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Incorporating Biodiversity-Ecosystem Function Relationships into Models and Conservation Planning

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**INCORPORATING BIODIVERSITY-ECOSYSTEM FUNCTION
RELATIONSHIPS INTO MODELS AND CONSERVATION PLANNING**

A Dissertation Presented

by

SARAH R. WEISKOPF

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

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Department of Environmental Conservation

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SARAH R. WEISKOPF

Approved as to style and content by:

Susannah Lerman, Co-Chair

Toni Lyn Morelli, Co-Chair

Forest Isbell, Member

Paige Warren, Department Head
Department of Environmental Conservation

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ABSTRACT

INCORPORATING BIODIVERSITY-ECOSYSTEM FUNCTION RELATIONSHIPS INTO MODELS AND CONSERVATION PLANNING

SEPTEMBER 2023

SARAH R. WEISKOPF, B.S., UNIVERSITY OF DELAWARE

M.S., UNIVERSITY OF DELAWARE

Ph.D., UNIVERSITY OF MASSACHUSETTS AMHERST

Directed by: Dr. Susannah Lerman and Dr. Toni Lyn Morelli

Unsustainable use of nature and climate change are leading to unprecedented biodiversity declines. These declines have cascading impacts on ecosystem function and ecosystem services, and ultimately on human well-being. International agreements have been adopted that aim to address both crises. The Paris Agreement, adopted in 2015, set global emission reductions targets. In 2022, most countries agreed to the Kunming-Montreal Global Biodiversity Framework (GBF). The GBF sets 23 ambitious targets for 2030 ranging from reducing threats to biodiversity, meeting people's needs through sustainable use and benefit sharing, and solutions for implementation.

Although adopting global goals and targets is an important first step, additional work is required for on-the-ground implementation. Important knowledge gaps include understanding how biodiversity, ecosystem functions, and ecosystem services are linked, modeling how policy scenarios could lead to different outcomes for biodiversity and ecosystem services, and guidance for where and how to prioritize conservation actions. This dissertation aims to fill some of these gaps. Chapters 1 and 2 explore how biodiversity conservation can affect important ecosystem functions and services. Chapter

3 moves from improving our baseline knowledge to thinking about how we can achieve our conservation goals through prioritizing restoration actions.

In chapter 1, I focus on the importance of biodiversity-ecosystem function relationships for urban systems. The proportion of people living in urban areas is growing globally. Thus, understanding how to manage urban biodiversity, ecosystem functions, and ecosystem services is important. Biodiversity can increase ecosystem functioning in natural systems. However, few studies have assessed the relationship between biodiversity and ecosystem functioning in urban areas, which differ in abiotic factors, species compositions, food webs, and turnover rates. I systematically reviewed documented evidence of biodiversity-ecosystem function relationships in urban environments and assessed factors that influenced the direction of the relationships.

I show that increasing biodiversity, even in small areas, can increase local ecosystem functioning in urban areas. Therefore, local management that increases biodiversity can have positive benefits for ecosystems and people. I also identify research gaps and opportunities to improve biodiversity-ecosystem function research in the urban realm moving forward and discuss how to improve urban green space management.

In chapter 2, I explored how biodiversity-ecosystem functioning relationships can be incorporated into modeling. Models of how changes in drivers, including land use change and climate change, lead to changes in biodiversity and ecosystem services are useful tools for policymakers as they consider how to sustainably manage natural resources. Despite known interactions between biodiversity, ecosystem functioning, and ecosystem services, models projecting changes in these domains typically operate independently and do not account for interactions or feedbacks, which may lead to

inaccurate estimates in ecosystem functioning and ecosystem service projections. In this chapter, I focused on how plant species diversity affects biomass production and carbon storage. I used the Biogeographic Infrastructure for Large-scaled Biodiversity Indicators (BILBI) model, a macroecological community-level model, to estimate plant species persistence under different climate and land use change scenarios in 2050. I linked this with empirical data on biodiversity-biomass production relationships to assess how biodiversity loss will affect carbon storage globally.

I found that biodiversity has the potential to cause as much carbon loss as emissions from other sources (i.e., they are within the range of uncertainty from biodiversity-mediated carbon loss), so achieving Sustainable Development Goal 15 (Life on Land) is essential to achieving Goal 13 (Climate Action). Because the Paris Agreement does not account for emissions from biodiversity loss, science on its carbon impacts, and action as a result, could be underestimated. This analysis points to the important role that maintaining and/or enhancing the diversity of plant species within areas of natural vegetation, rather than simply maximizing the extent of these areas, can play in addressing the climate change crisis. Alongside increasing the global extent of protected areas to prevent rapid carbon loss from ecosystem degradation, increasing plant species diversity in degraded ecosystems can increase carbon storage potential. However, existing international initiatives like the Bonn Challenge and the Paris Agreement focus on forest extent rather than forest quality for protection, afforestation, and reforestation, and thus are missing a key opportunity for action.

In chapter 3, I looked at how we can achieve proposed biodiversity conservation goals. Reversing trends in biodiversity loss and achieving the Convention on Biological

Diversity (CBD) 2050 vision of “Living in harmony with nature” will require not only conserving remaining biodiversity, but also restoring degraded areas. Recent legislative and executive actions in the U.S. have recognized the importance of restoration. Given limited budgets, deciding where to restore habitat will be an important need in the coming decade. In this chapter, I developed a modeling approach to maximize conservation benefit/restoration cost ratios that can be used to map restoration priorities. I illustrated this approach using a case study for highly threatened grassland ecosystems in the Great Plains region of Kansas.

I found that for the indicator species that we chose, shortgrass and mixed-grass prairies had the highest conservation benefit to cost ratio. Setting a minimum restoration threshold for each habitat type allowed me to identify high priority tallgrass prairie sites. The modeling approach is flexible and can be updated for different ecosystems, species, and conservation priorities. I outlined potential alterations that can be made in future analyses, depending on desired restoration goals.

Biodiversity conservation can increase ecosystem functioning and services. In this dissertation, I show that conserving biodiversity is important for urban ecosystem functioning and global carbon sequestration. Restoring biodiversity will have positive outcomes for ecosystem functions, ecosystem services, and people. My restoration prioritization model can therefore be used to implement conservation actions to achieve global and national biodiversity conservation goals and targets.

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CHAPTER 1

BIODIVERSITY PROMOTES URBAN ECOSYSTEM FUNCTIONING

Abstract

The proportion of people living in urban areas is growing globally. Understanding how to manage urban biodiversity, ecosystem functions, and ecosystem services is becoming more important. Biodiversity can increase ecosystem functioning in non-urban systems. However, few studies have assessed the relationship between biodiversity and ecosystem functioning in urban areas, which differ in species compositions, abiotic environments, food webs, and turnover rates. We systematically reviewed evidence of biodiversity-ecosystem functioning relationships in urban environments and assessed factors that influence the relationship direction. Based on 42 studies, relationships between biodiversity and ecosystem functioning were more positive than negative, especially for pollination and nutrient cycling and retention. Surprisingly, relationships between biodiversity and biomass production and storage were equally likely to be positive or negative, perhaps due to extensive plant management in urban areas. When we removed studies that relied on spatial correlation, the effects of biodiversity were mostly positive or neutral. Inference method, ecosystem function, and ecosystem type best predicted whether biodiversity had a positive impact on functioning. However, the number of studies and geographic coverage of my review was too low to provide a general predictive framework. We identify gaps and opportunities to improve urban biodiversity-ecosystem functioning research and discuss how my findings can improve urban green space management.

Introduction

Human activities are leading to declines in biodiversity that are unprecedented in human history (Díaz et al., 2019). The effects of biodiversity on ecological processes can be substantial, and are expected to grow stronger at large spatial and temporal scales (Cardinale et al., 2011; Isbell et al., 2017; Loreau et al., 2022; O'Connor et al., 2017). In fact, the loss of biological diversity is a leading driver of ecosystem functioning change, especially at high levels of species loss (Hooper et al., 2012). Biodiversity loss decreases ecosystem functions like productivity and nutrient recycling across ecosystems, although the relationship is generally non-linear and decelerates at high diversity levels (Cardinale et al., 2012; Reich et al., 2012; Schmid et al., 2009). Much of the research on how biodiversity influences ecosystem functioning has focused on forests, grasslands, and other non-urban systems. Research on the role of biodiversity in promoting ecosystem functioning in urban areas has been limited; a recent review of biodiversity-ecosystem functioning (BEF) relationships included only three urban studies (van der Plas, 2019).

Improved understanding of how biodiversity supports ecosystem functioning in urban areas could inform management. While urban planners often consider locations and users of green spaces and other ecological amenities, they often do not consider ecosystem functioning (Pickett et al., 2011). This is perhaps a relic of the origin of the urban ecology discipline, which was heavily influenced by the social sciences and urban planning and is only more recently emerging as a mainstream ecological research field (Grimm et al., 2000; Ramalho & Hobbs, 2012; Young, 2009). With most people now living in cities and the percentage of people living in urban areas increasing globally (United Nations, 2018), understanding how to manage the urban biodiversity, ecosystem

functioning, and ecosystem services that an increasingly urban population depends upon is especially important.

Biodiversity-ecosystem functioning relationships could differ between non-urban and urban ecosystems

Many species are not adapted to the highly altered conditions in urban ecosystems, yet others thrive (Aronson et al., 2014; Lerman, Narango, Andrade, et al., 2021). Urban biodiversity is influenced by local climate, time since development, land use histories, and human management activities (M. L. Avolio et al., 2018; Hope et al., 2003; Lerman, Narango, Andrade, et al., 2021; J. S. Walker et al., 2009). This can be especially true for plant diversity, which is influenced by landowner planting preferences, neighborhood characteristics, and the composition of plants sold in local nurseries, which are often non-native ornamentals (M. L. Avolio et al., 2018). In addition, urban animal assemblages often have more generalist species that tolerate and thrive in urban conditions (Lerman, Narango, Andrade, et al., 2021; Nielsen et al., 2013). Moving from non-urban areas to more urbanized areas, overall species richness decreases, and the abundance of certain species increases, leading to reduced evenness (Shochat et al., 2010).

Complementarity and selection effects (Box 1) are common drivers of positive biodiversity-ecosystem functioning relationships in non-urban ecosystems. Dominance by one or a few species can reduce complementarity; fewer niches in the system get filled (Hillebrand et al., 2008). For example, in headwater streams in northeast France, increasing benthic invertebrate species richness led to faster leaf decomposition when species were more evenly distributed than when one or a few species dominated (Dangles

& Malmqvist, 2004). Dominance can also affect selection effects, depending on whether the dominant species is better or worse at providing particular ecosystem functions (Hillebrand et al., 2008). A small number of urban-adapted species can dominate urban ecosystems. For example, in Phoenix, AZ, the most efficient foraging species dominated urban bird populations, while nearby desert communities were more even (Shochat et al., 2010). As a result, species dominance could more likely affect the relationship between biodiversity and ecosystem functioning in urban areas than in non-urban ecosystems. This could reduce the strength of complementarity, and also reduce selection effects if dominant species are not the highest function-providing species (Tilman et al., 2014). A further consideration is the role of native vs. invasive species. Native species assemblages show greater complementarity than exotic species assemblages, likely because they share a longer coevolutionary history (Wilsey et al., 2009). Indeed, negative relationships between biodiversity and functioning often involve invasive species (Harrison et al., 2014).

The benefits of diverse assemblages through time and space, **temporal and spatial selection effects**, (Box 1) have also been clearly documented in urban settings. For example, large scale pest outbreaks such as Dutch elm disease that killed millions of dominant city street trees throughout the eastern US underlined the benefits of greater species diversity (Santamour, 1990). More connected landscapes can recover quicker after disturbances (Gonzalez, 2009; Loreau et al., 2003). Given that urban ecosystems are patchy (Pickett et al., 2017), local land management decisions, such as plant composition and configuration, can influence the quality of local habitat and environmental heterogeneity (Lerman, Narango, Avolio, et al., 2021; Lerman & Warren, 2011). Larger

scale landscape decisions such as urban green space placement can affect patch structure and dispersal (Andrade et al., 2021; Beninde et al., 2015). This patchiness affects local (alpha) diversity and species turnover (beta diversity).

Considering entire ecosystems, more species are needed to maintain multiple ecosystem functions, i.e., **multifunctionality** (Box 1) (Hector & Bagchi, 2007; Lefcheck et al., 2015). For example, a grassland experiment found tradeoffs between total plant nitrogen and invasive species resistance but that, in some years, increasing species richness reduced these tradeoffs or even removed them (Zavaleta et al., 2010).

Multifunctionality has not yet been extensively studied in urban systems (Schwarz et al., 2017), even though ecosystems are often managed or valued for multiple functions and services.

Because urban environments can differ so dramatically from the surrounding non-urban environment, the same relationships between biodiversity and ecosystem functioning may not hold. Two major factors could disrupt the relationship. First, in non-urban environments, stable coexistence between species occurs when competition between species is weaker than competition between individuals of the same species; the same conditions drive positive effects of biodiversity on ecosystem functioning (Loreau, 2004; Vandermeer, 1981). In managed urban environments, plant species are cultivated and do not need to stably coexist to persist, which may weaken the effects of biodiversity on ecosystem functioning. Second, chemical inputs like fertilizers and pesticides used in urban areas can lead to negative observed relationships between biodiversity and function, at least across space. Thus, studies can be designed to look at two different questions: (1) within a place, how will a change in biodiversity over time cause a change

in ecosystem functioning (i.e., causal relationship between biodiversity and ecosystem functioning)? or (2) at a given time, are the most diverse places also those with the highest levels of ecosystem functioning or services (i.e., spatial correlation between biodiversity and ecosystem functioning)? There can be negative spatial covariation between biodiversity and ecosystem functioning even when loss of biodiversity causes a decrease in functioning. For example, in grasslands, fertilization increases productivity, but decreases biodiversity, which leads to loss of productivity over time (Isbell et al., 2013). Similarly, supplemental bird feeding in urban areas can influence bird community structure and increase the abundance of introduced species and reduce community evenness (Galbraith et al., 2015). Thus, when compared only across space, the most productive places may also be the least diverse, even when biodiversity loss leads to an eventual loss of productivity within the fertilized and food-supplemented locations.

Ecosystem functioning promotes ecosystem services

Ecosystem functioning is important for promoting ecosystem services. For example, the amount of services produced is related to the quantity and quality of various ecosystem components (Daily et al., 2009). Ecosystem functions include the flow of energy and materials through the biotic and abiotic components of an ecosystem (IPBES 2019), while ecosystem services directly link ecosystem components or functions to benefits that people receive ((Haase et al., 2014), Box 1). Although a focus on the relationship between biodiversity and ecosystem functioning in urban areas has been uncommon, assessments of urban ecosystem services have grown in recent years (Haase et al., 2014; Luederitz et al., 2015). Studies have assessed the benefits of urban green spaces for services such as local climate regulation, carbon sequestration, and mental and

physical health support (Haase et al., 2014; Ziter, 2016). However, many studies only consider the extent or location of green spaces (e.g., (Osborne & Alvares-Sanches, 2019; Peng et al., 2021), and few studies consider species composition in urban green spaces or the role of biodiversity in supporting ecosystem services (Cameron & Blanuša, 2016; Haase et al., 2014). While some studies do consider which species or species traits might provide the greatest level of ecosystem services, these studies do not incorporate the role of biological diversity itself. A recent review found that this was quite common; most studies did not quantitatively link the magnitude of a biodiversity metric with ecosystem service provision, but instead described the service as dependent on a particular composition of species, functional traits, or structures, or used biodiversity as an indicator of the service itself (Ziter, 2016). Moreover, relationships between biodiversity and ecosystem services in urban areas are often assumed rather than explicitly tested (Schwarz et al., 2017). A better understanding of how urban biodiversity links to ecosystem services has been identified as a key research gap (Knapp et al., 2021). Studying the underlying ecological components that contribute to ecosystem functioning, and ultimately to service provision, is an important step.

In this study, I focus on the relationship between biodiversity and ecosystem functioning (BEF), given that these ecosystem functions underpin several urban ecosystem services. The focus on ecosystem functioning allows us to consider the underlying conceptual relationships between biodiversity and ecosystem functioning as described in the ecological literature and to test whether these theories apply in urban environments where abiotic and biotic conditions have been significantly altered (Grimm et al., 2008). In addition, we build on previous review papers (e.g., (Schwarz et al., 2017;

Ziter, 2016)) by examining factors that may influence the direction of BEF relationships such as habitat type and spatial and temporal scale of the study. My overall objectives were to systematically review documented evidence of BEF relationships in urban environments and assess factors that may influence the direction of the relationships. Given the generally positive BEF relationships found in non-urban ecosystems, I expected increasing biodiversity in urban ecosystems will also increase ecosystem functioning, although this relationship may be obscured when other inputs (e.g., use of fertilizer or insecticides) are not accounted for.

Box 1: What is biodiversity?

Biodiversity is a broad term that captures multiple facets of the variability among living organisms (Box 1). Some aspects of biodiversity, such as species richness and functional diversity, are particularly important for ecosystem functioning (Díaz & Cabido, 2001; Harrison et al., 2014). Although species richness and functional diversity are related, high species richness does not always correspond to high functional diversity (Aguirre-Gutiérrez et al., 2017; Díaz & Cabido, 2001). Species richness and functional diversity may respond differently to drivers of change; therefore, it may be important to examine both for consequences to ecosystem functioning. Despite the importance of these different metrics, assessments of biodiversity and ecosystem service relationships in urban areas have most often assessed species richness, and few studies have looked at more than one metric of diversity (Schwarz et al., 2017; Ziter, 2016).

