:map:mat:map_var	0.0105926	-0.2902179	0.2873030	10000.000	0.9298
hf:map:mat:map_var	-0.1411884	-0.3259688	0.0384576	10000.000	0.1276
vel:hf:map:mat_var	-0.1400235	-0.3271282	0.0353409	10000.000	0.1360
vel:hf:mat:mat_var	0.0781706	-0.0845278	0.2552973	10000.000	0.3676
vel:map:mat:mat_var	-0.1562076	-0.3573036	0.0376093	10000.000	0.1234
hf:map:mat:mat_var	0.0479033	-0.1293718	0.2114754	12319.128	0.5668
vel:hf:map_var:mat_var	-0.0471079	-0.3251100	0.2095918	10000.000	0.7274
vel:map:map_var:mat_var	0.1747484	-0.0180147	0.3555036	10000.000	0.0688
hf:map:map_var:mat_var	-0.1337646	-0.4574935	0.1637584	10000.000	0.3966
vel:mat:map_var:mat_var	0.0356590	-0.2052847	0.2791346	9788.282	0.7636
hf:mat:map_var:mat_var	-0.2966082	-0.5301662	-0.0590095	9265.910	0.0160
map:mat:map_var:mat_var	0.0353470	-0.1742153	0.2592193	10000.000	0.7460
vel:hf:map:mat:map_var	-0.1437938	-0.3771061	0.0758364	10000.000	0.2126
vel:hf:map:mat:mat_var	-0.0473634	-0.1856859	0.0917470	10000.000	0.4976

Table B.1.5. Patch shape complexity maximal model outputs. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. Post.mean = posterior estimate mean, l-95% CI = lower 95% credibility interval, u-95% CI = upper 95% credibility interval, eff.samp = effective sample size, pMCMC = Bayesian p-values. Colon indicates interaction between main effects. Terms in blue have significant positive effects, terms in red have significant negative effects.

Model terms	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
vel:hf:map:map_var:mat_var	-0.0072096	-0.1872252	0.1641469	10000.000	0.9392
vel:hf:mat:map_var:mat_var	0.0266046	-0.1765870	0.2545212	10000.000	0.8042
vel:map:mat:map_var:mat_var	0.0112054	-0.1668555	0.1910464	10716.011	0.9038
hf:map:mat:map_var:mat_var	-0.0039979	-0.1845999	0.1938306	10399.666	0.9766
vel:hf:map:mat:map_var:mat_var	0.0972256	-0.0557454	0.2444319	10000.000	0.2000

Table B.2 Temperature variability. Summary statistics for mean annual temperature variation in degrees Celsius in Europe (extent: -33,67,30, 82 arc degrees) compared to Tropical latitudes (extent: -180,180,-30, 30 arc degrees). Calculated from 30 second resolution (179pprox.. 1km^2) maps from WorldClim version 2.1 (Fick & Hijmans, 2017).

Statistic	**Europe**	**Tropics**
Mean	9.22	3.26
Range	0 – 15.47	0 – 9.63
Standard deviation	2.48	2.42

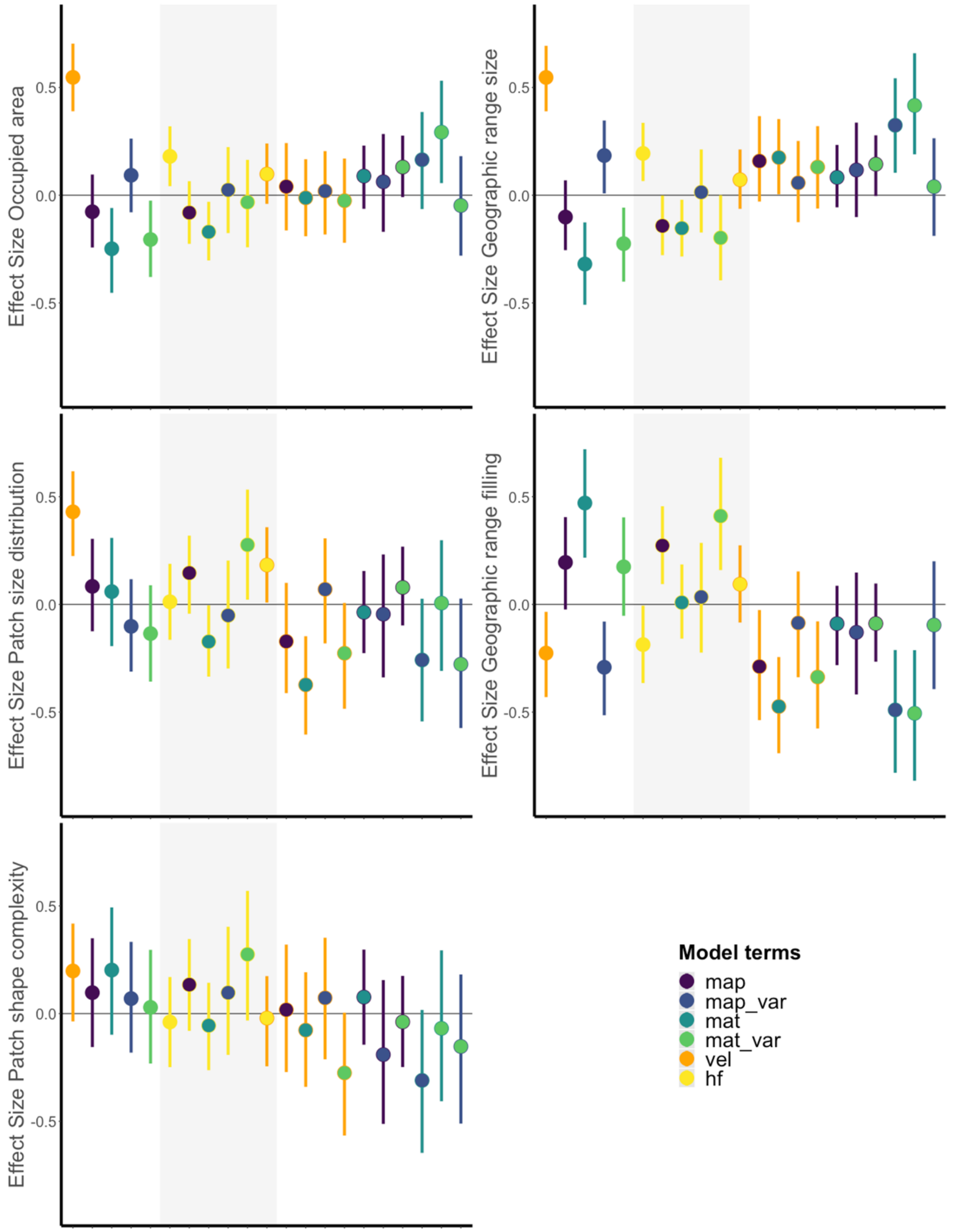

Figure B.1. Effect sizes for main effects and two way interactions from maximal models showing the strength of the correlation between Climate and Human footprint, and Range Metrics. Solid circles represent the slope of relationship, i.e. change in range metric associated with 1 SD change in climate or human footprint value. Vertical lines represent 95% credibility interval. Hf = human footprint, map(_var) = mean annual precipitation (variation), mat(_var) = mean annual precipitation (variation), vel = past climate change velocity. The colour of points and vertical lines refers to the terms in the model. If a point and vertical line are the same colour, this represents a main effect. If point and vertical line are different colours, this represents the interaction between two main effects as per the legend. Light grey vertical bar highlights terms associated with human footprint. The geographic range fractality model was not included as it was not deemed reliable based on diagnostic tests.