Definitions used in this paper:

Biodiversity - The variability among living organisms from all sources, including diversity within species, between species and of ecosystems (United Nations Convention on Biological Diversity, 1992)

Ecosystem Function - The flow of energy and materials through the biotic and abiotic components of an ecosystem. Common processes include biomass production, trophic relationships, nutrient cycling, water dynamics, and heat transfer (IPBES, 2019)

Species Richness - The total number of species in an area of interest

Species Evenness - The equity of relative abundance of species in an area of interest (Wilsey & Polley, 2004).

Functional or Trait Diversity - The range, values, relative abundance, and distribution of functional traits in a given community or ecosystem (IPBES, 2019)

Species composition/identity - The array of species present in an ecosystem or study area (IPBES, 2022)

Complementarity - An effect of biodiversity where greater species richness or functional diversity allows for greater niche differentiation (Díaz & Cabido, 2001; Hooper et al., 2005; Loreau & Hector, 2001; Tilman et al., 1997)

Selection Effects - An effect of biodiversity where more diverse assemblages are more likely to contain the best function-providing species, which can increase overall functioning when these species are dominant (Aarssen, 1997; Hooper, 1998)

Temporal and Spatial Selection Effects - An effect of biodiversity where because there is selection for different 'best' species at different times and places, increased temporal and spatial beta diversity can increase ecosystem functioning (Isbell et al., 2018; Loreau et al., 2021; Yachi & Loreau, 1999)

Multifunctionality - When more species are needed to maintain multiple ecosystem functions and services (Hector & Bagchi, 2007; Lefcheck et al., 2015). This is especially true over time because different species support different functions in different contexts (Isbell et al., 2011)

Methods

Article search and screening

For my systematic review, I ran a Web of Science search using the search term “TS = ((biodiversity) AND ("ecosystem function*" OR "ecosystem service") AND (urban OR city OR cities))” on December 4, 2020. The search yielded 535 results. To be included in my analysis, studies needed to explicitly assess how at least one metric of biodiversity (Box 1) related to at least one ecosystem function and must have been conducted in an urban setting (as defined by the study author). There are many definitions of “urban”, but common components include demography and structural attributes (Mcintyre et al., 2000; Moll et al., 2019). In some cases, I included ecosystem services that directly relate to ecosystem functioning (e.g., water capture or filtration, air pollution reduction). I excluded studies related to cultural services and human health, as these are harder to link directly to ecosystem functioning (Chan et al., 2016). I only included studies that explicitly assessed correlations between biodiversity and ecosystem functioning or tested cause/effect models or experiments. I included both experimental and observational studies.

I included 27 papers after my initial full text review. I then conducted a snowball search (i.e., I reviewed the citation lists of all included papers for relevant titles). This process yielded an additional 15 papers for a total of 42 papers included in my review.

Data extraction and analysis

I extracted data related to basic study information and methodology, including study location, ecosystem and habitat type, spatial scale (grain and extent), study type (i.e., observational experimental, or modeled), sample size, and length of study (see Supplemental Table 1.1 for complete description). Next, I extracted information regarding the BEF relationship. This included the ecosystem function assessed, focal taxonomic group, biodiversity metric, whether the study also considered species identity and if so, was species identity important, direction of BEF relationship, and whether the study assessed the impact of invasive species. As noted above, different relationships between biodiversity and ecosystem functioning might be expected when comparisons are made only across space, rather than across time within the same place (Loreau, 1998). Therefore, I recorded the inference type based on whether the study assessed how changes in biodiversity within a place over time affected functioning or made an effort to statistically consider the causal effects of changes in biodiversity after controlling for other abiotic (e.g., soil fertility or fertilizer or pesticide inputs) or biotic (e.g., composition) factors that are also known to affect ecosystem functioning (i.e., biodiversity isolation), or whether only spatial correlations between biodiversity and ecosystem functioning were made (i.e., spatial correlation).

I split observations into separate rows by focal taxonomic group, ecosystem type, and biodiversity metric, such that a single paper could have multiple rows in the analysis. Hereafter, I refer to each row as a ‘case’ (n=109). Given that studies measured a variety of response variables and interventions, sample sizes for comparable studies were too small to conduct a formal meta-analysis of effect sizes. Therefore, I focused on the

direction of biodiversity-ecosystem functioning relationships so that I could compare across all cases. I first assessed whether positive BEF relationships were more likely than negative ones (i.e., did biodiversity increase or decrease ecosystem functioning) using χ^2 -goodness of fit tests. I removed neutral and mixed responses for this analysis. I ran the tests with all cases combined, and individually for functions that had at least ten positive or negative responses. When possible, I also ran the χ^2 -goodness of fit tests on only the biodiversity isolation studies to see how results differed. To see how these results compared to BEF relationships observed in non-urban systems, I used the data from van der Plas (2019, n=1,232 cases), removing any observations that came from urban/suburban study areas (n=13, resulting in a total of 1,219 cases for comparison). I used the direction of relationships between ecosystem function and each specific biodiversity indicator (i.e., the “Relationship” column in the data). In some cases, I re-categorized the data to match my ecosystem function and/or taxonomic classifications (e.g., I combined terrestrial, aquatic, and belowground invertebrates into one “invertebrates” category).

I used random forest classification to assess whether any of the study methodology, diversity metric, ecosystem function, or inference type variables could predict the direction of BEF relationships. Specifically, I used conditional inference trees to select the values of the covariates that best differentiate the dependent variable (in this case, direction of BEF relationships) using significance tests. Response variables only included positive, negative, or no effect of biodiversity on ecosystem functioning; I excluded the 1 case of mixed responses. I ran the model using only the four ecosystem functions with the greatest number of cases: biomass, nutrient cycling and retention,

pollination, and water dynamics (e.g., water capture, water filtration). Biomass included biomass production and biomass stock (commonly used as a proxy for production), although I note that in some cases these metrics may not be tightly linked (TerHorst & Munguia, 2008). I used the conditional tree function *ctree* (Hothorn et al., 2006) in the package *partykit* (Hothorn & Zeileis, 2015) to run 10,000 iterations using the variables taxonomic group, ecosystem function category, biodiversity metric, spatial scale of the data, sample size, study years, whether the study considered species identity, and inference type as predictors. I set the significance level for tree splits to $\alpha=0.05$. I then used the *ggparty* package (Borkovec & Madin, 2019) to visualize the significant tree splits. I conducted all analyses in R version 4.0.4 (R Core Team, 2021).

Results

Distribution of evidence

The 42 papers included in my review contained 109 unique cases and studied 20 ecosystem functions in urban systems, which I grouped into seven major categories. The most studied urban ecosystem functions were nutrient cycling and retention, biomass/carbon storage, and pollination (Figure 1.1, Supplemental figure 1.1). Study length averaged approximately one year, ranging from one day to four years. Study area plot sizes were small: 43% of study plots covered $<1\text{m}^2$, and only 3% covered areas $>1\text{km}^2$. Most cases came from terrestrial ecosystems (N=88), with a few from freshwater ecosystems (especially streams; N=18), and only three cases from marine/coastal ecosystems. Like non-urban system studies (O'Connor et al., 2017), plants were by far the most studied taxonomic group, followed by invertebrates (Figure 1.1). However, no studies assessed how the diversity of vertebrates affected urban ecosystem functions.

Study locations were highly skewed, with 86% of papers in North America, Europe, or Australia (Supplemental Figure 1.2). Species richness was the most common biodiversity metric (N=64), compared to functional trait diversity (N=17), evenness (N=11), or another diversity metric (N=17).

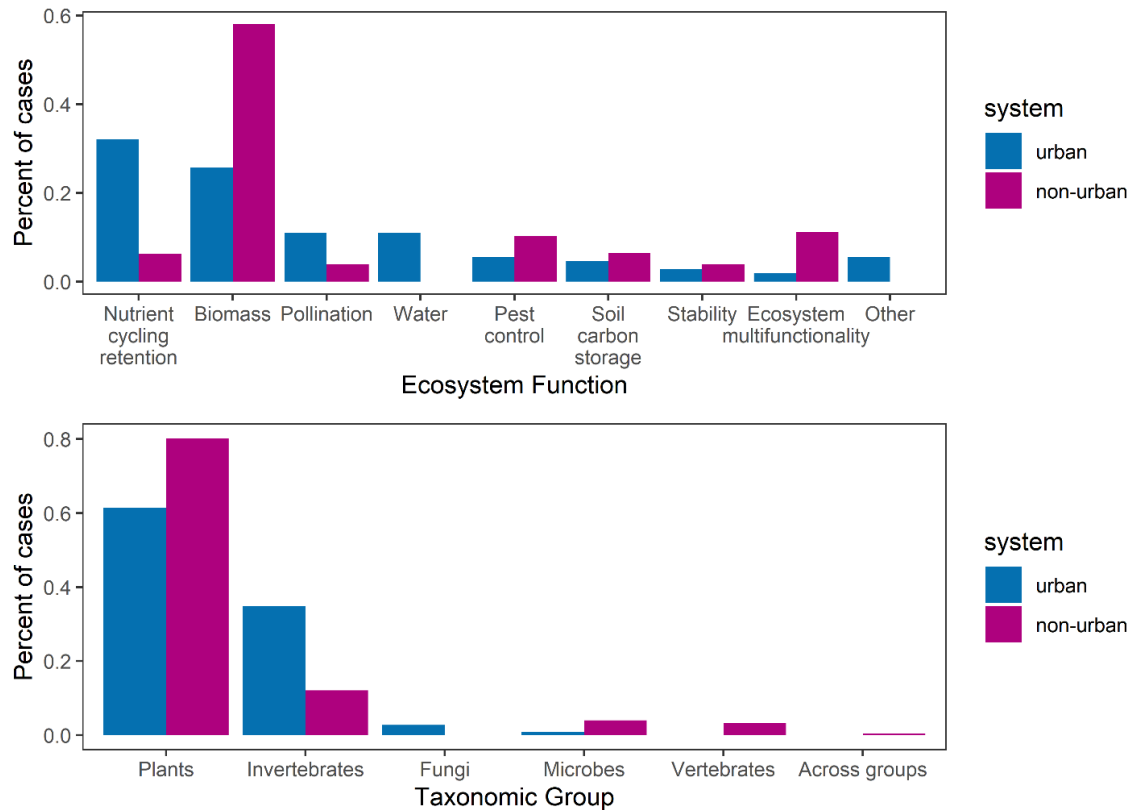


Figure 1.1: Spread of evidence on biodiversity-ecosystem functioning relationships by ecosystem function (a) and taxonomic group (b) for urban areas (this study, n=109 cases) compared to non-urban areas (data drawn from (van der Plas 2019), n=1,219 cases)

BEF relationships

Urban ecosystem functioning was significantly more likely to have a positive than a negative relationship with biodiversity, but neutral relationships were also common (Supplemental Table 1.2). When spatial correlation studies were removed, the

relationship was even stronger (Supplemental Table 1.2). Three functions had at least ten positive or negative cases. Of these, greater biodiversity increased pollination and nutrient cycling and retention, while biodiversity was equally likely to increase or decrease biomass production and storage (Supplemental Table 1.2). Compared to non-urban systems, pollination and nutrient cycling had a higher proportion of positive relationships between biodiversity and function in urban systems, while biomass had a higher proportion of negative relationships (Figure 1.2). When spatial correlation studies were removed, pollination results were not changed (Supplemental Table 1.2). Biomass and nutrient cycling and retention did not have enough observations for the χ^2 -goodness of fit tests, but the proportion of positive relationships between biodiversity and function increased when spatial correlations were removed (seven positive vs. two negative for biomass, eight positive vs. zero negative for nutrient cycling and retention).

My random forest model identified inference type (i.e., biodiversity isolation or spatial correlation), ecosystem function, and ecosystem type as the three most important variables for classification (Figure 1.3). Although 43% of studies also considered whether species identity influenced the level of functioning, this was not an important classification variable. The classification tree showed that studies assessing spatial correlations between biodiversity and ecosystem functioning were more likely to find negative relationships for biomass and water dynamics than for nutrient retention and recycling. Among studies that assessed biodiversity isolation, freshwater ecosystems showed more neutral and negative effects of biodiversity than terrestrial systems.

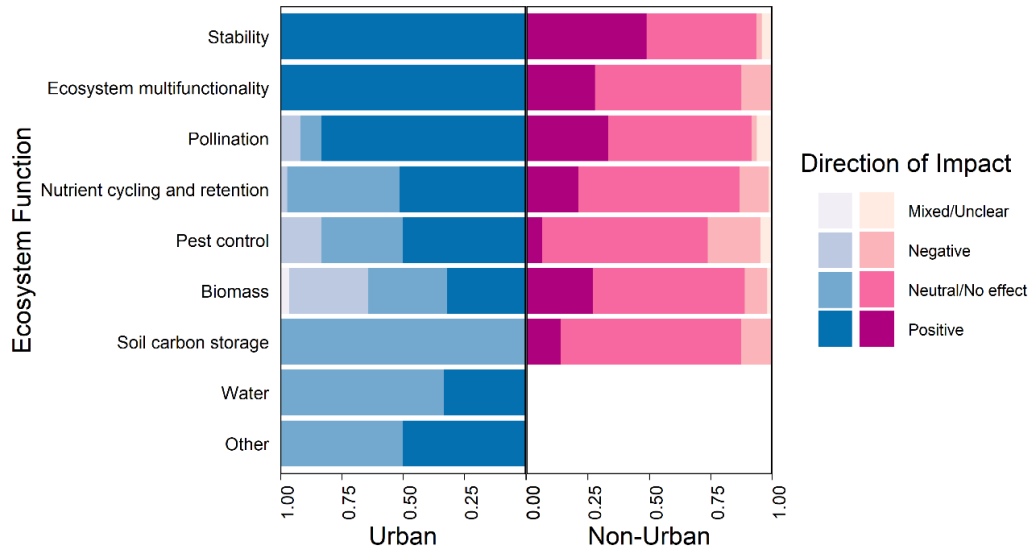


Figure 1.2: Comparison of proportion of positive, negative, neutral, and mixed responses of biodiversity-ecosystem functioning relationships by ecosystem function in urban (this study, n=109 cases) vs non-urban systems (data drawn from (van der Plas 2019), n=1,219)

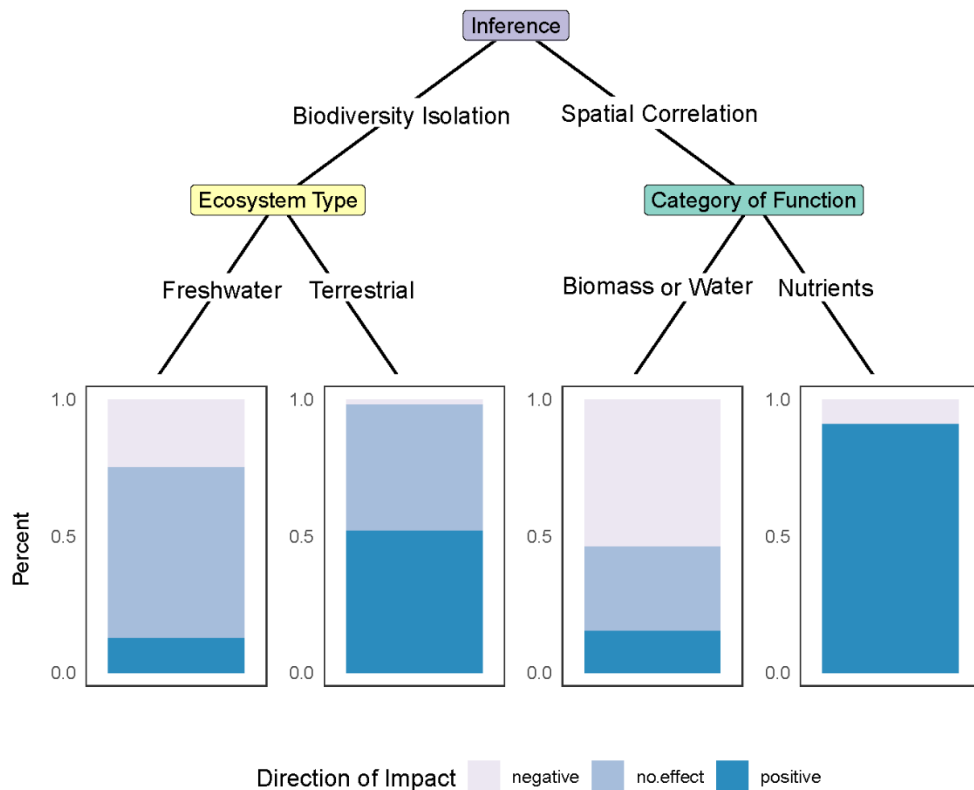


Figure 1.3: Random forest classification tree resulting from 10,000 model iterations with the significance level for tree splits set to $\alpha=0.05$. Studies assessing spatial correlations between biodiversity and ecosystem functioning were more likely to find negative relationships for biomass and water dynamics, but more likely to find positive relationships for nutrient retention and recycling. Among studies that attempted to isolate the effects of biodiversity on ecosystem functioning, freshwater ecosystems showed more neutral and negative effects of biodiversity than terrestrial systems, which showed almost exclusively positive or neutral effects.

Discussion

I found that biodiversity was positively associated with ecosystem functioning in urban areas, especially in terrestrial urban environments and studies that attempted to isolate biodiversity effects. However, similar to findings for urban biodiversity-ecosystem service relationships, neutral relationships were also quite common (Schwarz

et al., 2017; Ziter, 2016). Among the most studied functions, greater biodiversity was associated with increased pollination and nutrient cycling and retention, whereas biomass was equally likely to increase or decrease with biodiversity (Figure 1.2). Removing spatial correlation studies greatly reduced the number of negative cases for biomass. While water dynamics were also frequently studied, biodiversity often did not affect functioning.

Pollination: Studies that explored floral resource diversity and pollinator diversity documented an increase in pollination. Complementarity between pollinator species could drive this relationship. For example, in a Chicago urban garden experiment, different plant species benefited from a different suite of pollinators so, at the plant community level, pollinator species diversity increased overall yield (Lowenstein et al., 2015). Further, most of the common pollinator species in urban areas are generalists (Lerman & Milam, 2016). Thus, each additional pollinator species might increase overall pollination rates. Interestingly, multiple studies reported higher pollinator abundance, richness, and/or pollination rates in higher population density neighborhoods or urban compared to rural areas (Hall et al., 2017; Lowenstein et al., 2014; Theodorou et al., 2016). Many bees and other pollinators can benefit from native and non-native plants, and urban yards can have high plant diversity that provides nectar and pollen throughout the growing season (Frankie et al., 2009; Hall et al., 2017; Lerman et al., 2018). For example, in Chicago, more neighborhoods with higher human densities had a higher diversity of flowering plants (Lowenstein et al., 2014), and pollinators may be willing to travel farther to get to diverse floral patches (Jha & Kremen, 2013). This could explain

why biodiversity was more likely to increase pollination in urban compared to non-urban systems.

Nutrient cycling and retention: I found that decomposer diversity generally increased nutrient recycling in urban areas. Multiple studies found greater invertebrate species richness increased leaf litter decomposition (e.g., (Lemes da Silva et al., 2020; Tresch et al., 2019)). However, one study found a negative relationship; in this case, the presence of a highly efficient invasive ant species (*Tetramorium sp. E*) overpowered any effect of arthropod diversity on decomposition (Youngsteadt et al., 2015). Plant diversity also increased the rate of decomposition in non-urban systems (Mori et al., 2020), but most urban studies focused on decomposer diversity only. Increased plant and arthropod species diversity increased nitrogen retention in soils, including in urban grasslands and green roofs (C. Johnson et al., 2016; G. L. Thompson & Kao-Kniffin, 2016). In some cases, other site factors like impervious surface and land use had stronger effects on nitrogen cycling than biodiversity effects (Onandia et al., 2019). In particular, high percentages of impervious surfaces can lead to more runoff and greater nitrogen leaching (Grimm et al., 2008; Kaye et al., 2006), rendering urbanized areas as sources of nutrient pollution.

Biomass: The lack of a strong biodiversity effect on biomass is surprising given the strong evidence for increased biomass with increased diversity in non-urban systems (Cardinale et al., 2011, 2012; Hooper et al., 2012; Loreau et al., 2022; O'Connor et al., 2017). One explanation for a weak effect of biodiversity on biomass may be the high level of plant species manipulation in urban environments, which happens via planting and maintenance of trees, shrubs, and other vegetation. Urban residents plant high

numbers of ornamental exotic species, leading to distinctive plant communities (M. Avolio et al., 2020; Padullés Cubino et al., 2020). Human manipulation of the plant community can alter the patterns of succession and disrupt coexistence mechanisms (Loreau, 2004; Vandermeer, 1981) that typically take place in non-urban systems, which could weaken biodiversity-ecosystem functioning relationships. Selection effects occur when the highest performing species becomes dominant, but the effect on biomass could be dampened if humans artificially select for less productive species, perhaps to gain other desirable benefits unrelated to biomass production. Pesola et al. (2017) compared biodiversity and aboveground biomass in urban forest plots of varying ages in Milan, Italy. Selective silvicultural thinning over time reduced competition and resulted in a few dominant species in the oldest, highest biomass plots, thus leading to a negative relationship between biodiversity and biomass (Pesola et al., 2017).

On a theoretical level, positive relationships between biodiversity and function are not always expected from observational field data that measure realized diversity (i.e., diversity at the time of the survey) (Hagan et al., 2021; Loreau, 1998). If complementarity is the main driver of positive BEF relationships, then we would expect increased realized diversity to increase ecosystem functioning. For example, an experimental urban green roof study found that increasing plant diversity increased plant biomass, and that this effect was due to complementarity (C. Johnson et al., 2016). However, if selection effects are the main driver of positive BEF relationships, then biodiversity leads to the increases in function when initial diversity is high, but then the highest functioning species outcompete other species, leading to lower realized diversity. Therefore, using observational field data to measure BEF relationships may

underestimate the importance biodiversity has to ecosystem functioning (Hagan et al., 2021). This may have played a role in the lack of an effect of plant species diversity on biomass in urban forests in San Juan, Puerto Rico, where tree and shrub species identity influenced aboveground carbon storage, while overall species diversity (measured in a single year) did not (Timilsina et al., 2014). Moreover, environmental variation (e.g., soil fertility) can also mask biodiversity effects by inducing a negative correlation across space, even when there is a positive covariance over time (Isbell et al., 2013; Loreau, 1998). Indeed, when I removed spatial correlation studies, the percentage of cases with positive effects of biodiversity on biomass increased. This suggests that although the urban places that are most diverse will not necessarily be those that have the most biomass, increasing (or decreasing) biodiversity within a particular urban environment may still increase (or decrease) biomass.

Water dynamics: Most studies found that biodiversity did not affect water dynamics, despite expectations from non-urban communities that diverse communities capture more resources, including water (Cardinale et al., 2012). One green roof study found that diverse plant species mixtures had higher water capture rates than nearly all monocultures (Lundholm et al., 2010). This may be due to complementarity of growth phenology; because different species used water at different times, species mixtures were able to provide more stable water uptake over time (Lundholm et al., 2010). In contrast, a different green roof experiment did not find an effect of diversity on water capture, possibly due to the shorter length of the study or lower overall vegetation density (C. Johnson et al., 2016). Similarly, an afforestation experiment in New York City did not

find significant effects of plant diversity on water holding capacity after one year, which may not have been enough time for trees and shrubs to establish (Oldfield et al., 2014).

Research gaps and future directions

My random forest model identified inference type, ecosystem function category, and ecosystem type as useful metrics to predict how biodiversity might affect ecosystem functioning in urban areas. Differences between spatial correlation and biodiversity isolation inference studies is unsurprising given that positive relationships between biodiversity and function are not always expected when comparisons are made only across space. Nor is it surprising that ecosystem function would influence the relationship, given the variation observed across functions in both urban and non-urban systems (Figure 1.2). However, the more negative relationships in freshwater ecosystems was unexpected, as biodiversity-ecosystem functioning relationships were found to be similar for terrestrial and aquatic primary producers and even stronger for aquatic herbivores and detritivores (O'Connor et al., 2017). My result could be driven by a limited number of freshwater studies (n=4), including one where urban runoff added nutrients to the experimental wetland, leading to fewer, more productive species becoming dominant over the course of the experiment (Doherty & Zedler, 2014). Similar findings have been observed in fertilized terrestrial systems (Isbell et al., 2013). This highlights that, overall, the number of studies and geographic coverage of my study was too low to create a general predictive framework for how these metrics might lead to differential biodiversity-ecosystem functioning relationships. Therefore, to better understand urban biodiversity-ecosystem functioning relationships, I use my results to

identify limitations of existing studies, research gaps, and directions for future research which are summarized in Table 1.1 and described below.

Temporal and spatial scales: Most studies included in my review occurred over very short time frames (all under five years, and many less than one year). BEF relationships grow stronger over time (Isbell et al., 2011; Reich et al., 2012), and longer studies would provide an opportunity to assess whether biodiversity leads to more stable functioning in urban areas. Both studies of stability included in my review found positive effects of biodiversity (Lundholm et al., 2010; Manes et al., 2012). In addition to temporal scales, studies at greater spatial scales are needed to understand the effects of larger scale processes like dispersal and the influence of beta diversity. Ninety one percent of cases in my study were measured at scales of $<1\text{km}^2$, while 92% covered only one urban area. In addition, as the evidence base for urban biodiversity-ecosystem functioning relationships increases, it would be informative to explore differences across types of urban habitats (e.g., highly managed greenspaces vs. remnant forest patches). Further, urban areas included in my study were highly skewed towards North America. Increasing geographical scope is important because different urban areas have different levels of biodiversity, which can be driven by factors such as local climate, time since development, and land use histories (Lerman, Narango, Andrade, et al., 2021; Ramalho & Hobbs, 2012), and thus might show different biodiversity-ecosystem functioning relationships.

Assess more ecosystem functions and multifunctionality: Most papers in my review assessed BEF relationships for biomass or nutrient retention or cycling (Figure 1.1). The bias towards biomass-related functions is also predominant in BEF studies in

non-urban systems (van der Plas, 2019). Most papers looked at individual functions, while only one assessed the importance of biodiversity for multifunctionality. Since higher diversity is needed to maintain multiple functions (Cardinale et al., 2012; Hector & Bagchi, 2007; Tilman et al., 2014), single-function studies may underestimate the importance of biodiversity for ecosystem functioning in urban areas. It is also important to measure ecosystem functions directly; changes in the composition of species traits or abundances do not always result in changes to ecosystem functioning, thus inferences between functional traits and function cannot be assumed (Mayer-Pinto et al., 2018).

Taxonomic diversity and multiple trophic levels: I found that most studies assessed how plant diversity affected ecosystem functioning, while animal, fungi, and microbes were rarely assessed (Figure 1.1, supplemental figure 1.1). Additionally, most studies assessed horizontal diversity (i.e., diversity within a trophic level), while few considered vertical diversity (i.e., diversity across trophic levels). Loss of diversity across trophic levels can impact ecosystem functioning by altering food webs, leading to trophic cascades (Dirzo et al., 2014; Hooper et al., 2005). For instance, urban plant and predator diversity can influence pathogen damage both through direct effects on pest species and by influencing the composition of the non-urban enemy community (Bennett & Gratton, 2012). Despite the general knowledge that disruptions of food webs are possible, it is still unclear how species loss in one trophic level may impact other levels of the food web (Tilman et al., 2014). Feedbacks across trophic levels remain an important gap in my understanding of BEF relationships (Eisenhauer et al., 2019).

Assess multiple metrics of diversity: The majority of cases in my study assessed species richness as the diversity metric. However, species richness, functional diversity,

and evenness are not always correlated (Aguirre-Gutiérrez et al., 2017; Díaz & Cabido, 2001; Hillebrand et al., 2008; Stirling & Wilsey, 2001; Wilsey, Chalcraft, et al., 2005), and all metrics of community composition can be affected by global change (M. L. Avolio et al., 2021). Urban areas can have reduced evenness compared to non-urban areas (Shochat et al., 2010), and as discussed above, species dominance can influence BEF relationships by reducing complementarity and influencing selection effects. Therefore, studies of multiple metrics of biodiversity are important for understanding BEF relationships in urban areas. Additionally, most studies in my review measured alpha diversity, but did not account for important large-scale processes like species dispersal or species turnover (beta diversity) that may be important for maintaining diversity and ecosystem functioning.

Impact of non-native species: Non-native invasive species can disrupt ecosystem functioning (Pejchar & Mooney, 2009). Only 22% of the cases in my study considered the impact of invasive or non-native species on BEF relationships. Of those, the majority found negative (30%) or neutral impacts (30%) of non-native species, while only 5% found positive impacts, and 35% were unclear. Non-native species assemblages may have lower complementarity than native species assemblages (Wilsey et al., 2009). For example, (Doherty & Zedler, 2014) found negative correlations between species richness and biomass in un-weeded field sites where non-native invasive species became dominant, but not in a controlled mesocosm experiment. Given that urban areas can have high non-native species richness, especially for plants (Aronson et al., 2014), greater consideration of how non-native plants influence ecosystem functioning is warranted to better understand how invasive species might disrupt BEF relationships.

Mechanisms for biodiversity-ecosystem functioning relationships: Most studies did not explicitly test mechanisms behind observed biodiversity-ecosystem functioning relationships. Understanding mechanisms can help inform management decisions. For example, if complementarity was the main driver of positive biodiversity-ecosystem functioning relationships, then planting diverse assemblages in urban managed ecosystems could increase functioning. If, however, selection effects were a stronger driver, then managers might instead choose to manage for species that are “best” at providing desired functions (Ranalli & Lundholm, 2008). Even so, different species are the “best” at different times and places (including through time as the climate changes), making it challenging to correctly identify these species. Techniques such as structural equation modeling and Bayesian hierarchical modeling can provide insight into causal mechanisms.

Table 1.1: Future research directions for understanding urban BEF relationships

Future research direction	Rationale
Conduct studies over longer timescales	BEF relationships grow stronger over time. Longer studies can better assess the impacts of diversity on ecosystem function stability.
Increase diversity of urban areas where BEF relationships are measured	BEF relationships may differ depending on urban area characteristics such as time since development, level of urbanization/urban density, amount of

	biodiversity in the area, and climate. More data is needed to parse these differences.
Increase taxonomic coverage of biodiversity metrics	Most studies assessed BEF relationships for plants or invertebrates. While plant diversity is easier to measure, other taxonomic groups (e.g., mammals, birds) also provide important functions that have yet to be assessed.
Assess BEF relationships across trophic levels	Most studies assessed the impact of horizontal (i.e., within trophic level) diversity but did not assess vertical (i.e., across trophic level) diversity. Loss of diversity across trophic levels can impact ecosystem functioning by altering food webs, leading to trophic cascades
Assess multiple metrics of diversity	Most studies investigated the impact of species richness on ecosystem functioning. However, species richness and other diversity metrics may not respond the same way to environmental changes. In addition, species evenness may be an especially important metric in urban areas where a few species dominate.

Assess more functions and multifunctionality	A greater diversity of species are needed to provide multiple services. Single function studies may underestimate the level of diversity required.
Investigate the impact of invasive species	Urban areas can have high numbers of invasive species. Native species assemblages often show greater complementarity than exotic species assemblages, but few studies included an assessment of the impact of invasive species on BEF relationships.
Assess mechanisms behind BEF relationships rather than only correlations	Understanding whether BEF relationships are driven by complementarity or selection effects, and how spatial and temporal beta diversity within urban areas affects temporal and spatial selection effects, can change management strategies.

Management implications

Landscape planners often consider the extent and location of green spaces without considering the role of species diversity for providing important ecosystem functions or services (Haase et al., 2014; Pickett et al., 2011). However, as I have shown, biodiversity

can increase functioning in urban areas and warrants consideration in management plans. A recent review of urban planning documents from 40 cities around the world found that most plans included some goals related to biodiversity or ecosystem services, but few comprehensively included both (Nilon et al., 2017), which means they may be missing opportunities to synergistically achieve both goals. Managers may wish to consider not only species richness, but also species evenness, dominance, and functional traits that are important for providing functioning ecosystems over time (Schmitt-Harsh et al., 2013). For example, including a mixture of small and large tree species, could increase overall carbon storage by increasing overall resource use (Schmitt-Harsh et al., 2013). Moreover, considering the distribution of biodiversity within cities is important. Low income and minoritized communities often have lower access to green space and biodiversity (Astell-Burt et al. 2014, Haaland and van den Bosch 2015, Schell et al. 2020), which translates to lower access to important ecosystem functions and services.

In practice, management for biodiversity in urban areas can be more complicated than non-urban systems because managers also consider economic, social, and cultural factors (Aronson et al., 2017). Urban plants are often selected because of aesthetics, what will survive, and what is affordable and available for sale in local stores (M. Avolio et al., 2020; M. L. Avolio et al., 2018; Cameron & Blanuša, 2016). For example, residents in Salt Lake City, Utah, ranked beauty and shade as the two most important services provided by street trees (M. L. Avolio et al., 2018). Ease of maintenance is also a major consideration for local landowners and urban greenspace managers (M. Avolio et al., 2020; Larson et al., 2009). However, having a diversity of street trees can increase maintenance costs and even overall CO₂ emissions if pruning and other life cycle care

need to be performed at different time intervals (Strohbach et al., 2012). As a way to balance these considerations, managers in Santa Monica, California, have been planting a single species along some streets, and different tree species along other streets to increase city-wide diversity (Morgenroth et al., 2016). Although such a strategy may not promote complementarity, it could allow for increased stability of functions across the city over time. Another major consideration for urban planners is how to manage for non-native invasive species. Invasive species removal can be costly, and it is still unclear how to strike a balance between invasive species removal and tolerance by people (Aronson et al., 2017). Improved understanding of the role of invasive species in biodiversity-ecosystem functioning relationships could help us understand this balance. For example, if fast-growing invasive species are likely to take over before species-rich mixes can establish, it may be advisable to restore urban areas with a few native cover crops first before adding additional species (Doherty & Zedler, 2014).

Conclusion

As urban areas continue to develop and grow, understanding how to manage urban biodiversity, ecosystem functioning, and associated ecosystem services is especially important. One major challenge for urban biodiversity management is that urban green spaces are managed by millions of individuals spanning public and private land. Thus collectively managing urban green spaces can be challenging, and might hinder biodiversity goals (Aronson et al., 2017). In this review, I have shown that increasing biodiversity, even in small areas, can increase local ecosystem functioning. Therefore, local management that increases biodiversity can have positive benefits for ecosystems and people.