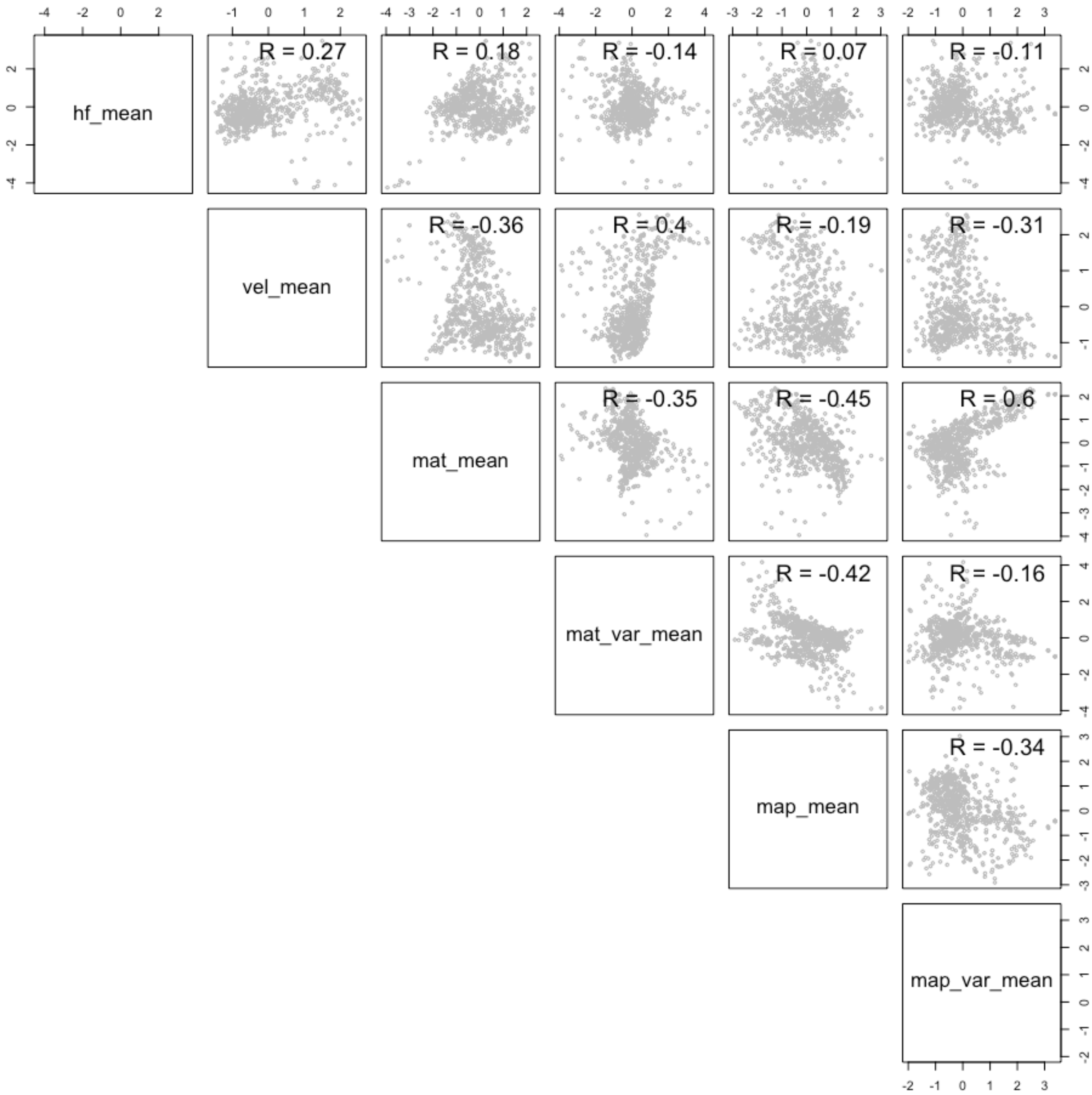

Figure B.2a. Correlations between explanatory variables.

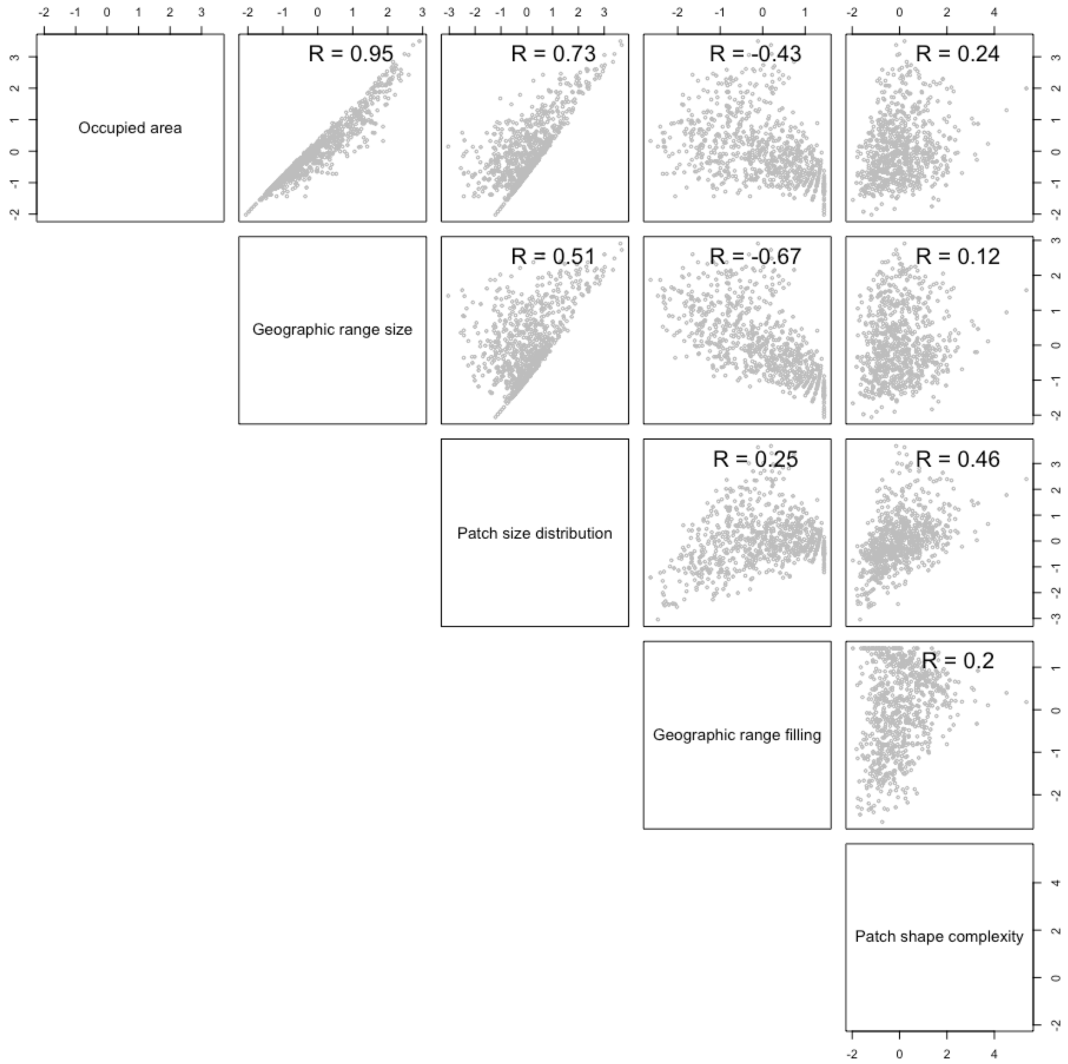

Figure B.2b. Correlations between range metrics.