CHAPTER 2

BIODIVERSITY LOSS REDUCES GLOBAL TERRESTRIAL CARBON STORAGE

Abstract

Biological carbon sequestration and biodiversity are tightly linked, but many models projecting carbon storage change do not account for the role which biodiversity plays in shaping the sequestration capacity of terrestrial ecosystems. I link a macroecological model projecting changes in vascular plant diversity with empirical biodiversity-biomass production relationships, to assess the relationship between biomass (carbon storage) loss and biodiversity loss under multiple climate and land-use change scenarios. I found that biodiversity decline could lead to the loss of *7.44-103.14* PgC of vegetation carbon under a global sustainability scenario and *10.87-145.95* PgC under a fossil-fueled development scenario. Carbon loss estimates are even higher when I consider both vegetation and soil carbon (*18.87 – 262.09* PgC and *26.49 – 356.71* PgC). Projected carbon emissions from biodiversity loss could rival emissions expected from other sources such as land-use change (53.8-61.1 PgC (Ciais et al., 2013)) or melting permafrost (20-125.32 (Canadell et al., 2021; Meredith et al., 2019; Schneider Von Deimling et al., 2015)), occurring gradually over the coming decades. This engenders a self-reinforcing feedback wherein higher levels of climate change lead to greater biodiversity loss, which in turn leads to greater carbon emissions and ultimately more climate change. Thus, biodiversity conservation and restoration can help achieve both biodiversity and climate change mitigation goals.

Introduction

Climate change and biodiversity loss have been increasingly recognized as related crises that are most effectively addressed together (Di Marco et al., 2016; Mori et al., 2021; H. O. Pörtner et al., 2021; Soto-Navarro et al., 2020; Strassburg et al., 2020). Hundreds of experimental studies have consistently found that within a place, more diverse assemblages, and in particular more diverse plant assemblages, can more efficiently use available resources and have higher standing biomass production and carbon sequestration (Cardinale et al., 2011, 2012; Duffy et al., 2017; O'Connor et al., 2017). Indeed, biodiversity loss can be one of the major drivers of productivity loss within ecosystems, on par with elevated carbon dioxide or effects of drought (Hooper et al., 2012). Thus, while climate change can affect biodiversity, biodiversity change can also affect climate change by altering carbon sequestration and storage (Mori et al., 2021; Weiskopf et al., 2020). Despite the contribution that biodiversity itself could make to carbon sequestration, high-level nature-based solution initiatives often focus on increasing the spatial extent of natural ecosystems, particularly forests, and not on their diversity or composition (Seddon et al., 2019).

This may, in part, be due to model limitations. Models projecting changes in biodiversity, ecosystem functioning, and ecosystem services typically operate independently and do not account for interactions or feedbacks (IPBES et al., 2016; O'Connor et al., 2021). For example, Earth System Models (ESMs) typically model terrestrial ecosystems using a small number of plant functional types and do not include biodiversity-productivity mechanisms (Wei et al., 2022; Zhou et al., 2021). Not accounting for biodiversity loss may lead to projections that overestimate levels of ecosystem function and ecosystem services, because these estimates assume that remnant

habitat patches will provide the same level of function even in the face of significant losses of species diversity within these patches (Isbell, Tilman, et al., 2015).

Incorporating these relationships could improve model accuracy, especially over long timescales. For example, an Australian ecosystem modeling exercise found that including species turnover in marine ecosystem models led to very different outcomes under different climate change scenarios (Fulton & Gorton, 2014).

Multiple pathways to integrate biodiversity and ecosystem function models have been proposed (Weiskopf et al., 2022). One approach that can be applied at the global scale is to connect biodiversity to ecosystem function and ecosystem service models using empirical, observational, or experimental biodiversity-ecosystem function data. Because of the extensive experimental data on the increase in biomass associated with increasing plant species richness (O'Connor et al., 2017, 2022), assessing how loss of plant diversity will affect carbon storage offers a feasible and important case study to demonstrate the utility of this modeling approach. Moreover, assessments of plant species diversity and carbon storage are relevant for monitoring biodiversity and climate change mitigation goals. Early analyses have been conducted that illustrate this method (Isbell, Tilman, et al., 2015; Mori et al., 2021). For example, Isbell et al. (2015b) linked regional estimates of species loss (using species-area relationships) with biodiversity-ecosystem function relationships derived from local-scale experiments. Yet, that work did not consider compositional turnover or how climate change or future land use change might affect spatial patterns of composition of species. Species turnover and regional species richness likely have important effects on functioning and stability (Isbell et al., 2017;

Mori et al., 2018; S. Wang & Loreau, 2016). Accounting for compositional turnover while estimating regional diversity loss can help address some of these assumptions.

I use the Biogeographic Infrastructure for Large-scaled Biodiversity Indicators (BILBI) model to project plant species loss (Hoskins et al., 2020), going beyond the species-area (Isbell, Tilman, et al., 2015) or endemics-area (Mori et al., 2021) relationships considered in previous studies by also accounting for variation in the species composition of communities (beta diversity) at fine spatial scales. This allows BILBI to be used to assess species persistence/loss over the long term under different scenarios of both land-use and climate change (Di Marco et al., 2019; Hoskins et al., 2020). I link my species loss estimates with empirical biodiversity-biomass production relationships (O'Connor et al., 2017) to assess the biomass, and ultimately carbon storage loss, associated with loss of vascular plant diversity. Like previous analyses (Isbell, Tilman, et al., 2015), I use data from local scale biodiversity experiments to estimate biodiversity-biomass production relationships at regional scales. This assumes that either 1) local loss of species diversity is similar to regional scale biodiversity loss, or 2) species loss occurring at the regional scale has consequences for ecosystem functioning. Although the first assumption may not always be met, there is considerable evidence for the second assumption (Isbell et al., 2017). Furthermore, the advantage of using experimental data is that by strictly controlling for species richness, composition, and other confounding factors, local experiments can disentangle the causal effects of species richness on biomass production. Importantly, my study explores how projected future climate and land-use change scenarios will affect biodiversity loss, and estimates the additional, long-term loss of carbon storage from biodiversity loss that is expected on top

of greenhouse gas emissions projected to arise from direct land-use change or other climate change impacts on carbon stocks (Figure 2.1).

I used BILBI model projections of the proportion of vascular-plant species expected to persist under “global sustainability” and “fossil-fueled development” scenarios that were produced for a recent model intercomparison project (Kim et al., 2018). The BILBI model uses generalized dissimilarity models fitted with more than 52 million records from over 254,000 plant species to map beta diversity at $\sim 1\text{km}^2$ scale globally (see (Di Marco et al., 2019; Hoskins et al., 2020) for complete model fitting information). Following Weiskopf et al. 2022 (pathway A, Figure 4), I combined beta diversity estimates with species-area relationships to assess plant species losses in each ecoregion globally, and then used empirical estimates of biodiversity-biomass production relationships from (O’Connor et al., 2017) to assess proportional changes in plant biomass. Finally, I used projected terrestrial carbon storage maps (which do not include biodiversity losses) from the Coupled Model Intercomparison Project Phase 5 (CMIP5) IPSL-CM5A-MR model to estimate aboveground plant and soil carbon storage losses associated with projected biodiversity loss in each ecoregion (Dufresne et al., 2013).

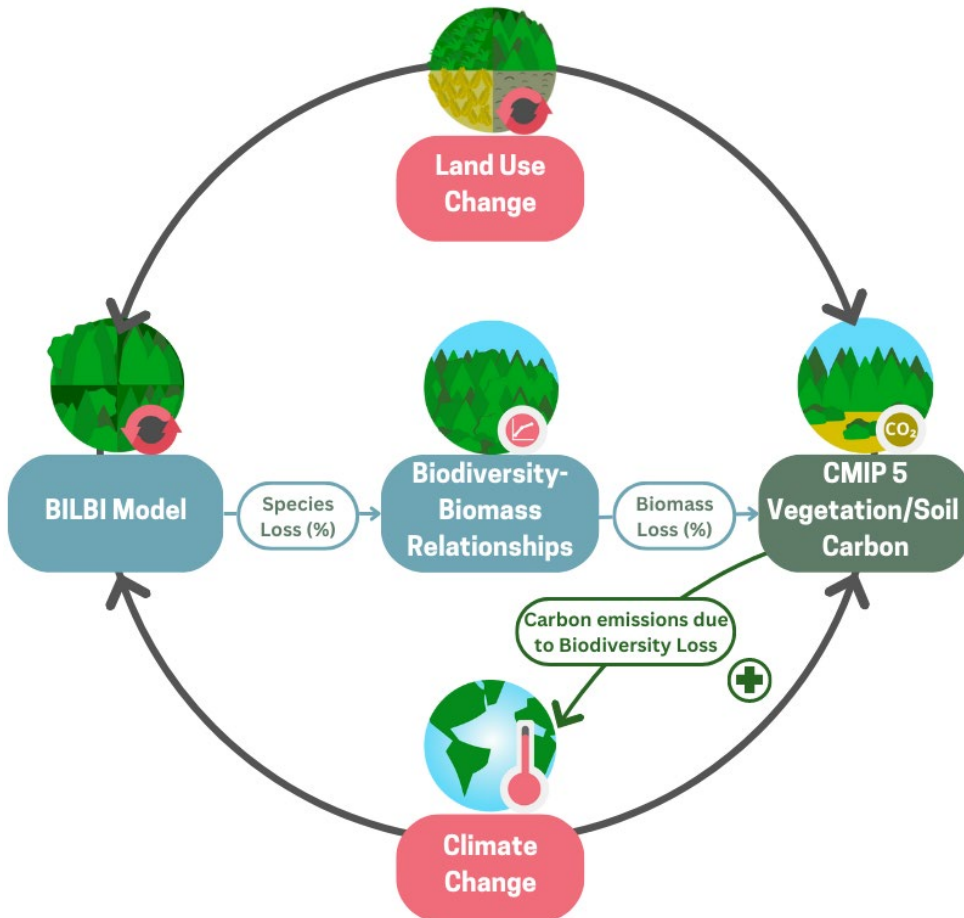


Figure 2.1: Modeling framework for this analysis. Land-use and climate change are used to estimate changes in vegetation and soil carbon (CMIP models) and biodiversity loss (BILBI model). In this analysis, I use BILBI model output of percent species loss and empirical biodiversity-biomass relationships to estimate the effects of biodiversity loss on vegetation and soil carbon storage (blue lines). Biodiversity-driven changes in carbon storage impacts the level of climate change (green line). This engenders a positive feedback wherein higher levels of climate change leads to greater biodiversity loss, which in turn leads to even greater carbon emissions and ultimately more warming (plus symbol).

Results

Under the global sustainability scenario, ecoregions lost an average of 16.0% plant species (ranging from 0.0% to 45.9%; Figure 2.2), leading to an average biomass loss of 4.4% (ranging from 0.0% to 14.7%) (Supplemental Figure 2.1). For reference, it is estimated that 39% of vascular plant species are currently threatened with extinction (Lughadha et al., 2020). This biomass loss is from within remaining vegetation as a result of biodiversity loss, over and above any biomass loss resulting from the direct impact of land-use change under a given scenario. Biodiversity and biomass losses were higher under the fossil-fueled development scenario, with ecoregions losing an average of 20.9% of plant species (ranging from 0.0% to 46.2% across individual ecoregions; Figure 2.2), leading to an average biomass loss of 5.9% (ranging from 0.0% to 14.87%; Supplemental Figure 2.1). In both scenarios, plant species loss, and therefore biomass loss driven by plant species loss were especially high in the tropics. Southern Australia, eastern Europe, and some regions of South America also had high losses.

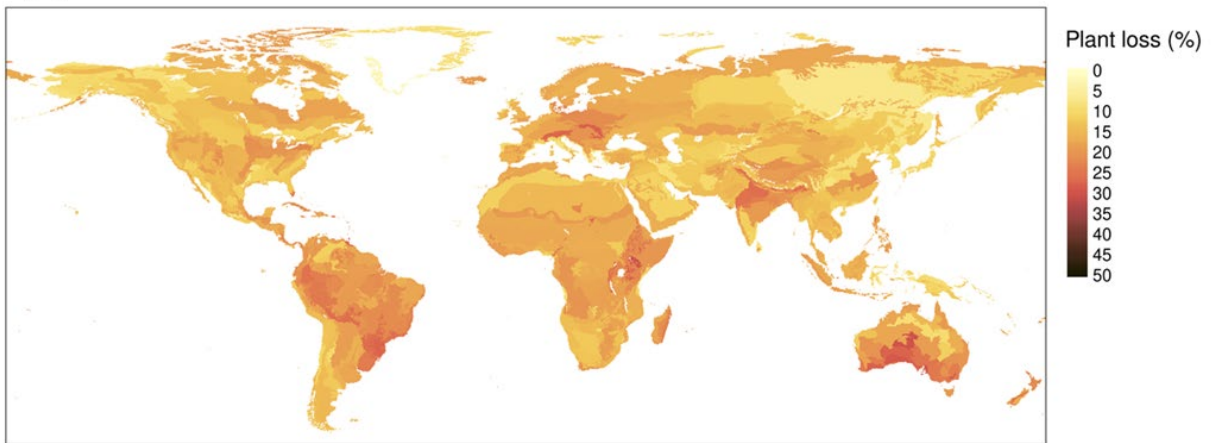
When I applied the biomass loss values to projected carbon storage maps, I found that overall vegetation carbon loss was greatest in the tropical regions of South America, Central Africa, and Southeast Asia, which was driven by which regions store the greatest amount of vegetation carbon and by the level of biodiversity loss (Figure 2.3). For example, biodiversity loss projections and vegetation carbon are both high in the Amazon, making this a hotspot of biodiversity-driven carbon loss. In contrast, biodiversity loss projections are also high in Southern Australia, but because this region has lower vegetation carbon, it is not an area with high biodiversity-driven carbon loss.

When summed across all terrestrial ecoregions, biodiversity declines lead to loss of 7.44-103.14 PgC of vegetation carbon in the long term under global sustainability and 10.87-145.95 PgC under fossil-fueled development. Again, this refers to losses within remaining habitat, above those resulting from direct impacts of land-use change on vegetation extent. When soil carbon is also considered, given that they may also strongly depend on plant diversity (Yang et al., 2020), potential carbon loss increases dramatically to 18.87 – 262.09 PgC under the global sustainability scenario and 26.49 – 356.71 PgC under the fossil-fueled development scenario (Supplemental figures 2.7 and 2.8). The range of carbon loss values is estimated from the full range of species-area relationships and biodiversity-biomass production estimates, thus capturing a large range of uncertainty in the strengths of these relationships within and among sites (Supplemental Figure 2.6). These carbon losses per ecoregion depend not only on how much plant diversity is lost from the ecoregion, but also the remaining area of the ecoregion, given that they are summed up across all remaining habitat (Figure 2.4). For example, under the global sustainability scenario, the overall loss of carbon is higher from the ecoregions that have lost 10-20% of plant species diversity compared to ecoregions that lost >20% of their diversity because the former cover larger areas (Figure 2.4).

Projected carbon emissions from biodiversity loss could rival emissions expected from other sources such as land-use change or melting permafrost (Supplemental Table 2.1). My models predicted long-term vegetation carbon emissions from long-term biodiversity loss (i.e., over the coming decades as the system moves towards a new equilibrium state) driven by climate and land-use change projections for 2050 were equivalent to about 12-169% of the total emissions expected from land-use change by

2100 for the global sustainability scenario, and about 20-271% for the fossil-fueled development scenario (Supplemental Table 2.1).

A



B

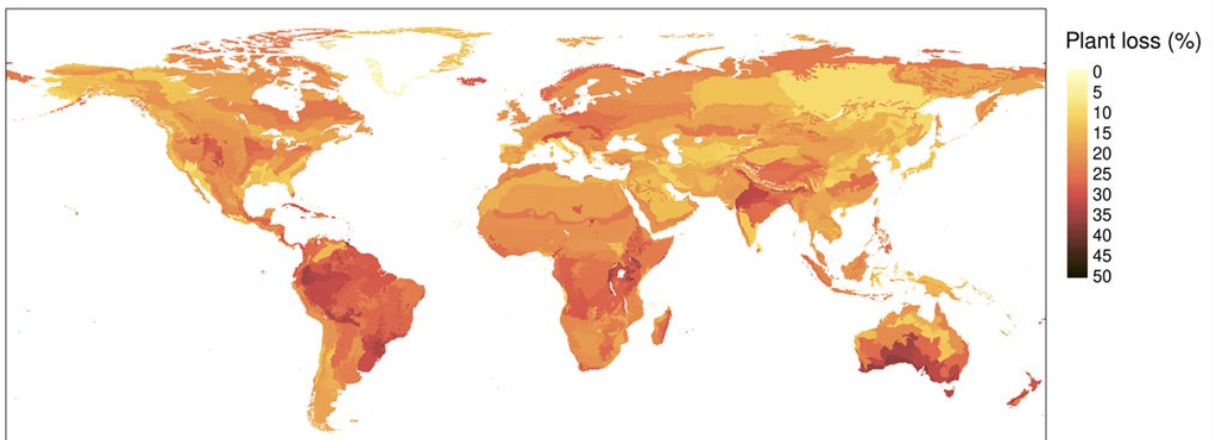


Figure 2.2: Species loss - Plant species loss by ecoregion projected by the BILBI model under a global sustainability (SSP1/RCP2.6, panel A) and fossil-fueled development (SSP5/RCP8.5, panel B) scenario using a species-area relationship of $z=0.25$. Darker areas indicate greater plant species loss.