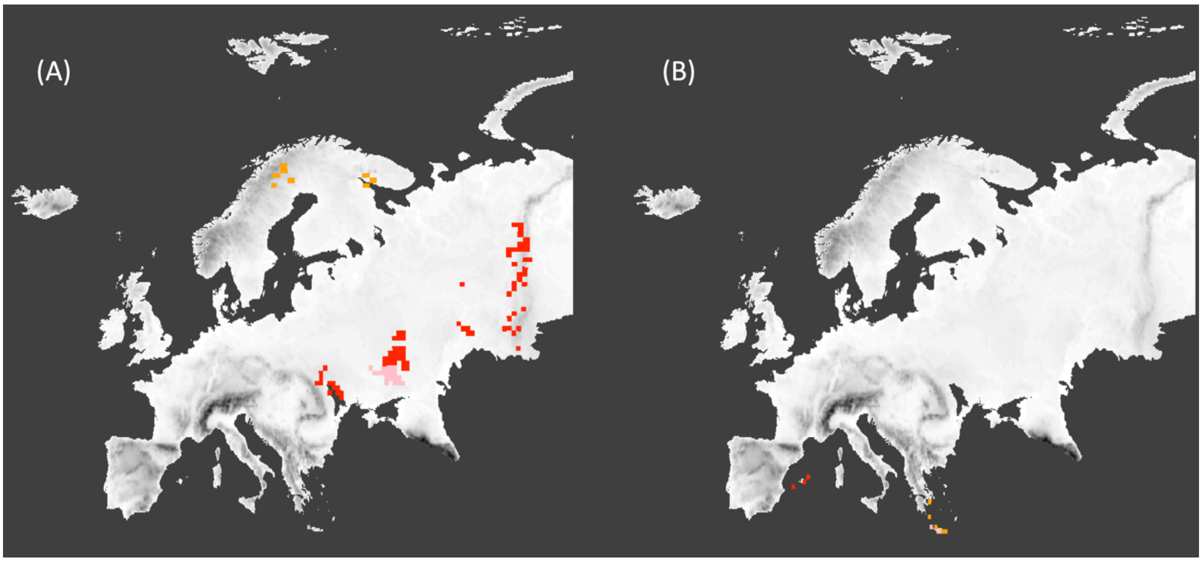

Figure B.3. Maps of example species. (A) Occurrence of *Schivereckia podolica, Dianthus pseudoversicolor* and *Potentilla arcticai* in red, pink and orange respectively. (B) Occurrence of *Silene mollissimais, Silene sieberi* and *Papaver purpureomarginatum* in red, pink and orange respectively. Gradient from light to dark colour on land mass represents increasing elevation.

Appendix C | Supplementary information for Chapter 4

Table C.1.1. PC1 model outputs for communities at the level of haul. Effects of SST, depth and fishing pressure and their two-way interactions on community weighted mean of PC1 (representing pace of life Life history axis). Estimate = model estimate, std.error = standard error, statistic = z value. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Colon indicates interaction between main effects. All continuous covariates are average values at resolution of community. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects.

term	**estimate**	**std.error**	**statistic**	**p.value**
SNSP	0.0007324	0.0094492	0.0775052	0.9382216
SNWI	-0.0107423	0.0136006	-0.7898359	0.4296236
sst_var	-0.0425324	0.0096018	-4.4296280	0.0000094
Depth	0.0095239	0.0083311	1.1431770	0.2529651
fp	-0.0060697	0.0048709	-1.2461291	0.2127170
Year	0.0420576	0.0042265	9.9509659	0.0000000
Quarter	-0.0201404	0.0048378	-4.1631237	0.0000314
SNSP:SNWI	-0.0210114	0.0047969	-4.3801617	0.0000119
SNSP:sst_var	-0.0160950	0.0074910	-2.1485891	0.0316670
SNSP:Depth	0.0297707	0.0094783	3.1409339	0.0016841
SNSP:fp	0.0001087	0.0073920	0.0147021	0.9882699
SNWI:sst_var	0.0371037	0.0094627	3.9210328	0.0000882
SNWI:Depth	0.0262821	0.0091794	2.8631562	0.0041944
SNWI:fp	0.0011311	0.0077543	0.1458626	0.8840298
sst_var:Depth	-0.0033670	0.0058465	-0.5758934	0.5646872
sst_var:fp	-0.0182651	0.0065988	-2.7679271	0.0056414
Depth:fp	-0.0192486	0.0060419	-3.1858406	0.0014433

Table C.1.2. PC1 model outputs for communities in grid cells aggregated by a factor of 5. Effects of SST, depth and fishing pressure and their two-way interactions on community weighted mean of PC1 (representing pace of life Life history axis). Estimate = model estimate, std.error = standard error, statistic = z value. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Colon indicates interaction between main effects. All continuous covariates are average values at resolution of community. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects.

term	estimate	std.error	statistic	p.value
SNSP	-0.0533713	0.0113090	-4.7193690	0.0000024
SNWI	0.0667113	0.0154716	4.3118532	0.0000162
sst_var	-0.0005028	0.0103425	-0.0486143	0.9612267
Depth	0.0237507	0.0085099	2.7909632	0.0052551
fp	-0.0280859	0.0051505	-5.4530106	0.0000000
Year	0.0411676	0.0051946	7.9250499	0.0000000
Quarter	-0.0159428	0.0067601	-2.3583815	0.0183548
SNSP:SNWI	-0.0256168	0.0056062	-4.5693993	0.0000049
SNSP:sst_var	0.0033227	0.0092518	0.3591360	0.7194933
SNSP:Depth	0.0523198	0.0112566	4.6479150	0.0000034
SNSP:fp	0.0009095	0.0095725	0.0950155	0.9243025
SNWI:sst_var	0.0053211	0.0117096	0.4544185	0.6495277
SNWI:Depth	-0.0189191	0.0109038	-1.7350852	0.0827257
SNWI:fp	0.0060738	0.0097342	0.6239626	0.5326521
sst_var:Depth	-0.0133695	0.0065347	-2.0459168	0.0407646
sst_var:fp	-0.0163752	0.0081397	-2.0117725	0.0442439
Depth:fp	-0.0290416	0.0071557	-4.0585104	0.0000494

Table C.1.3. PC1 model outputs for communities in grid cells aggregated by a factor of 10. Effects of SST, depth and fishing pressure and their two-way interactions on community weighted mean of PC1 (representing pace of life Life history axis). Estimate = model estimate, std.error = standard error, statistic = z value. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Colon indicates interaction between main effects. All continuous covariates are average values at resolution of community. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects.

term	estimate	std.error	statistic	p.value
SNSP	-0.0695746	0.0138317	-5.0300977	0.0000005
SNWI	0.1255570	0.0161860	7.7571378	0.0000000
sst_var	0.0418785	0.0115374	3.6298108	0.0002836
Depth	-0.0179588	0.0101582	-1.7679209	0.0770741
fp	-0.0235350	0.0067840	-3.4692108	0.0005220
Year	0.0312068	0.0060148	5.1883812	0.0000002
Quarter	-0.0322285	0.0074998	-4.2972424	0.0000173
SNSP:SNWI	-0.0396525	0.0067795	-5.8488792	0.0000000
SNSP:sst_var	-0.0161051	0.0118872	-1.3548262	0.1754729
SNSP:Depth	0.0635711	0.0148833	4.2713062	0.0000194
SNSP:fp	0.0007040	0.0137875	0.0510593	0.9592783
SNWI:sst_var	0.0044732	0.0152973	0.2924187	0.7699665
SNWI:Depth	-0.0008380	0.0142747	-0.0587027	0.9531889
SNWI:fp	-0.0036054	0.0139600	-0.2582674	0.7962006
sst_var:Depth	-0.0234171	0.0082640	-2.8336133	0.0046025
sst_var:fp	-0.0197432	0.0111656	-1.7682109	0.0770256
Depth:fp	-0.0387937	0.0100905	-3.8445902	0.0001208

Table C.1.4. PC1 model outputs for communities in grid cells aggregated by a factor of 20. Effects of SST, depth and fishing pressure and their two-way interactions on community weighted mean of PC1 (representing pace of life Life history axis). Estimate = model estimate, std.error = standard error, statistic = z value. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Colon indicates interaction between main effects. All continuous covariates are average values at resolution of community. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects.

term	estimate	std.error	statistic	p.value
SNSP	-0.0601258	0.0196879	-3.0539406	0.0022586
SNWI	0.1274055	0.0228824	5.5678427	0.0000000
sst_var	0.0286471	0.0167988	1.7053037	0.0881378
Depth	-0.0242884	0.0150421	-1.6147008	0.1063755
fp	-0.0270915	0.0108553	-2.4957004	0.0125709
Year	0.0249878	0.0080118	3.1188727	0.0018154
Quarter	-0.0231069	0.0094353	-2.4489931	0.0143256
SNSP:SNWI	-0.0590012	0.0099241	-5.9452708	0.0000000
SNSP:sst_var	-0.0402375	0.0166231	-2.4205779	0.0154959
SNSP:Depth	0.0246220	0.0206937	1.1898260	0.2341148
SNSP:fp	0.0189352	0.0236724	0.7998839	0.4237780
SNWI:sst_var	0.0386598	0.0222722	1.7357831	0.0826022
SNWI:Depth	0.0539850	0.0212198	2.5440875	0.0109564
SNWI:fp	-0.0290353	0.0238377	-1.2180394	0.2232090
sst_var:Depth	-0.0254691	0.0110623	-2.3023420	0.0213159
sst_var:fp	-0.0292567	0.0185681	-1.5756421	0.1151083
Depth:fp	-0.0321438	0.0180928	-1.7766100	0.0756324

Table C.1.5. PC1 model outputs for communities in grid cells aggregated by a factor of 50. Effects of SST, depth and fishing pressure and their two-way interactions on community weighted mean of PC1 (representing pace of life Life history axis). Estimate = model estimate, std.error = standard error, statistic = z value. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Colon indicates interaction between main effects. All continuous covariates are average values at resolution of community. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects.

term	estimate	std.error	statistic	p.value
SNSP	-0.0243659	0.0368433	-0.6613398	0.5083944
SNWI	0.1307355	0.0429559	3.0434843	0.0023386
sst_var	0.0773175	0.0344125	2.2467853	0.0246537
Depth	-0.0126957	0.0338461	-0.3751014	0.7075851
fp	0.0015894	0.0290795	0.0546575	0.9564114
Year	0.0300321	0.0139657	2.1504241	0.0315217
Quarter	0.0214776	0.0123874	1.7338257	0.0829490
SNSP:SNWI	-0.0830971	0.0189628	-4.3821027	0.0000118
SNSP:sst_var	0.0140268	0.0361875	0.3876151	0.6983009
SNSP:Depth	0.1631992	0.0497998	3.2771086	0.0010488
SNSP:fp	0.0973217	0.0552021	1.7630091	0.0778990
SNWI:sst_var	-0.0446378	0.0499806	-0.8931024	0.3718023
SNWI:Depth	-0.0557731	0.0505107	-1.1041845	0.2695131
SNWI:fp	-0.1365717	0.0550877	-2.4791691	0.0131689
sst_var:Depth	-0.0352358	0.0232346	-1.5165232	0.1293871
sst_var:fp	0.0164303	0.0491514	0.3342784	0.7381695
Depth:fp	0.0635962	0.0523807	1.2141156	0.2247036

Table C.2.1. PC2 model outputs for communities at the level of haul. Effects of SST, depth and fishing pressure on community weighted mean of PC2 (representing reproductive investment life history axis) at each community resolution. Estimate = model estimate, std.error = standard error, statistic = z value. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Colon indicates interaction between main effects. All continuous covariates are average values at resolution of community. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects.

term	estimate	std.error	statistic	p.value
SNSP	0.0001373	0.0108551	0.0126468	0.9899096
SNWI	0.0764011	0.0153892	4.9645871	0.0000007
sst_var	0.0208444	0.0108799	1.9158612	0.0553828
Depth	-0.0265372	0.0096984	-2.7362503	0.0062144
fp	0.0133763	0.0056348	2.3738684	0.0176028
Year	0.0112438	0.0048413	2.3224926	0.0202064
Quarter	-0.0085537	0.0055359	-1.5451276	0.1223154
SNSP:SNWI	-0.0175973	0.0054774	-3.2127073	0.0013149
SNSP:sst_var	0.0079565	0.0086250	0.9224856	0.3562754
SNSP:Depth	0.0409424	0.0109252	3.7475187	0.0001786
SNSP:fp	0.0080377	0.0085269	0.9426265	0.3458720
SNWI:sst_var	-0.0097128	0.0108858	-0.8922395	0.3722646
SNWI:Depth	-0.0288794	0.0105906	-2.7268895	0.0063934
SNWI:fp	-0.0029816	0.0089478	-0.3332261	0.7389636
sst_var:Depth	-0.0275306	0.0067382	-4.0857514	0.0000439
sst_var:fp	-0.0072594	0.0076064	-0.9543739	0.3398944
Depth:fp	-0.0141658	0.0069798	-2.0295430	0.0424030

Table C.2.2. PC2 model outputs for communities in grid cells aggregated by a factor of 5. Effects of SST, depth and fishing pressure on community weighted mean of PC2 (representing reproductive investment life history axis) at each community resolution. Estimate = model estimate, std.error = standard error, statistic = z value. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Colon indicates interaction between main effects. All continuous covariates are average values at resolution of community. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects.

term	estimate	std.error	statistic	p.value
SNSP	-0.0055379	0.0124951	-0.4432031	0.6576188
SNWI	0.0834603	0.0166906	5.0004278	0.0000006
sst_var	0.0141789	0.0112014	1.2658235	0.2055763
Depth	-0.0098403	0.0094585	-1.0403722	0.2981670
fp	0.0305479	0.0056988	5.3603712	0.0000001
Year	0.0027022	0.0056641	0.4770733	0.6333099
Quarter	-0.0019417	0.0073241	-0.2651172	0.7909192
SNSP:SNWI	-0.0177018	0.0060891	-2.9071236	0.0036477
SNSP:sst_var	0.0293638	0.0101959	2.8799543	0.0039773
SNSP:Depth	0.0627299	0.0123904	5.0627924	0.0000004
SNSP:fp	-0.0006867	0.0105621	-0.0650141	0.9481628
SNWI:sst_var	-0.0227623	0.0128955	-1.7651371	0.0775407
SNWI:Depth	-0.0449526	0.0120338	-3.7355240	0.0001873
SNWI:fp	-0.0004013	0.0107408	-0.0373613	0.9701969
sst_var:Depth	-0.0205521	0.0072033	-2.8531346	0.0043290
sst_var:fp	-0.0151881	0.0089791	-1.6915000	0.0907414
Depth:fp	-0.0209898	0.0079019	-2.6562768	0.0079009

Table C.2.3. PC2 model outputs for communities in grid cells aggregated by a factor of 10. Effects of SST, depth and fishing pressure on community weighted mean of PC2 (representing reproductive investment life history axis) at each community resolution. Estimate = model estimate, std.error = standard error, statistic = z value. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Colon indicates interaction between main effects. All continuous covariates are average values at resolution of community. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects.

term	estimate	std.error	statistic	p.value
SNSP	0.0084019	0.0147478	0.5697041	0.5688784
SNWI	0.0566111	0.0172467	3.2824271	0.0010292
sst_var	-0.0064653	0.0123073	-0.5253221	0.5993593
Depth	-0.0087860	0.0108480	-0.8099216	0.4179853
fp	0.0365941	0.0072367	5.0567351	0.0000004
Year	0.0013503	0.0064153	0.2104777	0.8332948
Quarter	-0.0089892	0.0078847	-1.1400841	0.2542513
SNSP:SNWI	-0.0228418	0.0072175	-3.1647806	0.0015520
SNSP:sst_var	0.0139336	0.0126799	1.0988762	0.2718221
SNSP:Depth	0.0616479	0.0158743	3.8835036	0.0001030
SNSP:fp	-0.0330013	0.0147079	-2.2437748	0.0248469
SNWI:sst_var	-0.0160215	0.0163171	-0.9818864	0.3261558
SNWI:Depth	-0.0338404	0.0152270	-2.2223881	0.0262571
SNWI:fp	0.0360324	0.0148894	2.4200045	0.0155203
sst_var:Depth	-0.0088080	0.0088149	-0.9992129	0.3176916
sst_var:fp	-0.0121624	0.0119089	-1.0212869	0.3071185
Depth:fp	-0.0354012	0.0107633	-3.2890758	0.0010052