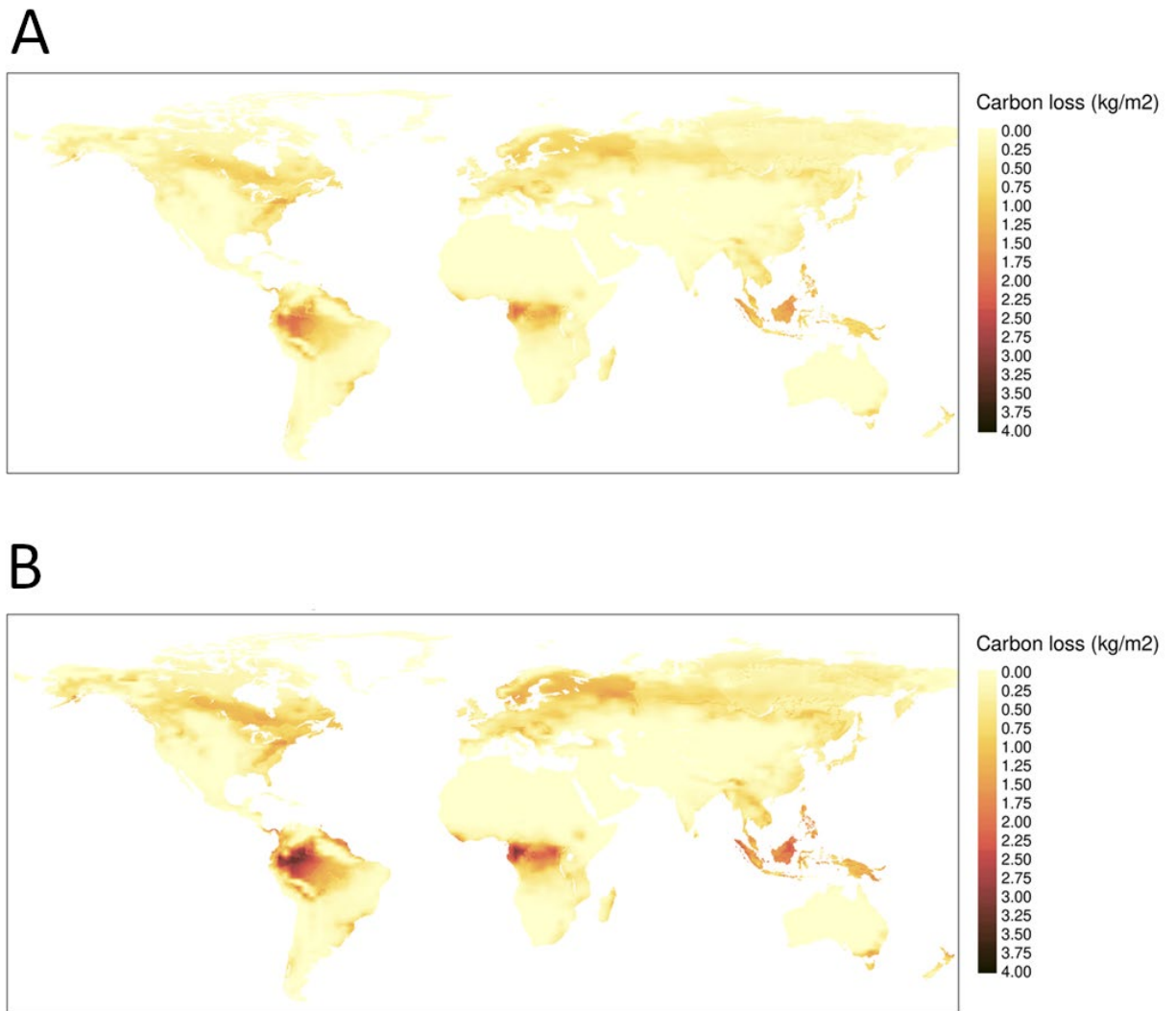


Figure 2.3: Carbon loss (kg/m^2) driven by long-term loss of plant biodiversity by ecoregion under a global sustainability (SSP1/RCP2.6, panel A) and fossil-fueled development (SSP5/RCP8.5, panel B) scenario using the mean BEF slope $b = 0.26$ and a species-area relationship slope $z=0.25$. Darker areas indicate greater carbon loss. This carbon loss is from within remaining vegetation as a result of biodiversity loss, over and above any carbon loss resulting from the direct impact of land-use change (e.g., deforestation) under a given scenario.

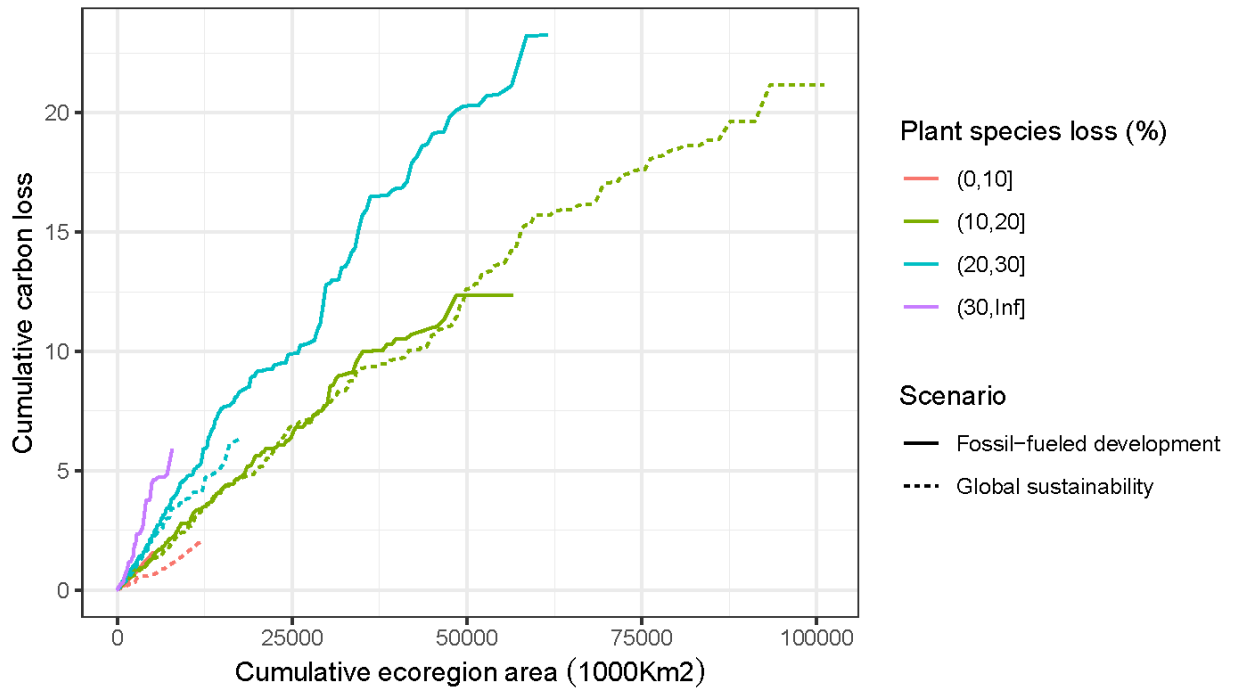


Figure 2.4: Cumulative carbon loss by cumulative ecoregion area (added from smallest to largest ecoregion size) grouped by proportion of plant species diversity lost in the ecoregion for a global sustainability scenario (SSP1/RCP2.6) and fossil-fueled development scenario (SSP5/RCP8.5). Because carbon losses are summed across all remaining habitat, places with moderate biodiversity loss can contribute more to overall carbon loss than areas of high biodiversity loss.

Discussion

I used a macro-ecological model to predict changes in overall plant species richness and linked it with empirical estimates of the plant biodiversity-biomass production relationship based on experimental data. Biodiversity loss can reduce global

carbon storage potential leading to high loss of vegetation carbon, and very high loss of total carbon (vegetation + soil). Substantially greater loss is projected under the more intense climate change and land-use change scenario, but even a sustainability scenario (compliant with the Paris target of 2°C) carries high risks, similar to findings for mammals and wilderness areas (Asamoah et al., 2022; Mendez Angarita et al., 2023). This engenders a positive feedback wherein higher levels of climate change lead to greater biodiversity loss, which in turn leads to even greater carbon emissions.

Another recent analysis using a different approach (linking species distribution models and other relationships for 2005-2070s) found an even greater productivity loss associated with climate and land-use driven biodiversity loss, such that mitigation activities that maintain tree diversity could avoid a 9-39% loss of productivity across terrestrial biomes (Mori et al., 2021). Together, these findings indicate that biodiversity loss can be a strong driver of carbon emissions.

Priority areas for biodiversity conservation and climate change mitigation could change by accounting for the role of biodiversity in promoting carbon storage. For example, (Soto-Navarro et al., 2020) identified few priority areas in Central Africa in the top 20% of overlap areas between biodiversity and carbon importance. However, I found that carbon losses due to biodiversity loss were high in this area (Figure 2.3), and therefore that biodiversity protection and restoration here could be highly valuable for climate mitigation (Cimatti et al., 2022). Projected biodiversity loss and associated percent biomass loss were higher in the Amazon and Central Africa under the fossil-fueled development scenario compared to the global sustainability scenario, but are consistently high in the European Alps and Southern Australia across scenarios. For total

carbon emissions, interactions between biodiversity loss and ecosystem-level carbon storage led to consistently high losses of carbon in the tropics under both scenarios, specifically in the Amazon, Central Africa, and Southeast Asia, and moderately high losses in boreal forests. These places thus represent potential hotspots in terms of biodiversity and carbon storage loss.

A recent global model intercomparison of ecosystem function models, including dynamic global vegetation models (DGVMs), found similar patterns of carbon loss across South America and Central Africa (Pereira et al. 2020). These models also found high losses in northern Africa that I did not find from biodiversity loss alone. In contrast, the model intercomparison estimated ecosystem carbon gains in high northern latitudes, whereas I found that these areas may experience carbon losses from biodiversity loss. Interestingly, the model intercomparison found little difference in total ecosystem carbon between global sustainability and fossil fueled development scenarios, likely due to CO₂ fertilization with higher levels of climate change (Pereira et al., 2020). These differences are not unexpected, given that the DGVMs represent global plant diversity as a small set of plant functional types and simulate their distribution and biogeochemical cycles across the world under different climate and land-use change scenarios. Thus, these models are not accounting for how changes in species diversity within an area will affect biomass. Incorporating biodiversity-biomass relationships could be a useful way to improve DGVMs in the future.

Earth system models generally project increasing land carbon accumulation in high latitudes and decreasing accumulation in the tropics (Canadell et al., 2021). Similar to (Mori et al., 2021), I found that total carbon loss from biodiversity loss was also

greatest in the tropics (driven by the interaction between biodiversity loss and the location of high carbon stores), which may represent additional losses not captured in current models. Moreover, when proportional loss is considered, other areas such as southern Australia and the European Alps become hotspots of biodiversity and carbon loss (Supplemental Figure 2.1).

The IPCC estimates that the remaining carbon budgets - the amount of carbon that can be emitted by human activities while still limiting global warming to specified levels - is 140 PgC for limiting warming to 1.5°C, and 310 PgC for limiting warming to 2°C, although there is substantial uncertainty around these estimates (Canadell et al., 2021). My high-end estimates for carbon loss from biodiversity loss exceed these limits (262.09 PgC under the global sustainability scenario and 356.71 PgC under the fossil-fueled development scenario). Not considering biodiversity loss in emissions scenarios could lead to severe overestimates of terrestrial carbon stocks and remaining carbon budgets.

Overall, my analysis points to the important role that maintaining and/or enhancing the diversity of plant species within areas of natural vegetation, in addition to increasing the extent of these areas, can play in addressing the climate change crisis. Alongside increasing the global extent of protected areas (to prevent rapid carbon loss from ecosystem degradation), increasing plant species diversity in degraded ecosystems can increase carbon storage potential (Strassburg et al., 2020). However, existing international initiatives like the Bonn Challenge and the Paris Agreement focus on forest extent rather than forest quality for protection, afforestation, and reforestation (Mori, 2020; Seddon et al., 2019). Further, initiatives that include biodiversity goals may not provide clear definitions of what constitutes a biodiverse restoration (Andres et al., 2022).

This can lead to planting monocultures with non-native species, which could ultimately be detrimental to biodiversity and carbon storage over the long-term (Seddon et al., 2019). Higher biodiversity, with the right species in the right places (van der Plas et al., 2023), could even help reduce the impacts of climate change on biodiversity, and therefore indirectly help maintain carbon storage potential of ecosystems (Hisano et al., 2018).

Restoring biodiversity is necessary to achieve the recently adopted goals and targets of the Kunming-Montreal Global Biodiversity Framework, including those related to biodiversity conservation and nature's contributions to people (United Nations Convention on Biological Diversity, 2022a). In addition to increasing carbon storage, restoring biodiversity has co-benefits for other Sustainable Development Goals, including human health and well-being (Goal 3), zero hunger (Goal 2) and clean water and sanitation (Goal 6) (Díaz et al., 2019). For example, restoring biodiversity can decrease pathogen transmission and disease incidence (Keesing et al., 2010; Ostfeld, 2009; Pongsiri et al., 2009). Increasing genetic diversity of crops can increase yields, and increasing tree species diversity can increase the production of wood in plantations (Cardinale et al., 2012; Feng et al., 2022). Diverse systems can also be more resistant to climate extremes (Isbell, Craven, et al., 2015). Thus, ecological restoration with explicit focus on biodiversity has a major role to play in achieving global sustainability goals.

Accounting for Limitations

I estimate how projected biodiversity loss could reduce global terrestrial ecosystem carbon storage, and how much of this loss can be prevented by achieving targets set under the Paris Agreement. Although informative, there are a number of

uncertainties and limitations that should be refined in future assessments. First, my empirical relationship between biodiversity and biomass production comes from a meta-analysis of hundreds of experiments conducted at the local scale (O'Connor et al., 2017), which does not directly match the ecoregion scale of the BILBI model analysis. As discussed above, this assumes that either 1) local loss of species diversity is similar to regional scale biodiversity loss, or 2) species loss occurring at the regional scale has consequences for ecosystem functioning of a similar magnitude to those for species loss at a local scale. As well, turnover between sites is most likely to support positive biodiversity-biomass production relationships in abiotically heterogeneous landscapes with intermediate dispersal (Isbell et al., 2017; van der Plas et al., 2023).

However, there are several theoretical reasons why I expect biodiversity-ecosystem functioning relationships observed at a local level to be equally strong, and perhaps even stronger, across larger spatial extents. Larger spatial and temporal extents will encompass a greater range of environmental conditions. In turn, this provides greater opportunity for niche partitioning, and thus positive BEF relationships (Gonzalez et al., 2020; Isbell et al., 2017). Additionally, whole landscapes require more species to maintain ecosystem functioning than do individual locations, with more diversity needed at broader spatial and temporal scales (P. L. Thompson et al., 2021). Indeed, the effects of biodiversity grow stronger (and less saturating) over time (Reich et al., 2012). Accounting for local compositional turnover while estimating regional diversity loss, as I did here, can help address some of these assumptions. Additionally, I presented estimated carbon losses over a large range of potential BEF relationship values to capture some of the uncertainties introduced by these assumptions.

Second, the BILBI model assumes that if changes result in non-analog climatic conditions, species will not persist (and thus does not allow for adaptation or tolerance of conditions not experienced at present) and it does not consider the possibility of increasing species richness in some ecoregions with climate change induced range shifts. Thus, the model presents a somewhat pessimistic estimate of biodiversity loss from climate change, a common issue with many species distribution model approaches. However, native species assemblages have greater complementarity than exotic species assemblages due to longer histories of interactions. Thus, increasing species richness by adding species not previously present in the ecosystem may have a relatively small effect on productivity (Wilsey et al., 2009).

Third, it is important to correctly interpret the findings from my analysis. The BILBI model uses the species-area relationship to assess plant species persistence, meaning that it projects plant species losses expected in the *long term* due to habitat conditions in a given year (e.g., poor conditions in 2050 might generate losses beyond 2050). Therefore, my carbon storage loss estimates are also what is expected over the *long term*, when ecosystems approach to their new equilibrium states, based on climate and land-use changes projected for 2050, whereas land-use and permafrost emissions were estimated from climate and land-use changes from present conditions up to 2100. Although long term is not easily defined, the way that species loss scales with area becomes larger over longer timeframes (Rosenzweig, 1999). Thus, estimates produced using smaller species-area estimates are more likely over shorter timescales, while larger losses become increasingly likely as more time elapses. By using a range of species-area

relationship values, I attempt to capture the range of future biodiversity-driven emissions that I might see over different time scales.

Fourth, my estimates of total carbon loss are based on projected carbon maps from a single CMIP5 model (IPSL-CM5A-MR). My goal was to compare scenarios with each other and provide a range of reasonable carbon loss estimates rather than absolute losses, and ESM uncertainty is a minor source of uncertainty compared to scenarios and model settings (Thuiller et al., 2019). I used projected carbon maps from the IPSL-CM5A-MR model to be consistent with my biodiversity model input parameters, but land carbon uptake estimates vary across CMIP5 and CMIP6 models (Arora et al., 2020). Among CMIP5 models assessed, IPSL-CM5A-MR correctly reproduced the global land sink in comparisons with historical data, but was not the best performing model for the cVeg variable that I used in this analysis (Anav et al., 2013). Recent analysis found that IPSL-CM5A-MR produced estimates of near-present plant carbon within the range of observation-based estimates in the non-circumpolar region, but overestimated the circumpolar regions (Wei et al., 2022).