Table C.2.4. PC2 model outputs for communities in grid cells aggregated by a factor of 20. Effects of SST, depth and fishing pressure on community weighted mean of PC2 (representing reproductive investment life history axis) at each community resolution. Estimate = model estimate, std.error = standard error, statistic = z value. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Colon indicates interaction between main effects. All continuous covariates are average values at resolution of community. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects.

term	**estimate**	**std.error**	**statistic**	**p.value**
SNSP	0.0038246	0.0200752	0.1905157	0.8489050
SNWI	0.0595917	0.0232853	2.5591969	0.0104914
sst_var	-0.0125478	0.0171393	-0.7321045	0.4641048
Depth	0.0028466	0.0153946	0.1849068	0.8533021
fp	0.0571214	0.0110786	5.1560062	0.0000003
Year	0.0062909	0.0081760	0.7694307	0.4416377
Quarter	-0.0054144	0.0093863	-0.5768401	0.5640475
SNSP:SNWI	-0.0356180	0.0100722	-3.5362806	0.0004058
SNSP:sst_var	0.0147647	0.0169659	0.8702583	0.3841593
SNSP:Depth	0.0682834	0.0211193	3.2332240	0.0012240
SNSP:fp	-0.0462787	0.0241639	-1.9152042	0.0554665
SNWI:sst_var	-0.0140160	0.0227243	-0.6167839	0.5373773
SNWI:Depth	-0.0135312	0.0216582	-0.6247600	0.5321286
SNWI:fp	0.0519799	0.0243300	2.1364516	0.0326426
sst_var:Depth	0.0033536	0.0112974	0.2968456	0.7665844
sst_var:fp	0.0011796	0.0189575	0.0622223	0.9503858
Depth:fp	-0.0402350	0.0184662	-2.1788451	0.0293432

Table C.2.5. PC2 model outputs for communities in grid cells aggregated by a factor of 50. Effects of SST, depth and fishing pressure on community weighted mean of PC2 (representing reproductive investment life history axis) at each community resolution. Estimate = model estimate, std.error = standard error, statistic = z value. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Colon indicates interaction between main effects. All continuous covariates are average values at resolution of community. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects.

term	estimate	std.error	statistic	p.value
SNSP	0.0219792	0.0382533	0.5745697	0.5655823
SNWI	0.0486139	0.0445998	1.0900012	0.2757126
sst_var	0.0730687	0.0357295	2.0450519	0.0408497
Depth	0.0973040	0.0351414	2.7689248	0.0056242
fp	-0.0315789	0.0301924	-1.0459238	0.2955962
Year	0.0101231	0.0145001	0.6981391	0.4850902
Quarter	-0.0403011	0.0128615	-3.1334792	0.0017275
SNSP:SNWI	-0.0373425	0.0196886	-1.8966600	0.0578728
SNSP:sst_var	0.0051999	0.0375724	0.1383972	0.8899265
SNSP:Depth	0.1214822	0.0517056	2.3494975	0.0187988
SNSP:fp	0.1585762	0.0573147	2.7667633	0.0056616
SNWI:sst_var	0.0121234	0.0518934	0.2336210	0.8152792
SNWI:Depth	-0.0533714	0.0524438	-1.0176884	0.3088261
SNWI:fp	-0.1407792	0.0571959	-2.4613490	0.0138416
sst_var:Depth	-0.0715721	0.0241238	-2.9668701	0.0030085
sst_var:fp	0.0387425	0.0510325	0.7591741	0.4477484
Depth:fp	0.0862545	0.0543853	1.5859876	0.1127421

Table C.3.1. PC3 model outputs for communities at the level of haul. Effects of SST, depth and fishing pressure on community weighted mean of PC3 (representing trophic level) at each community resolution. Estimate = model estimate, std.error = standard error, statistic = z value. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Colon indicates interaction between main effects. All continuous covariates are average values at resolution of community. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects.

term	estimate	std.error	statistic	p.value
SNSP	0.0467849	0.0118458	3.949480	0.0000783
SNWI	-0.0948616	0.0163983	-5.784833	0.0000000
sst_var	0.0163580	0.0115754	1.413165	0.1576071
Depth	-0.1299941	0.0101033	-12.866503	0.0000000
fp	0.0277045	0.0059464	4.659060	0.0000032
Year	-0.0108772	0.0053400	-2.036909	0.0416591
Quarter	0.1036965	0.0061213	16.940337	0.0000000
SNSP:SNWI	0.0446391	0.0058938	7.573909	0.0000000
SNSP:sst_var	0.0291248	0.0093710	3.107973	0.0018838
SNSP:Depth	0.0291926	0.0117860	2.476887	0.0132534
SNSP:fp	-0.0284485	0.0092587	-3.072614	0.0021219
SNWI:sst_var	-0.0248706	0.0117784	-2.111552	0.0347249
SNWI:Depth	-0.0491182	0.0113846	-4.314459	0.0000160
SNWI:fp	0.0171788	0.0096976	1.771451	0.0764857
sst_var:Depth	-0.0283674	0.0072222	-3.927787	0.0000857
sst_var:fp	0.0171448	0.0082536	2.077242	0.0377792
Depth:fp	-0.0280845	0.0074744	-3.757420	0.0001717

Table C.3.2. PC3 model outputs for communities in grid cells aggregated by a factor of 5. Effects of SST, depth and fishing pressure on community weighted mean of PC3 (representing trophic level) at each community resolution. Estimate = model estimate, std.error = standard error, statistic = z value. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Colon indicates interaction between main effects. All continuous covariates are average values at resolution of community. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects.

term	estimate	std.error	statistic	p.value
SNSP	0.0726765	0.0131778	5.5150485	0.0000000
SNWI	-0.1228534	0.0178627	-6.8776460	0.0000000
sst_var	0.0072918	0.0119775	0.6087869	0.5426657
Depth	-0.1620081	0.0099364	-16.3045934	0.0000000
fp	0.0315799	0.0060110	5.2536689	0.0000001
Year	0.0069508	0.0061075	1.1380772	0.2550882
Quarter	0.0934031	0.0079323	11.7750780	0.0000000
SNSP:SNWI	0.0400123	0.0064979	6.1577569	0.0000000
SNSP:sst_var	0.0066789	0.0107911	0.6189247	0.5359660
SNSP:Depth	0.0235315	0.0131382	1.7910761	0.0732811
SNSP:fp	-0.0399727	0.0111711	-3.5782392	0.0003459
SNWI:sst_var	0.0086291	0.0136602	0.6316985	0.5275839
SNWI:Depth	-0.0067171	0.0127229	-0.5279484	0.5975352
SNWI:fp	0.0367186	0.0113598	3.2323194	0.0012279
sst_var:Depth	-0.0287531	0.0076271	-3.7698699	0.0001633
sst_var:fp	0.0198830	0.0094981	2.0933794	0.0363153
Depth:fp	-0.0290881	0.0083515	-3.4829574	0.0004959

Table C.3.3. PC3 model outputs for communities in grid cells aggregated by a factor of 10. Effects of SST, depth and fishing pressure on community weighted mean of PC3 (representing trophic level) at each community resolution. Estimate = model estimate, std.error = standard error, statistic = z value. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Colon indicates interaction between main effects. All continuous covariates are average values at resolution of community. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects.

term	estimate	std.error	statistic	p.value
SNSP	0.0719762	0.0157346	4.5744015	0.0000048
SNWI	-0.1009041	0.0184298	-5.4750452	0.0000000
sst_var	0.0056667	0.0131335	0.4314682	0.6661280
Depth	-0.1543714	0.0115573	-13.3570918	0.0000000
fp	0.0281857	0.0077189	3.6515199	0.0002607
Year	0.0141750	0.0068432	2.0714090	0.0383206
Quarter	0.0964068	0.0085438	11.2838919	0.0000000
SNSP:SNWI	0.0445266	0.0077160	5.7706761	0.0000000
SNSP:sst_var	0.0338687	0.0135253	2.5040910	0.0122766
SNSP:Depth	0.0320098	0.0169336	1.8903129	0.0587161
SNSP:fp	-0.0324188	0.0156880	-2.0664710	0.0387840
SNWI:sst_var	0.0021924	0.0174058	0.1259559	0.8997668
SNWI:Depth	-0.0264990	0.0162424	-1.6314705	0.1027911
SNWI:fp	0.0310059	0.0158829	1.9521555	0.0509198
sst_var:Depth	-0.0352836	0.0094008	-3.7532386	0.0001746
sst_var:fp	0.0304309	0.0127021	2.3957470	0.0165865
Depth:fp	-0.0252832	0.0114813	-2.2021241	0.0276565

Table C.3.4. PC3 model outputs for communities in grid cells aggregated by a factor of 20. Effects of SST, depth and fishing pressure on community weighted mean of PC3 (representing trophic level) at each community resolution. Estimate = model estimate, std.error = standard error, statistic = z value. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Colon indicates interaction between main effects. All continuous covariates are average values at resolution of community. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects.

term	estimate	std.error	statistic	p.value
SNSP	0.0980061	0.0226940	4.3185912	0.0000157
SNWI	-0.1318297	0.0264121	-4.9912717	0.0000006
sst_var	0.0016249	0.0193849	0.0838218	0.9331981
Depth	-0.1521471	0.0173431	-8.7727540	0.0000000
fp	0.0278544	0.0125174	2.2252538	0.0260642
Year	0.0112226	0.0092373	1.2149209	0.2243963
Quarter	0.0819837	0.0108917	7.5271888	0.0000000
SNSP:SNWI	0.0643015	0.0114416	5.6199607	0.0000000
SNSP:sst_var	0.0460968	0.0191675	2.4049451	0.0161749
SNSP:Depth	0.0595213	0.0238601	2.4945930	0.0126102
SNSP:fp	-0.0525040	0.0272965	-1.9234689	0.0544212
SNWI:sst_var	-0.0257890	0.0256838	-1.0040961	0.3153323
SNWI:Depth	-0.0648794	0.0244687	-2.6515290	0.0080128
SNWI:fp	0.0696040	0.0274859	2.5323506	0.0113301
sst_var:Depth	-0.0340149	0.0127518	-2.6674539	0.0076428
sst_var:fp	0.0353768	0.0214081	1.6524972	0.0984332
Depth:fp	-0.0643031	0.0208631	-3.0821413	0.0020552

Table C.3.5. PC3 model outputs for communities in grid cells aggregated by a factor of 50. Effects of SST, depth and fishing pressure on community weighted mean of PC3 (representing trophic level) at each community resolution. Estimate = model estimate, std.error = standard error, statistic = z value. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Colon indicates interaction between main effects. All continuous covariates are average values at resolution of community. Terms highlighted in blue have significant positive effects, terms highlighted in red have significant negative effects.

term	estimate	std.error	statistic	p.value
SNSP	0.0426383	0.0425665	1.0016864	0.3164951
SNWI	-0.1607680	0.0496286	-3.2394195	0.0011977
sst_var	-0.0865337	0.0397581	-2.1765025	0.0295177
Depth	-0.2121269	0.0391038	-5.4247155	0.0000001
fp	0.0009719	0.0335967	0.0289296	0.9769207
Year	0.0036384	0.0161351	0.2254951	0.8215942
Quarter	0.0341347	0.0143116	2.3850991	0.0170745
SNSP:SNWI	0.0893014	0.0219085	4.0761033	0.0000458
SNSP:sst_var	0.0097947	0.0418088	0.2342747	0.8147717
SNSP:Depth	-0.0922172	0.0575356	-1.6027847	0.1089822
SNSP:fp	-0.2153765	0.0637771	-3.3770170	0.0007328
SNWI:sst_var	0.0708564	0.0577446	1.2270662	0.2197977
SNWI:Depth	0.0954972	0.0583570	1.6364303	0.1017496
SNWI:fp	0.1825344	0.0636450	2.8680089	0.0041306
sst_var:Depth	-0.0204090	0.0268438	-0.7602859	0.4470837
sst_var:fp	-0.0406893	0.0567866	-0.7165296	0.4736644
Depth:fp	-0.1634896	0.0605175	-2.7015250	0.0069022