Finally, I ran my model using vegetation carbon only, or using both vegetation and soil carbon. I did not account for potential changes in litter carbon. Increasing biodiversity increases the rate of litter decomposition (i.e., less litter mass storage), which could add to increasing decomposition from warming, and thus I would expect biodiversity loss to increase litter carbon storage. While the strength of the biodiversity-carbon relationships for soil and litter are not fully established, the effects on litter carbon are likely weaker than those on plant biomass or soil carbon (Balvanera et al., 2006; Cardinale et al., 2011; Mori et al., 2020). For example, decomposition was 34.7% higher

in mixed species forests compared to monocultures, while soil carbon storage was 178% higher in mixed grasslands than in monocultures (Mori et al., 2020; Yang et al., 2019). Moreover, the estimated effects of diversity on plant biomass and soil carbon were driven by short-term studies, and these relationships grow stronger over time in long-term experiments (Reich et al., 2012; Yang et al., 2019, 2020).

Conclusion

Biological carbon sequestration and biodiversity are tightly linked. Biodiversity-mediated carbon loss rivals emissions for other sources, so achieving Sustainable Development Goal 15 (Life on Land) is essential to achieving Goal 13 (Climate Action). While meeting the Paris Agreement would prevent a large amount of carbon loss compared to a fossil-fueled economic development strategy, this scenario is still associated with high carbon loss via biodiversity loss. Therefore, additional mitigation measures may be needed to meet Paris agreement expectations even if current emissions reductions targets are met. Improving my understanding of how biodiversity will adapt to climate change will be key to improving climate impact predictions.

Addressing climate change and biodiversity loss together will be the most effective way to address these crises. Although policymakers are starting to think about climate change mitigation initiatives that have co-benefits for biodiversity, the role of biodiversity itself in promoting carbon storage is often overlooked, with much focus simply on biomass or ecosystem extent. On one hand, this may mean that the scientific community is underestimating future carbon emissions by not accounting for biodiversity-driven carbon losses, thus increasing the urgency for mitigating climate and land use impacts. On the other hand, this highlights the important role that ecosystem

restoration, focusing on the composition of these ecosystems, can play in climate change mitigation. In other words, there is potential to link the restoration target (T2) of the CBD Kunming-Montreal Global Biodiversity Framework with that for climate change mitigation (T8) and enhancing nature's contributions to people (T11), emphasizing a need to reconsider the functional value of biodiversity rather than focusing only on area-based measures for conservation (e.g., so-called 30 by 30; T3) (United Nations Convention on Biological Diversity, 2022a). Building on and improving the modeling approach used in this study can help identify areas for conservation and restoration and contribute to ongoing processes such as national biodiversity strategy and action plans under the Convention on Biological Diversity, nationally determined contributions for emissions reduction under the Paris Agreement, and payment for ecosystem services programs, and also benefit ESM development.

Methods

Step 1 - Use BILBI model to estimate proportion of plant species expected to persist in each ecoregion under different climate and land-use scenarios

To assess how land-use change and climate change affect biodiversity, the BILBI model uses land-use data and projections to create a map of habitat condition, which is expressed in units of the proportion of native species expected to remain in each grid-cell, given the land-use type of that cell (Table S1 in (Di Marco et al., 2019)). The model is also able to project climate-driven change in beta-diversity patterns, expressed in terms of the predicted dissimilarity (or conversely similarity) in species composition between any specified pair of grid-cells over both space and time. These projections are coupled

with a modified form of species-area analysis to estimate the proportion of species expected to persist (i.e., avoid extinction) under a given scenario of land-use and climate change, within any given region. See supplement 1 and (Di Marco et al., 2019; Hoskins et al., 2020) for full model details, but briefly, this is achieved by:

- 1) Calculating the total area of similar ecological environments relative to a given cell, by summing the predicted compositional similarity with all other cells under the present climate, and hypothetically assuming the habitat of all cells is in perfect condition.
- 2) Calculating the potential area of similar ecological environments under a given future scenario, accounting for both the projected change in climate and the expected condition of habitat under that scenario.
- 3) Expressing the effective area of habitat, across similar ecological environments, expected under a given scenario (from step 2 above), as a proportion of the total area of similar environments prior to climate and land-use change (from step 1 above), and then using the species-area relationship to translate this proportion into the predicted proportion of species expected to persist over the long term. A constant species-area exponent of $z=0.25$ was used in these calculations, as widely employed in other studies predicting the proportion of species expected to persist in fragmented habitats. However, intact habitats also experience species relaxation (i.e., long-term loss of species as the community approaches equilibrium species richness (Diamond, 1972)), commonly estimated at $z=0.15$. To estimate the additional loss of species due to climate and land-use change, I subtracted these two estimates

of z to obtain a lower bound of $z=0.1$ (Gonzalez, 2009; Isbell, Tilman, et al., 2015). I used a range of z values between 0.1 and 0.65, similar to Isbell et al. (2015b), to capture some of the uncertainty around the magnitude of species extinction debts.

I used two scenarios: SSP1/RCP 2.6 (“global sustainability”¹), a low land-use change and low climate change scenario which is compliant with the Paris target of keeping global warming to below 2°C by the end of the century compared to pre-industrial times, and SSP5/RCP8.5 (“fossil-fueled development”), a high climate change and intermediate land-use change scenario (Kriegler et al., 2017; van Vuuren et al., 2017). I chose these scenarios to represent the extreme low- and high-end outcomes to provide a full range of uncertainty estimates. To obtain estimates of the proportion of species expected to persist at the ecoregion level (p_{region}), I used a weighted geometric mean of all cells in the ecoregion. The weight applied to each cell is inversely proportional to the total effective area covered by cells with a similar environment to the cell of interest. This means that cells within less extensive environments have a higher weight, since these areas are likely to support more unique species and thus are expected to contribute more to regional species persistence.

Step 2: Use empirical relationships to link changes in species richness to changes in biomass

I use empirical biodiversity-biomass relationships from a recent meta-analysis based on 374 experiments (>500 entries from primary producers, dominated by terrestrial

¹ Note that SSP1/RCP2.6 still entails a significant amount of land- use change due to bioenergy production and increased food demand (Ciais et al., 2013).

plant studies). They found general support for using a power function to describe how changes in species richness lead to changes in biomass for primary producers as follows (O'Connor et al., 2017):

$$\text{Biomass} = a * (\text{richness})^b \quad (1)$$

where a is a constant representing the average biomass of a monoculture for the ecosystem, and b describes the power relationship between a change in richness and biomass. As species richness increases, the biomass of the system will increase compared to the monoculture baseline, but the amount of increase per species decelerates as more species are added. This equation can be converted to proportional change in biomass (ΔB) based on proportional change in species richness per ecoregion as follows:

$$\Delta B = (p_{region})^b \quad (2)$$

I apply this transformation to the BILBI model output to assess percent change in biomass from change in plant species richness, using the mean $b = 0.26$, as well as the 95% CI to provide uncertainty estimates around my results. O'Connor et al (2017) found that for primary producers, $b = 0.26$ (with a 95% CI of 0.16-0.37) was valid for most assemblages and was robust to differences in experimental design and the range of species richness levels considered. Although b values can vary spatially (Liang et al., 2016; Mori et al., 2021), there is still uncertainty in how biodiversity-ecosystem functioning relationships differ across space and in how factors like climate, environmental conditions, and species trait compositions might systematically affect the observed relationship (O'Connor et al., 2017). If the places where habitat destruction is highest are correlated with BEF relationships, then using a narrower range of spatially explicit values could systematically bias results. To address this concern, I estimated

productivity losses associated with the full confidence interval range from O'Connor et al (2017). This range is wider than spatially explicit values estimated for forests globally (range =0.198-0.299, mean = 0.26) (Liang et al., 2016). Therefore, my range of b values provides a conservative range of estimates of productivity loss associated with biodiversity loss.

Step 3: Estimate total changes in carbon storage and compare to other global change drivers

The previous step provided spatially explicit estimates of percent change in biomass associated with loss of biodiversity for each scenario. To convert biomass change to carbon storage change, I multiplied the gridded estimates of percent change in biomass by a global map of terrestrial carbon storage.

I used terrestrial carbon storage maps that considered only vegetation carbon, as well as maps considering vegetation and soil carbon. To be consistent with my BILBI model, I downloaded the total carbon in vegetation (cVeg) and total carbon in soil (cSoil) layer from the CMIP5 IPSL-CM5A-MR model (Dufresne et al., 2013). The BILBI model scenarios used climate data downscaled from the lower resolution IPSL-CM5A-LR, but I chose to use the mid-resolution 1.25° x 2.5° model to obtain higher resolution carbon maps. I obtained cVeg and cSoil for both of my scenarios – global sustainability (SSP1/RCP 2.6) and fossil-fueled development (SSP5/RCP8.5) from the Earth System Grid Federation (ESGF; <https://esgf-node.llnl.gov/search/cmip5/>).

I excluded soil types that are more likely to be impacted by drying and warming than by changes in plant diversity, including wetland (Gleysols), peatland (Histosols), and permafrost (Cryosols) soils (Isbell, Tilman, et al., 2015). I therefore excluded these

soil types from the analysis. Specifically, I resampled the 250m predicted World Reference Base 2006 subgroup soil classification (ISRIC, <https://data.isric.org/geonetwork/srv/eng/catalog.search#/metadata/5c301e97-9662-4f77-aa2d-48facd3c9e14>; (Hengl et al., 2017)) to the same resolution as the cSoil raster layer using the nearest neighbor method in the R software program raster package (Hijmans, 2020), and then masked out these soil types from the cSoil raster.

I calculated the average cVeg and cSoil value over a 12-month period in 2050 (the end year for the BILBI model output). To obtain cVeg and cSoil values on the same scale as the biodiversity data, I resampled by ecoregion using bilinear interpolation. Then, I multiplied my raster layers (percent change in plant biomass and 2050 carbon maps), to obtain changes in carbon storage in 2050 in kg/m² (ΔC), such that:

$$\Delta C = cVeg * \Delta B \text{ for vegetation carbon only, or}$$

(3)

$$\Delta C = (cVeg + cSoil) * \Delta B \text{ for vegetation carbon and soil carbon.}$$

To convert this to total C storage in PgC (C_{total}), I used the area function in the raster package (Hijmans, 2020) to calculate the total area in m² of each ecoregion (A). I then multiplied this by the carbon storage layer to obtain total carbon storage lost per ecoregion, which I summed to obtain global C storage loss values.

$$C_{total} = 1.0E^{-12} \sum_{k=1}^n \Delta C_k * A_k$$

(4)

where k= a given ecoregion and n=total number of ecoregions.

I conducted all analyses in R version 4.1.1 (R Core Team, 2021), and produced all graphics using either the tmap or ggplot2 packages (Tennekes, 2018; Wickham, 2016) (Wickham 2016, Tennekes 2018).

CHAPTER 3

PRIORITIZING GRASSLAND RESTORATION: A PILOT STUDY IN THE GREAT PLAINS, UNITED STATES

Abstract

Global and domestic conservation targets highlight the growing recognition that ecological restoration will be needed to meet biodiversity conservation goals. Given limited conservation budgets, deciding where to restore habitat will be an important need in the coming decade. Here, I develop a modeling approach to maximize conservation benefit/restoration cost ratios that can be used to map restoration priorities, and I illustrate this approach using a case study for highly threatened grassland ecosystems in the Great Plains region of Kansas. I found that for the indicator species that I chose, shortgrass and mixed-grass prairies had the highest conservation benefit to cost ratio. Setting a minimum restoration threshold for each habitat type allowed us to identify high priority tallgrass prairie sites. The modeling approach is flexible and can be updated for different ecosystems, species, and conservation priorities. I outline potential alterations that can be made in future analyses, depending on desired restoration goals.

Introduction

Human activities are leading to unprecedented biodiversity declines, with land use change the leading driver of biodiversity loss at a global scale (Díaz et al., 2019; Jaureguiberry et al., 2022). Thus far, global conservation targets have not been met, but effective conservation actions exist (C. N. Johnson et al., 2017; Secretariat of the Convention on Biological Diversity, 2020). Conservation activities often focus on

protecting wild places. While such efforts are critical for maintaining existing diversity, they will not be sufficient (Pimm et al., 2018). Reversing trends in biodiversity loss and achieving the Convention on Biological Diversity (CBD) 2050 vision to live in harmony with nature will require not only conserving remaining biodiversity, but also restoring degraded areas (Leclère et al., 2020). In fact, a recent modeling exercise investigating how to stop biodiversity loss found that scenarios that halted declines and reversed trends included restoring 4.3-14.6 million km² of degraded land by 2050, along with increasing the extent and management of protected areas (Leclère et al., 2020). The scenarios included in Leclère et al. (2020) may actually underestimate the effort required, since they did not consider the effects of climate change, harvest, or invasive alien species on biodiversity (Bryan & Archibald, 2020). In addition to increasing biodiversity, restoration can significantly increase ecosystem functioning and services (Benayas et al., 2009; IPBES, 2018).

The benefits of investing in restoration generally far exceed the costs, and avoiding, reducing, and reversing land degradation is required to achieve the Sustainable Development Goals (IPBES, 2018). Recognizing the importance of restoration, the CBD Kunming-Montreal Global Biodiversity Framework includes a target that at least 30% of degraded freshwater, marine and terrestrial ecosystems be under restoration by 2030 (United Nations Convention on Biological Diversity, 2022b). Degraded ecosystems are places with persistent decline or loss in biodiversity and ecosystem functions and services that cannot fully recover within decadal timescales without intervention (Future Earth and GEO BON, 2022). At a national level, the U.S. has recognized the importance of restoration as well. The recently enacted Infrastructure Investment and Jobs Act (also

called the Bipartisan Infrastructure Law, passed in 2021) includes \$1.4 billion for ecosystem restoration and resilience (U.S. Department of the Interior, 2022). The 2021 America the Beautiful Report, which lays out a vision for U.S. government conservation activities over the next decade, consistently mentions both conservation and restoration, and specifically highlights that these activities should occur across the country on private, State, local, and Tribal lands, rather than focusing primarily on western public lands as has been historically the case (National Climate Task Force, 2021). In fact, some ecoregions in the U.S. have <20% of their historical area remaining, and thus restoration would be needed to achieve a 30% conservation target (Dinerstein et al., 2019).

Definitions of what constitutes restoration vary, which can challenge implementation (USDA Forest Service, 2006). The USDA Forest Service defines restoration as “The process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed. Ecological restoration focuses on reestablishing the composition, structure, pattern, and ecological processes necessary to facilitate terrestrial and aquatic ecosystems sustainability, resilience, and health under current and future conditions” (USDA Forest Service, 2013). When developing restoration plans, the USDA Forest Service considers the natural range of variability, ecological integrity, current and likely future ecological conditions (including climate), technical and economic feasibility, and enhancements of carbon stocks (USDA Forest Service, 2016). Knowledge of historical conditions can be useful to guide restoration activities. For example, afforestation of grassy biomes may not be effective restoration, although it is important to recognize that in some cases achieving historical baselines are no longer feasible (Temperton et al., 2019).

Given the increasing attention to restoration activities, it is important to consider where investments will be most effective to simultaneously achieve multiple biodiversity and ecosystem services goals while minimizing costs (Future Earth and GEO BON, 2022). Conservation benefits can be measured in different ways, for example by considering species of concern, rare species, or overall species richness (Dreiss & Malcom, 2022; Hamilton et al., 2022), while costs could include acquisition and management costs (Armsworth et al., 2011) or opportunity costs from protecting and restoring land rather than using it for agriculture or other activities (Naidoo & Iwamura, 2007; Venter et al., 2014). Considering both benefits and costs can allow for land management decisions that optimize conservation and economic returns (Polasky et al., 2008). There can be tradeoffs between conservation goals, such as minimizing deforestation vs. maximizing conservation of forest vertebrates (Di Marco et al., 2016), and so different restoration priorities might be identified depending on the objectives chosen. While considering costs as well as benefits (i.e., return on investment) can improve agreement over conservation priorities, it does not solve all disagreements (Armsworth et al., 2017). Researchers have produced restoration priority maps at the global scale (e.g., (Mappin et al., 2019; Strassburg et al., 2020)), as well as for some regions and ecosystems in regions including the U.S. (e.g., (Ager et al., 2013; Allan et al., 2015; Chimner et al., 2010)). While global priority maps are important, many conservation decisions are made at national and sub-national levels, so finer scale maps are needed for effective implementation (Nelson et al., 2009).

Some ecosystems are especially degraded and are therefore a prominent restoration focus. Globally, temperate grasslands are one of the most highly threatened

biomes (Hoekstra et al., 2005). Grasslands in North America are no exception, including native prairie loss as high as 99% in some areas since European settlement (Samson & Knopf, 1994). Tallgrass prairies have experienced the most extensive losses, but mixed-grass and shortgrass prairie loss has also been high (Augustine et al., 2021). Grassland conversion to cropland remains prevalent in the US, with recent hotspots of cropland expansion in western Kansas and the panhandles of Oklahoma and Texas (Lark et al., 2015). Grassland loss has negative consequences for native biodiversity. 74% of grassland bird species are declining, with grassland birds exhibiting the largest population declines compared to any other habitat type (Rosenberg et al., 2019). Grassland loss has resulted in range contractions for North American mammal species, including pronghorn (*Antilocapra americana*), elk (*Cervus canadensis*), bison (*Bison bison*), and grizzly bears (*Ursus arctos*) (Laliberte & Ripple, 2004; Morrison et al., 2007). Plant species have also been affected, not just by direct habitat loss, but also by loss of species in remnant patches due to fragmentation and interrupted ecological processes (Leach & Givnish, 1996). Although remnant prairie patches can harbor more plant species than would be expected based on traditional species area relationship expectations, the number of species found in these remnant patches is far lower than the number of species that were originally present (Wilsey, Martin, et al., 2005). Given the high rates of ecosystem degradation and biodiversity loss, restoring grassland ecosystems represents an important conservation priority. Indeed, unassisted recovery of biodiversity after agricultural abandonment can be slow and incomplete (e.g., with only three quarters of plant diversity returning nearly a century after agricultural abandonment (Isbell et al., 2019).