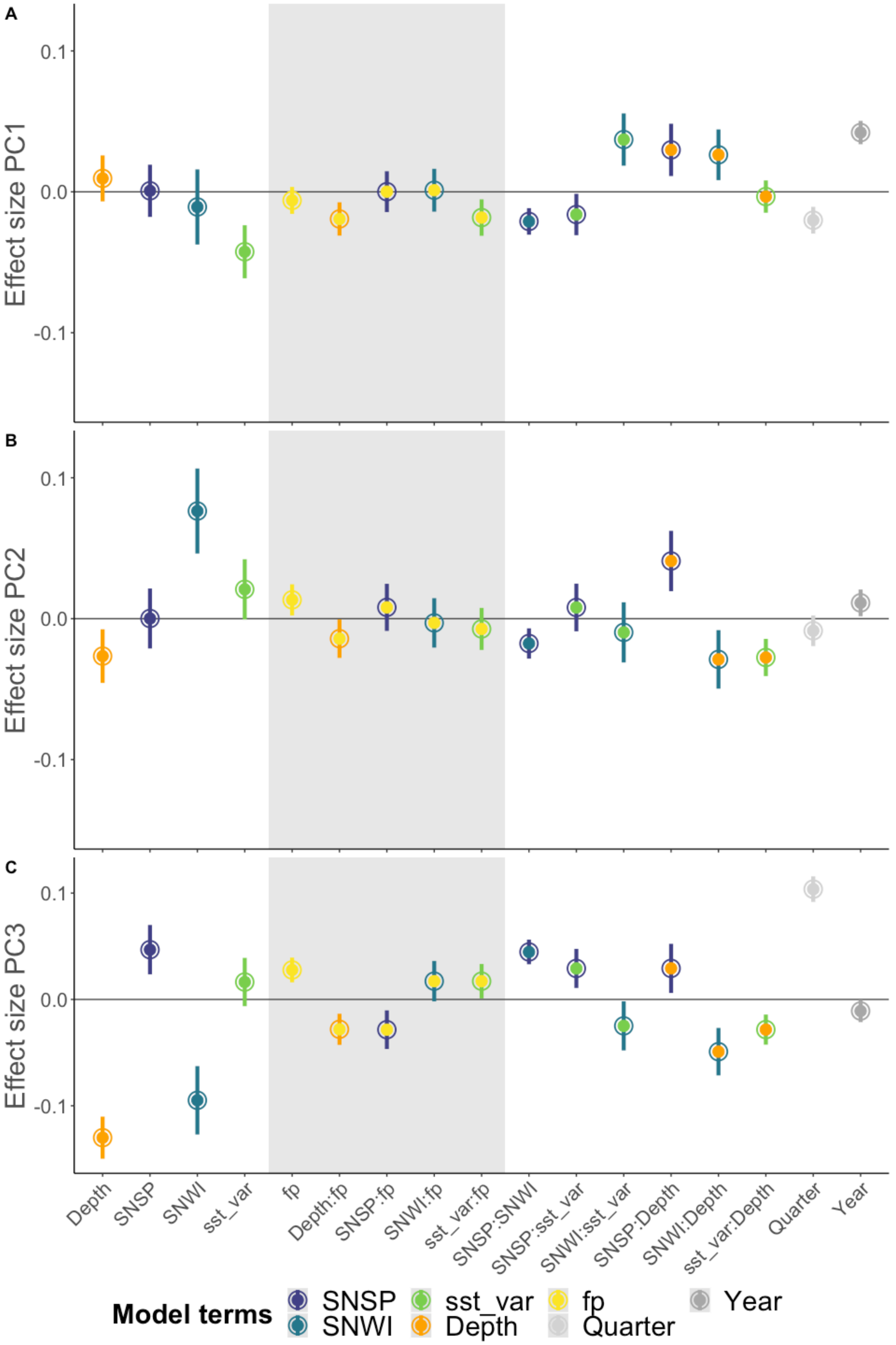

Figure C.1. Community weighted means of life history principle components at the level of haul. (A) Effects of SST, depth and fishing pressure on community weighted mean of PC1 (representing pace of life Life history axis). (B) Effects of SST, depth and fishing pressure on community weighted mean of PC2 (representing reproductive investment life history axis). (C) Effects of SST, depth and fishing pressure on community weighted mean of PC3 (representing trophic level). In all panels, the x axis represents change in community weighted mean value of PC associated with a one standard deviation change in each model term. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure, Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). The colour of points and vertical lines refers to the terms in the model. If a point and vertical line are the same colour, this represents a main effect. If point and vertical line are different colours, this represents the interaction between two main effects as per the legend. Light grey vertical bar highlight terms associated with fishing pressure. Vertical lines represent 95% Confidence interval. CIs overlapping continuous horizontal lines indicate that the slope of the relationship is not significantly different from zero (no effect). Total number of observations (communities) in the models = 8160.

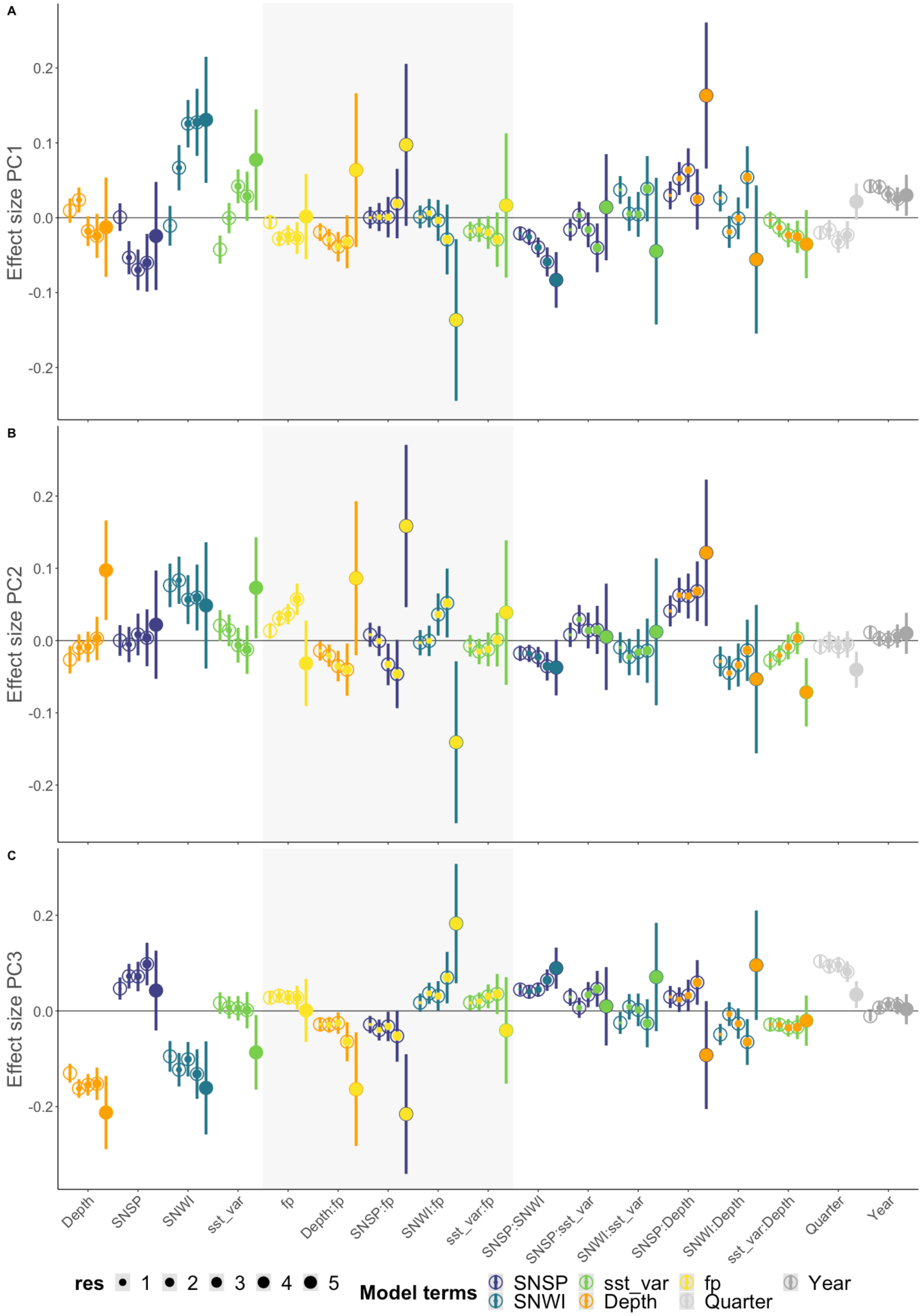

Figure C.2. Comparison of relative importance of covariates across community resolutions. A) Effects of SST, depth and fishing pressure and their two-way interactions on community weighted mean of PC1 (representing pace of life Life history axis) at each community resolution. B) Effects of SST, depth and fishing pressure on community weighted mean of PC2 (representing reproductive investment life history axis) at each community resolution. C) Effects of SST, depth and fishing pressure on community weighted mean of PC3 (representing trophic level) at each community resolution. Depth = depth, SNSP = spring sea surface temperature, SNSW = winter sea surface temperature, sst_var = sea surface temperature variation, fp = fishing pressure. All continuous covariates are average values at resolution of community. Year = year that sample was obtained, Quarter = difference in community composition in hauls caught in spring (reference level is hauls caught in winter). Communities were defined at the level of haul (1), or all hauls in grid cells aggregated by factors of 5, 10, 20 or 50 (see methods). Number of observations (communities) per model: res1 = 8160, res5 = 6030, res10 = 3945, res20 = 1963, res50 = 564. In all panels, x axis represents change in community weighted mean value of PC associated with a one standard deviation change in each model term. Vertical lines represent 95% Confidence interval. CIs overlapping continuous horizontal lines indicate that the slope of the relationship is not significantly different from zero (no effect). The colour of points and vertical lines refers to the terms in the model. If a point and vertical line are the same colour, this represents a main effect. If point and vertical line are different colours, this represents the interaction between two main effects as per the legend. The size of points refers to community resolution of the model as per the legend. Light grey vertical bar highlight terms associated with fishing pressure.

Table C.2. Consistent core areas. Values represent width in kilometers of a square containing the core areas of 48 species in our data set after Probst et al., (2021). Probst define consistent core areas as “grid cells containing 50% of cumulative population biomass in any given year and season”, with grid cells containing at least 50% of all core areas for the whole study duration considered consistent core areas. Winter = consistent core areas during winter, Summer = consistent core areas during summer, Annual = consistent core areas for both winter and summer.

Species	**Winter**	**Summer**	**Annual**
Merlangius merlangus	218	225	166
Trisopterus esmarkii	197	174	111
Melanogrammus aeglefinus	183	201	167
Pleuronectes platessa	210	238	155
Scyliorhinus canicula	138	120	76
Limanda limanda	244	229	148
Trisopterus minutus	143	165	114
Eutrigla gurnardus	188	176	47
Callionymus lyra	229	247	116
Hippoglossoides platessoides	244	246	173
Raja montagui	118	77	59
Squalus acanthias	227	183	78
Microstomus kitt	245	235	179
Platichthys flesus	61	110	61

Table C.2. Consistent core areas. Values represent width in kilometers of a square containing the core areas of 48 species in our data set after Probst et al., (2021). Probst define consistent core areas as “grid cells containing 50% of cumulative population biomass in any given year and season”, with grid cells containing at least 50% of all core areas for the whole study duration considered consistent core areas. Winter = consistent core areas during winter, Summer = consistent core areas during summer, Annual = consistent core areas for both winter and summer.

Species	**Winter**	**Summer**	**Annual**
Gadus morhua	242	216	148
Raja clavata	128	58	58
Callionymus maculatus	115	192	115
Trisopterus luscus	81	76	46
Merluccius merluccius	158	178	146
Agonus cataphractus	94	141	54
Zeus faber	182	122	93
Echiichthys vipera	108	103	41
Enchelyopus cimbrius	163	138	99
Raja brachyura	115	86	33
Gaidropsarus vulgaris	166	115	55
Glyptocephalus cynoglossus	170	212	141
Lophius piscatorius	176	207	160
Lepidorhombus whiffiagonis	102	90	74
Helicolenus dactylopterus	108	112	80
Taurulus bubalis	57	NA	NA
Pholis gunnellus	132	86	81
Leucoraja naevus	157	140	110
Scophthalmus rhombus	107	144	104
Ciliata mustela	98	NA	NA
Lophius budegassa	167	201	115
Galeorhinus galeus	145	102	0
Pollachius virens	135	158	119

Table C.2. Consistent core areas. Values represent width in kilometers of a square containing the core areas of 48 species in our data set after Probst et al., (2021). Probst define consistent core areas as “grid cells containing 50% of cumulative population biomass in any given year and season”, with grid cells containing at least 50% of all core areas for the whole study duration considered consistent core areas. Winter = consistent core areas during winter, Summer = consistent core areas during summer, Annual = consistent core areas for both winter and summer.

Species	**Winter**	**Summer**	**Annual**
Phycis blennoides	141	123	81
Pollachius pollachius	142	110	90
Molva molva	121	109	99
Scophthalmus maximus	260	240	143
Zeugopterus punctatus	160	167	0
Myoxocephalus scorpius	163	158	97
Cyclopterus lumpus	153	132	77
Sebastes viviparus	117	134	53
Brosme brosme	124	97	89
Triglops murrayi	118	83	53
Hippoglossus hippoglossus	209	212	130

Appendix D | Supplementary information for Chapter 5

Table D.1. Nutrient application rates. Nutrients were applied at a rate of 10 g m^{-2} y^{-1} by elemental mass. Plots = 25 m^{2}, 15 plots per nutrient treatment (5 treatments x 3 replicates). *Micronutrients (mixture of Ca, Mg, S, B, Cu, Fe, Mn, Mo, Zn) were only applied in the 1st treatment year.

Fertilizer	g plot^{-1} year^{-1}	kg experiment^{-1} year^{-1}
Slow-release Urea (43% N)	581	8.7
Triple Super Phosphate	1272	19.1
Potassium Sulphate	558	8.4
Micronutrients*	2500	37.5

Table D.2. Soil assay data. Assay of Slieve Carran soil samples collected in the pre-experiment year (2015). C, N, P and K refer to Carbon, Nitrogen, Phosphorus and Potassium respectively.

Block	plot	%C	%N	P (ppm)	K (ppm)	pH
1	1	8.258	0.643	7	185	5.5
	2	9.613	0.786	13	237	5.6
	3	7.715	0.62	8	184	5.5
	4	7.075	0.544	5	215	5.4
	5	6.556	0.525	6	146	5.4
	6	6.192	0.492	9	167	5.3
	7	6.113	0.48	5	162	5.4
	8	7.627	0.582	4	222	6.4
	9	7.354	0.572	4	205	5.5
	10	8.49	0.745	10	262	5.6
2	11	7.718	0.633	7	172	5.4
	12	7.102	0.554	5	163	5.2
	13	8.083	0.66	5	136	5.6
	14	7.517	0.546	4	147	5.3
	15	7.242	0.552	4	137	5.4
	16	9.411	0.711	7	176	5.9
	17	6.916	0.549	5	191	5.3
	18	9.24	0.792	6	238	5.7
	19	6.418	0.493	3	152	5.3
	20	8.439	0.612	4	176	5.3
3	21	8.146	0.577	7	182	5.6
	22	12.307	0.892	9	134	6
	23	7.111	0.502	3	168	5.5
	24	9.111	0.697	6	151	5.4
	25	8.945	0.649	5	155	5.3
	26	5.999	0.482	3	131	5.4
	27	9.011	0.625	4	152	6.3
	28	9.223	0.654	6	164	5.4
	29	7.956	0.612	5	127	5.4
	30	6.915	0.512	5	127	5.1
Site mean		**7.927**	**0.610**	**5.800**	**172.133**	**5.513**

Table D.3. Species list

1. *Achillea millefolium*
2. *Agrostis capillaris*
3. *Agrostis stolonifera*
4. *Ajuga reptans*
5. *Anemone nemorosa*
6. *Anthoxanthum odoratum*
7. *Briza media*
8. *Bryophyte*
9. *Calluna vulgaris*
10. *Campanula rotundifolia*
11. *Carex caryophyllea*
12. *Carex flacca*
13. *Carex panicea*
14. *Carex pulicaris*
15. *Centaurea nigra*
16. *Cerastium fontanum*
17. *Conopodium majus*
18. *Corylus avellana*
19. *Cynodon sp.*
20. *Cynosurus cristatus*
21. *Dactylis glomerata*
22. *Dactylorhiza fuchsii*
23. *Dactylorhiza maculata*
24. *Dactylorhiza sp.*
25. *Danthonia decumbens*
26. *Euphrasia sp.*

Table D.3. Species list

27. *Festuca ovina*
28. *Festuca rubra*
29. *Galium saxatile*
30. *Galium verum*
31. *Gymnadenia conopsea*
32. *Helictotrichon pubescens*
33. *Holcus lanatus*
34. *Hypericum pulchrum*
35. *Hypochaeris radicata*
36. *Koeleria macrantha*
37. *Lathyrus linifolius*
38. *Lathyrus pratensis*
39. *Leontodon autumnalis*
40. *Leontodon hispidus*
41. *Linum catharticum*
42. *Lotus corniculatus*
43. *Luzula campestris*
44. *Luzula multiflora*
45. *Mentha arvensis*
46. *Molinia caerulea*
47. *Neottia ovata*
48. *Odontites vernus*
49. *Orchis mascula*
50. *Parnassia palustris*
51. *Pedicularis palustris*
52. *Pedicularis sylvatica*

Table D.3. Species list

53. *Pilosella officinarum*
54. *Pimpinella saxifraga*
55. *Plantago lanceolata*
56. *Plantago maritima*
57. *Platanthera sp.*
58. *Poa pratensis*
59. *Poa trivialis*
60. *Potentilla erecta*
61. *Potentilla sterilis*
62. *Prunella vulgaris*
63. *Pteridium aquilinum*
64. *Ranunculus acris*
65. *Ranunculus repens*
66. *Rhinanthus minor*
67. *Rosa spinosissima*
68. *Rosa xanthina*
69. *Rubus vestitus*
70. *Rumex acetosa*
71. *Scorzoneroides autumnalis*
72. *Sesleria caerulea*
73. *Sonchus asper*
74. *Succisa pratensis*
75. *Taraxacum campylodes*
76. *Thymus polytrichus*
77. *Thymus praecox ssp. Polytrichus*
78. *Trifolium medium*

Table D.3. Species list

79. *Trifolium pratense*
80. *Trifolium repens*
81. *Trisetum flavescens*
82. *Unknown orchidaceae sp.*
83. *Veronica chamaedrys*
84. *Vicia cracca*
85. *Viola riviniana*