Here, I build a modeling framework to maximize conservation benefit/restoration cost ratios that can be used to map restoration priorities in the United States. I illustrate this framework using a case study in the Great Plains region of Kansas. I restricted possible restoration sites to current cropland or pasture that was formerly tallgrass, mixed-grass, or short-grass prairie. I selected cropland and pasture as these areas are likely easier to restore than more urbanized areas, and programs exist to target conservation activities on agricultural lands (e.g., the Conservation Reserve Program, (USDA Farm Service Agency, 2022)). I explore how different scenarios and model assumptions can change priorities.

Methods

Land area available for restoration

I downloaded estimated historical distribution of grassland communities of the Southern Great Plains from the U.S. Geological Survey, which provides gridded 30x30 m resolution estimates of 10 grassland communities prior to Euro-American settlement (Callan et al., 2016; Reese et al., 2016). I subset the raster to tallgrass, mixed-grass, or short-grass prairie communities in Kansas. I selected Kansas as my study site as the state has a large amount of cropland and rangeland, is a hotspot of ongoing agricultural expansion, and was located within the historical range of my indicator species (see species included in the model section below) (Lark et al., 2015). Kansas is also unique in that contains part of the Flint Hills – the largest remaining tallgrass prairie. Large areas of the Flint Hills are managed with cattle grazing and prescribed burning, which can be detrimental to grassland bird populations (Rahmig et al., 2009; With et al., 2008). Even so, tallgrass restoration in this region is likely easier than elsewhere in the Great Plains. I

identified current areas of cropland or pasture from the 2019 National Land Cover Dataset (NLCD; categories 81 and 82) (Dewitz & U.S. Geological Survey, 2021), and used this raster to mask the grassland community raster using the raster package (Hijmans, 2020) in R version 4.0.4 (R Core Team, 2021).

Restoration costs

Although acquisition costs and management or restoration costs are not always correlated (Armsworth et al., 2011), estimates of land value can be used as proxies for restoration costs, since they relate to costs of acquisition or other conservation strategies like conservation easements (Nolte, 2020). The spatial grain of economic and biodiversity data can have a strong effect on prioritization outcomes, and can be especially important when scaling between regional conservation plans and local actions (Sutton & Armsworth, 2014). Using coarse resolution cost proxies, such as county-level metrics, can lead to inaccurate estimates of conservation budgets (Armsworth, 2014; Sutton et al., 2016), but high resolution estimates provide much better proxies (Nolte, 2020). I downloaded land values in the United States estimated from 2000-2019 sales data at 480x480 m resolution from (Nolte, 2020) (Supplemental figure 3.1). I converted the cost data to USD/ha and used this dataset to estimate the cost (Cx_i) of each pixel (x_i).

Species included in the model

I selected five grassland species to serve as indicators of restoration benefit, including two bird species, two mammal species, and one insect species (Table 3.1, current and historical range maps in Figure 3.1). Lesser prairie chickens (*Tympanuchus pallidicinctus*) require large grasslands with limited anthropogenic disturbance, and have experienced substantial population declines from habitat loss and fragmentation (U.S.

Fish and Wildlife Service, 2021). Most of the existing population (67%) resides in shortgrass prairie (U.S. Fish and Wildlife Service, 2021). The Northern Distinct Population of lesser prairie chickens, which includes Kansas, was recently classified as threatened, while the Southern Distinct Population was classified as endangered (U.S. Fish and Wildlife Service, 2022). Greater prairie chickens (*Tympanuchus cupido*) are classified by the IUCN red list as near threatened due to loss of habitat (BirdLife International, 2020). Greater prairie chickens occupy tallgrass prairie ecosystems (Robb & Schroeder, 2005).

I included swift fox (*Vulpes velox*) and pronghorn (*Antilocapra americana*) as my two mammal species indicators. Swift fox are found primarily on shortgrass and mixed-grass prairies, and conversion of grasslands has been one of the main drivers for the reduction in their range (Moehrensclager et al., 2004). Pronghorn live in grassland ecosystems in Western North America. Although populations have recovered, habitat loss and conversion has been a driver of population declines (IUCN SSC Antelope Specialist Group, 2016).

Finally, I included regal fritillary (*Speyeria idalia*) as my insect indicator species. Regal fritillaries are classified as vulnerable on the IUCN red list, with habitat loss, fragmentation, and degradation as a primary driver of declines (Selby, 2007; A. Walker et al., 2022). They are restricted to habitats where their larval host plants – prairie endemic violet species – are present, and although it is not well studied, they appear to have limited dispersal ability (Selby, 2007; Shepherd & Debinski, 2005). Butterflies in the *Speyeria* genus are among the first organisms to disappear from human-altered

ecosystems, and are thus good indicators of undisturbed ecological communities (Hammond & Mccorkle, 1984).

Benefits for biodiversity

As species lose habitat, their extinction risk increases. I estimated the biodiversity benefits of restoration using a modified version of the species-area relationship to assess how restoration reduces extinction risk (Koncki & Aronson, 2015; Strassburg et al., 2020). For each species j , I downloaded a current range map from that I used to calculate the area of current habitat (A_c) and a historical range map that I used to calculate the area of original habitat A_o (see table 3.1 for sources). I calculated the current extinction risk (r_o) for each species (j) as (Strassburg et al., 2019, 2020; Thomas et al., 2004):

$$1) \quad r_{oj} = 1 - \left(\frac{A_c}{A_o}\right)^z$$

To create a restoration benefit map for each species, I estimated the new extinction risk (r_{1j}) if a particular pixel x_i was restored. I assumed that areas restored to each species' preferred habitat type would eventually become habitat for the species in the long-term and reduce extinction risk. Thus, if x_i is within the species preferred habitat type, the new extinction risk is:

$$2) \quad r_{1j} = 1 - \left(\frac{A_c + Ax_i}{A_o}\right)^z$$

Where Ax_i is the area of pixel x_i , and z is a constant representing how extinction risk scales with habitat loss. $z=0.25$ is commonly used for species area relationships, but I used a range of $z=0.1 - 0.4$ to assess the sensitivity of my priority maps.

I then calculated the restoration benefit of each individual pixel b_{ij} for each species as the reduction in extinction risk achieved by restoring a particular pixel.

$$3) b_{ij} = r_{0j} - r_{1j}$$

To create an overall benefit map considering all species (S), I calculated the restoration benefit of each pixel (Bx_i) by summing the benefit for each individual species per pixel:

$$4) Bx_i = \sum_{j=1}^S b_{ij}$$

Table 3.1: Sources of species range map and dispersal distances used in models

Species	Historical range map	Current range map	Dispersal distance	Habitat Type
Lesser prairie chicken (<i>Tympanuchus pallidicinctus</i>)	(BirdLife International and Handbook of the Birds of the World, 2008)	(U.S. Geological Survey (USGS) - Gap Analysis Project (GAP), 2018b)	50km (Hagen et al., 2004)	Shortgrass prairie, mixed-grass prairie (U.S. Fish and Wildlife Service, 2021)
Greater prairie chicken (<i>Tympanuchus cupido</i>)	(BirdLife International and Handbook of the Birds of the World, 2013)	(U.S. Geological Survey (USGS) - Gap Analysis Project (GAP), 2018a)	10 km (Robb & Schroeder, 2005)	Tallgrass prairie (Robb & Schroeder, 2005)
Swift fox (<i>Vulpes velox</i>)	(USGS & IUCN, 2016)	(U.S. Geological Survey (USGS) - Gap Analysis Project)	15 km (Moehrenschrager et al., 2004)	Shortgrass prairie, mixed-grass prairie (Moehrenschrager et al., 2004)

		(GAP), 2018d)		
Pronghorn (<i>Antilocapra americana</i>)	(Kauffman et al., 2018)	(U.S. Geological Survey (USGS) - Gap Analysis Project (GAP), 2018c)	267 km (JACQUES & JENKS, 2007)	Temperate grasslands (Shortgrass prairie, mixed-grass prairie, tallgrass prairie)(IUCN SSC Antelope Specialist Group, 2016)
Regal fritillary (Speyeria idalia)	(A. Walker et al., 2022)	(A. Walker et al., 2022)	Uncertain, but could some individuals seem able to disperse at least 3 km (Marschalek, 2020; A. Walker et al., 2022)	Mixed-grass prairie, tallgrass prairie (Selby, 2007)

Optimization model

I used integer linear programming (ILP) in the R package lpSolve to optimize restoration scenarios (Berkelaar & Others, 2023). ILP maximizes or minimizes an objective function (i.e., a mathematical equation describing the relationship between actions and outcomes) subject to a set of constraints (Beyer et al., 2016). When objectives can be converted into linear format, ILP will find an optimal solution given the constraints, which is a benefit over other heuristic methods like simulated annealing (Beyer et al., 2016).

I set my objective function to maximize the benefit/cost ratio subject to a total limit on area (in this case, set to 30% of the pixels available for restoration) and a minimum amount of each habitat type to be restored.

$$5) \quad \max \sum_{i=1}^N \frac{Bx_i}{Cx_i}$$

subject to:

$$\sum_{i=1}^N Ax_i \leq T_A$$

$$\sum_{i \in G_a} Ax_i \geq H_A$$

Where N = the total number of pixels available for analysis and T_A is the total area that can be restored in each model run. The second constraint sets a minimum area (H_A) that needs to be restored for each habitat type (a), and G_a represents the membership of each planning unit within a habitat type. To account for diminishing returns in species benefit as more suitable habitat is restored, I ran my optimization in 3 iterations. To do this, I set $T_A = 0.1 * N$ (i.e., after 3 iterations, I will have reached my 30% restoration target). To see whether the number of iterations affected results, I also ran my optimization with 30 iterations. However, results were very similar (supplemental figure 3.2), and I therefore present results from 3 iterations in the main text. I set $H_A = 0.067 * G_a$ (i.e., after 3 iterations I will restore at least 20% of each grassland habitat type). I also tested a 0 and 10% minimum threshold. After each iteration I added newly restored sites to the current area of habitat (A_c) for each species j as applicable and repeated equations 1-5 until total planned area was accounted for. I ran all optimizations on the USGS Denali Supercomputer (Falgout et al., n.d.).

Not all restored areas are equally likely to be colonized naturally by my species of interest (at least without translocations). I assessed how weighting biodiversity benefits by distance to current habitat could affect restoration outcomes. I ran three scenarios that

considered pixels outside of the dispersal distance of each species to have equal, partial, or no benefit:

- 1) Translocation scenario – all suitable habitat types were considered equally beneficial for the species regardless of distance to current habitat (i.e., benefits calculated as described in the benefits to biodiversity section above);
- 2) Intermediate scenario - Pixels whose Euclidean distance was within the known dispersal distance of the species current range were weighted as 1 (i.e., $b_{ij} = r_{0j} - r_{1j}$), whereas those outside were given 0.5 weight (i.e., $b_{ij} = 0.5 * (r_{0j} - r_{1j})$). To do this, I added a buffer equal to the dispersal distance (Table 3.1) around the current range map. I turned this shapefile into a raster such that areas inside the buffer were equal to 1, while those outside were equal to 0.5, and multiplied this by the restoration benefit of each pixel b_{ij} for each species. This assumes that either some translocation is possible, or that eventually species will move to further habitats, but that this may take longer and thus has lower immediate benefits than closer pixels;
- 3) Natural dispersal scenario – only pixels within the Euclidean dispersal distance were considered beneficial, while pixels outside of this distance were given a benefit of 0. To do this, I added a buffer equal to the dispersal distance (Table 3.1) around the current range map. I turned this shapefile into a raster such that areas inside the buffer were equal to 1, while those outside were equal to 0, and multiplied this by the restoration benefit of each pixel b_{ij} for each species.

I assessed sensitivity to pixel size of the restoration prioritization outcomes by varying the resolution between 480x480 m² (the original resolution of the cost map) and 960x960 m². I found that pixel size only slightly influenced the area of each habitat type selected or reduced extinction risk for each species (Supplemental figure 3.3), and I therefore present results for 960x960 m² for computational efficiency.

Results

Available restoration area ranged from 31,623.78 km² of shortgrass prairie in western Kansas to 58,290.28 km² of mixed-grass prairie in central Kansas to 35,054.90 km² of tallgrass prairie in eastern Kansas when I selected pixels at the 960x960 m² resolution (Figure 3.2). This included 97.3% croplands and 2.7% of pasture (Supplemental figure 3.4). Restoring 30% of this available area with at least 20% of each habitat type could cost on the order of \$13 billion (Table 3.2) and reduce extinction risk by an average of 1.6% (0.8% - 2.2% using the full range of z values) across all indicator species and dispersal scenarios.

Dispersal scenarios

As dispersal limitations became more influential in pixel selection (i.e., moving from the translocation scenario to the natural dispersal scenario), tallgrass prairie habitat selection moved farther north while mixed-grass and shortgrass prairie selection moved farther south (Figure 3.3). However, there were still quite a few areas that were prioritized in all three scenarios (Figure 3.3).

Although restoration location shifted, total area restored in each habitat type was similar under each of the restoration scenarios (Figure 3.4). Under the natural dispersal scenario, more shortgrass prairie and less mixed grass prairie was selected for restoration

compared to the intermediate or translocation scenario, while the total amount of tallgrass prairie remained the same. Lesser prairie chicken had the greatest reduction in extinction risk (2.3% - 6.7% when we set a 20% minimum habitat restoration threshold under the full range of z values considered), while greater prairie chickens had the least (0.12%-0.27%). Interestingly, because habitat selection between scenarios differed only in the amount of short vs. mixed-grass prairie selected, the scenarios only influenced extinction risk for the regal fritillary when I set a minimum restoration threshold of 20% per habitat type (1.6% reduction in extinction risk under the translocation scenario vs. 1.3% under the natural dispersal scenario; Figure 3.4).

The natural dispersal scenario was the most expensive, followed by the intermediate scenario and the translocation scenario (Table 3.2). The natural dispersal and intermediate scenarios were more expensive because the restriction on distance to current habitat necessitated the selection of more expensive areas. Even so, the natural dispersal scenario was only 10% more expensive than the translocation scenario.

Minimum habitat threshold scenarios

When I set a lower threshold for minimum area of habitat restored for each habitat type (0 or 10% instead of 20%), I saw similar patterns, but less tallgrass prairie was selected for restoration (Supplemental figure 3.5, Figure 3.5). Setting a higher minimum habitat threshold reduced extinction risk slightly for the tallgrass prairie species (greater prairie chicken and regal fritillary), but increased extinction risk for species that do not use tallgrass prairie (lesser prairie chicken and swift fox). Restoring more mixed-grass and shortgrass prairie was more expensive, but cost differences were negligible (~3%, Table 3.3).

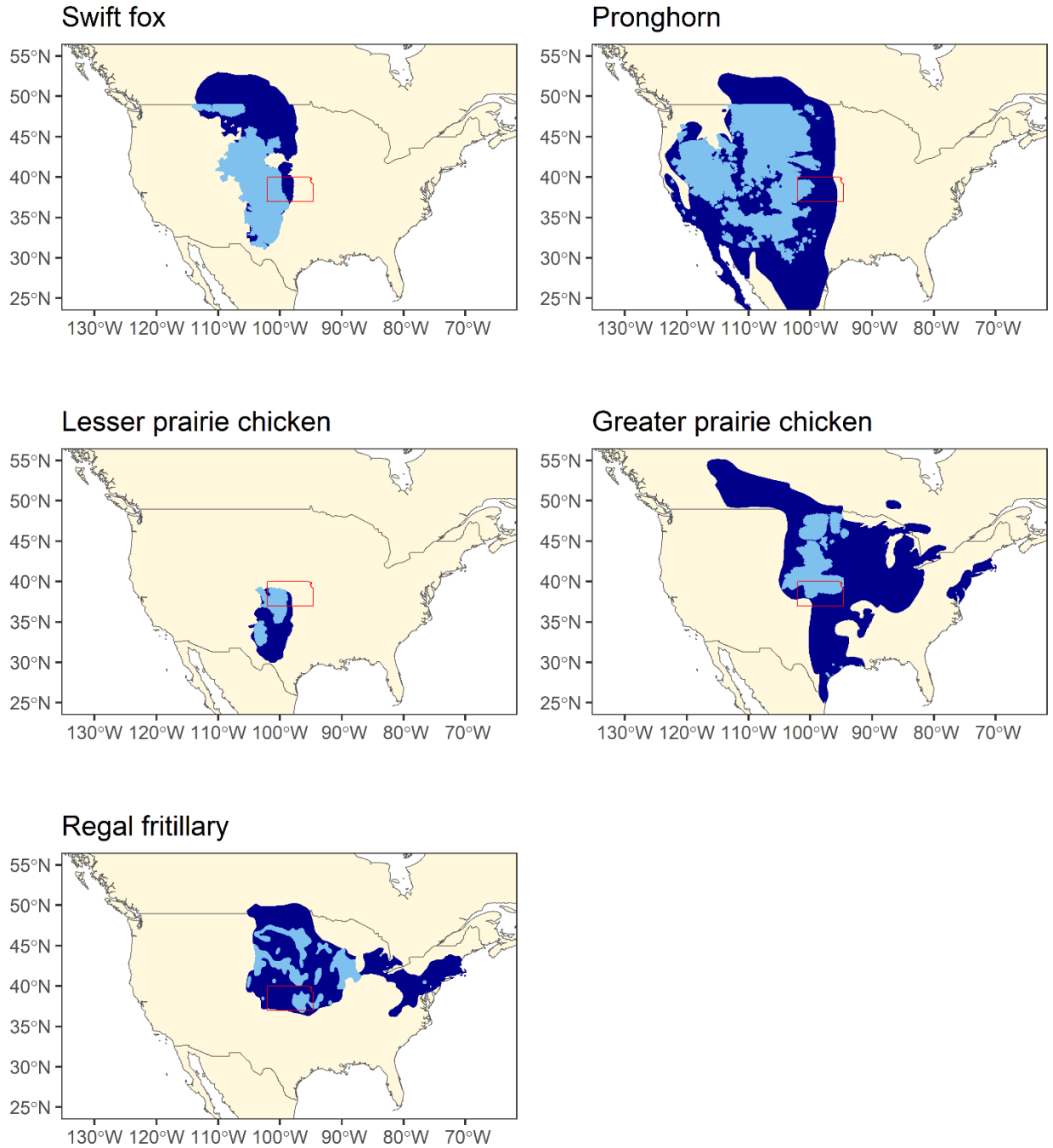


Figure 3.1: Current (light blue) and historical (dark blue) range maps for the species included in this analysis. The red box highlights Kansas in relation to the species range. Sources for the range maps are listed in Table 3.1. The base map comes from (South, 2017)

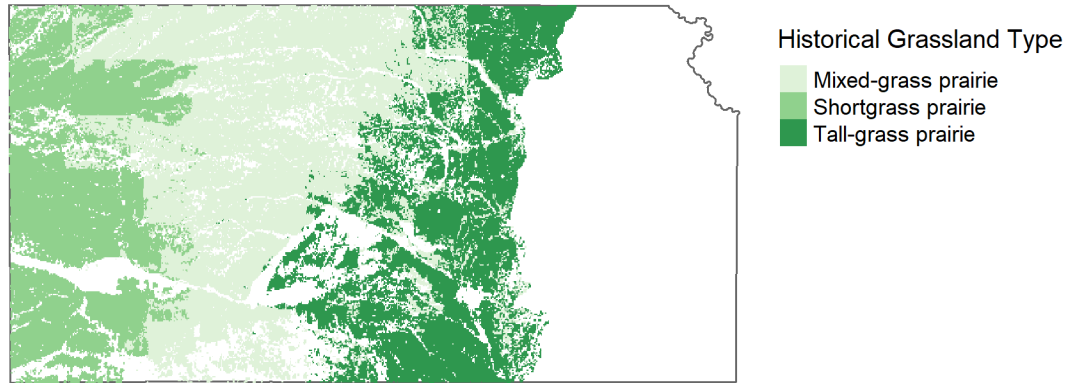
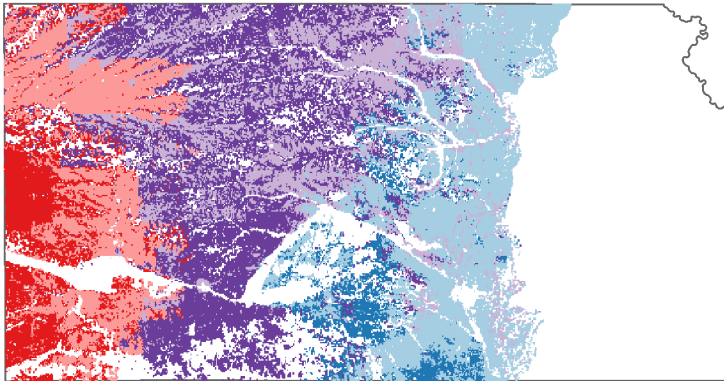


Figure 3.2: Area in Kansas that is currently cropland or pasture by historical grassland community type. This was considered the area available for restoration for this analysis. Historical grassland data comes from (Callan et al., 2016; Reese et al., 2016) and agricultural data comes from (Dewitz & U.S. Geological Survey, 2021).

Translocation



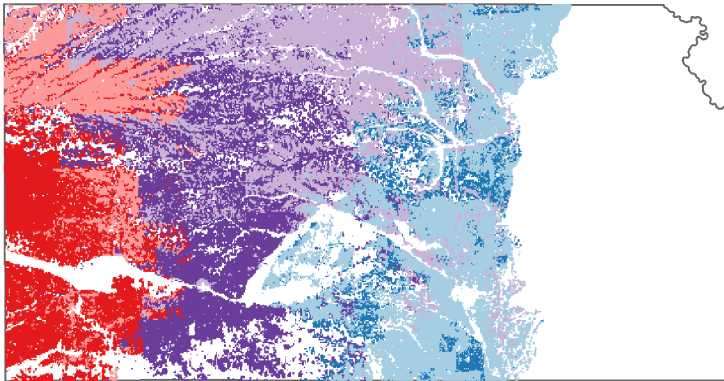
Historical grassland type

- Mixed-grass
- Shortgrass
- Tall-grass

Prioritized restoration sites

- Mixed-grass
- Shortgrass
- Tall-grass

Intermediate



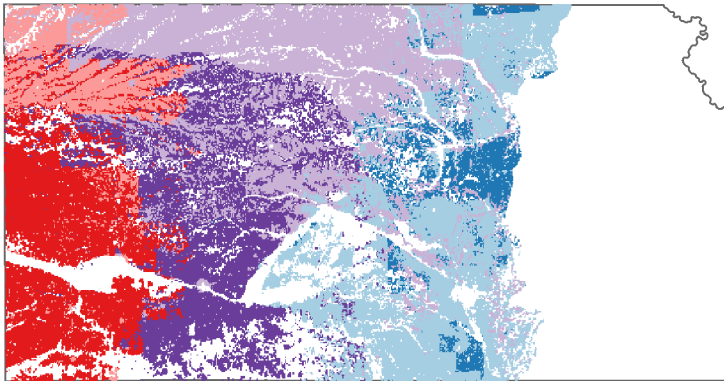
Historical grassland type

- Mixed-grass
- Shortgrass
- Tall-grass

Prioritized restoration sites

- Mixed-grass
- Shortgrass
- Tall-grass

Natural dispersal



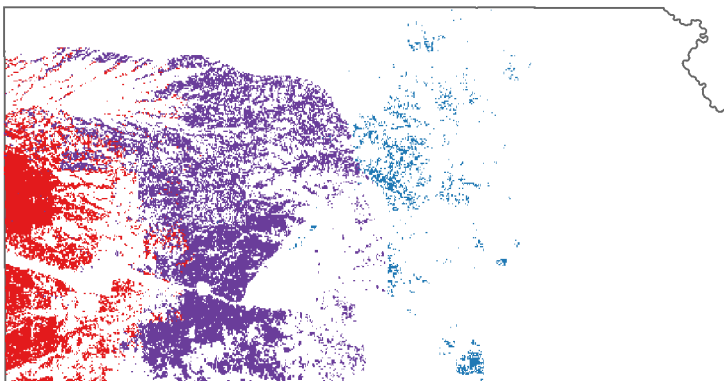
Historical grassland type

- Mixed-grass
- Shortgrass
- Tall-grass

Prioritized restoration sites

- Mixed-grass
- Shortgrass
- Tall-grass

Prioritized sites from all scenarios



Prioritized restoration sites

- Mixed-grass
- Shortgrass
- Tall-grass

Figure 3.3: Priority restoration sites when $z = 0.25$, minimum habitat area to be restored per habitat type is 20%, resolution = $960 \times 960 \text{ m}^2$, iterations = 3 for the translocation scenario (top), intermediate scenario (middle) and natural dispersal scenario (bottom)

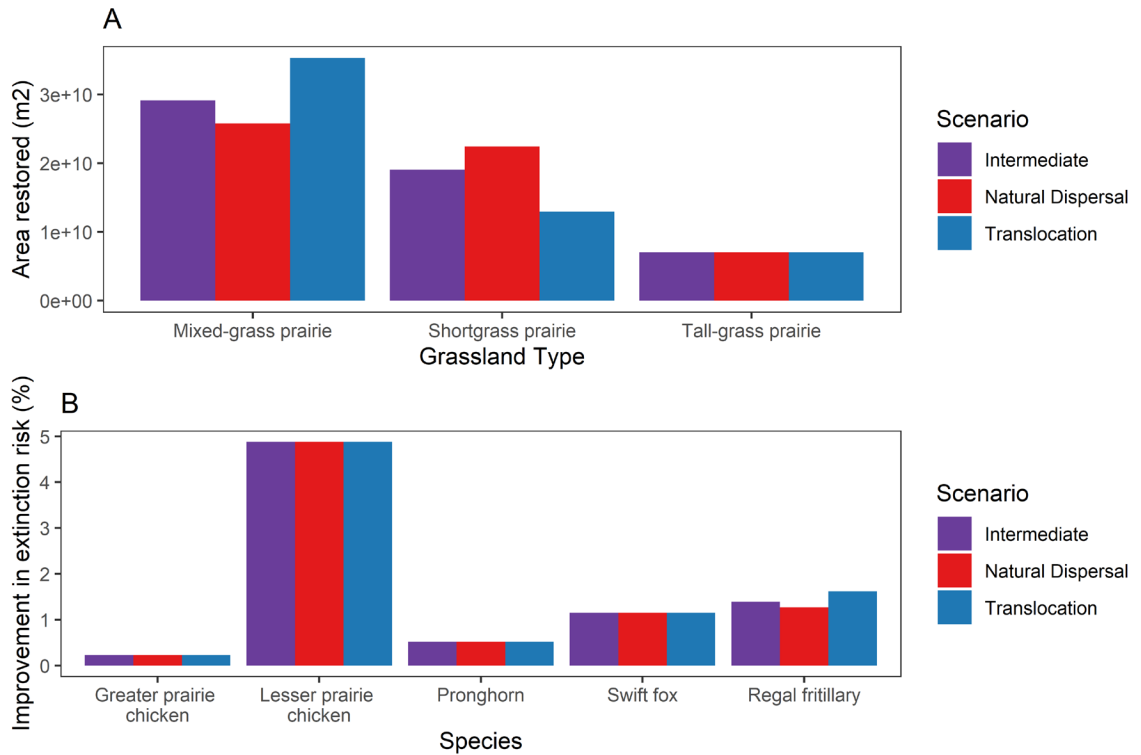


Figure 3.4: Area restored in each habitat type under the three restoration scenarios (A) and improved extinction risk for each species under the three restoration scenarios (B). Error bars represent the range of z -values from 0.1 – 0.4. Results are from scenarios where $z = 0.25$, minimum habitat area to be restored per habitat type is 20%, resolution = $960 \times 960 \text{ m}^2$, iterations = 3.

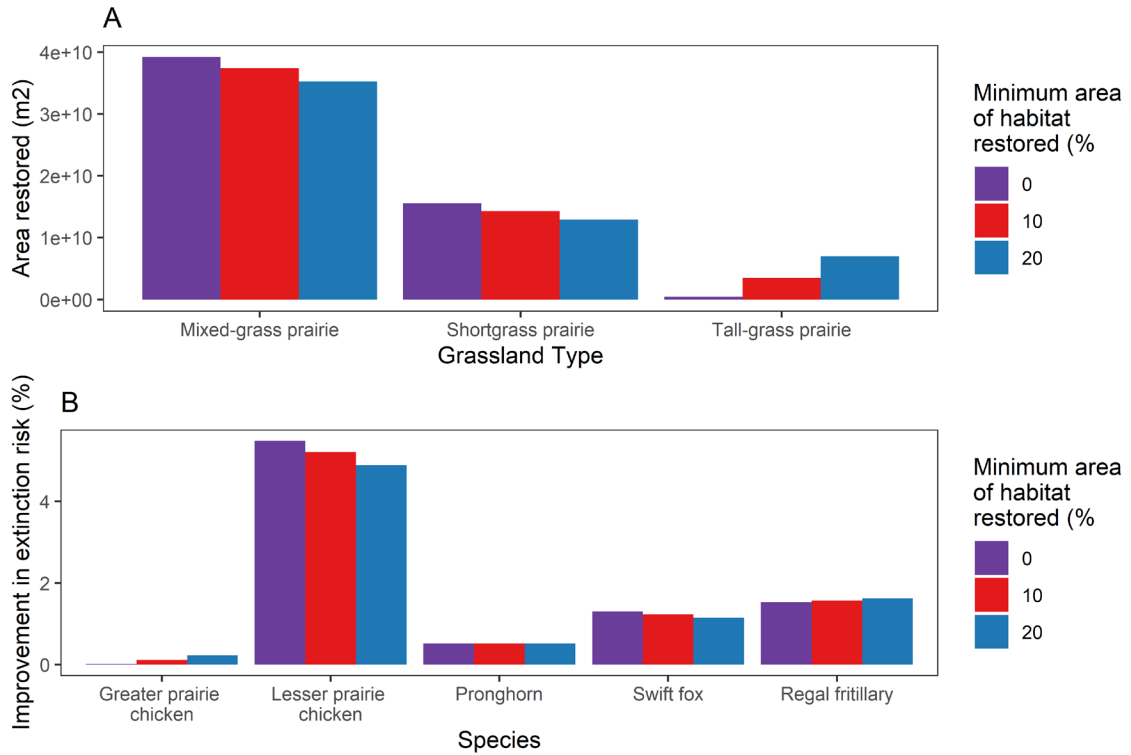


Figure 3.5: Comparison of how the minimum area of each habitat type restored affected area restored by grassland type (A) and improved species' extinction risk (B) under the translocation scenario (i.e., all suitable habitat types were considered equally beneficial for the species regardless of distance to current habitat).

Table 3.2: Total restoration costs for each restoration scenario (rounded to the nearest \$10) run at 960x960m resolution and a 20% minimum habitat restoration for each habitat type.

Scenario	Total Cost	Average cost/ha
Translocation	\$ 12,586,408,090	\$2,280
Intermediate	\$ 13,016,861,060	\$2,360
Natural Dispersal	\$ 13,838,448,080	\$ 2,510

Table 3.3: Total restoration costs for different minimum habitat thresholds for the translocation scenario at 960x960m resolution.

Minimum Habitat Scenario	Total Cost	Average cost/ha
0%	\$12,973,977,710	\$2,350
10%	\$12,689,216,130	\$2,300
20%	\$12,586,408,090	\$2,280

Discussion

Ecological restoration will be an important conservation option in the coming decade in the US and globally as countries work to achieve global biodiversity targets. Here, I developed a modeling approach to prioritize restoration actions and illustrated the model's utility using a case study in Kansas. I found that for the indicator species that I chose, shortgrass and mixed-grass prairies had the highest conservation benefit to cost ratio. Setting a minimum restoration threshold for each habitat type allowed us to identify high priority tallgrass prairie sites as well. Thresholds can be altered in future scenarios to reflect management needs.

Altering the number of iterations, weighting benefits based on dispersal distance, and using different pixel sizes and species-area relationships did not greatly change the prioritization results. When we considered current species ranges and dispersal

limitations in pixel selection, tallgrass prairie habitat selection moved farther north while mixed-grass and shortgrass prairie selection moved farther south (Figure 3.3). This is likely driven by where my selected species are currently found (Figure 3.1). For example, greater prairie chicken populations are located in northern Kansas, while lesser prairie chickens are located in southwest Kansas, thus driving their preferred habitat types in these directions when their dispersal distance is taken into account. Considering differential benefits based on dispersal distance and current range (i.e., the intermediate and natural dispersal scenarios) is useful, as the current species range may more closely reflect the species' niche than its historical range (Lenoir et al., 2020; Rubenstein et al., 2023). Although restoration location shifted, total area restored in each habitat type was similar under each of the restoration scenarios. The amount of tallgrass prairie likely remained constant due to the indicator species selected for my analysis. That is, because shortgrass and mixed-grass prairie reduced extinction risk more for the species that I chose (due to habitat preferences and level of remaining habitat for each species), the minimum amount of tallgrass prairie habitat was selected in each scenario.

Many conservation optimization analyses focus on identifying protected areas based on where species are currently found (e.g., (Hamilton et al., 2022; Venter et al., 2014)). Prioritizing restoration presents an additional challenge, because the user must prioritize based on ecosystem features that do not currently exist (Yoshioka et al., 2014). Different approaches have been used to address this challenge. For example, (Yoshioka et al., 2014) looked at bird species extirpations between 1978 and 1998 and used lost species as the restoration features to be prioritized in Japan. They also considered restoration constraints (e.g., area to be restored) and feasibility (level of urbanization) in

their prioritization. For my analysis, I used an approach similar to (Strassburg et al., 2020), where I used species-area relationships to estimate restoration benefits for biodiversity. My approach differed from theirs in several ways. For example, because (Strassburg et al., 2020) ran their model globally and used over 20,000 species, they used coarser metrics of historical habitat and conservation costs. Running the analysis on a smaller scale allowed us to consider more detailed historical habitat types and estimated historical ranges of my modelled species. Moreover, when considering return on investment globally, higher-income countries like the U.S. may not come out as the best locations for restoration (Luby et al., 2022). Indeed, most of the United States came out as low priority restoration sites in (Strassburg et al., 2020). However, there is strong interest in restoration within the US, as well as significant restoration funding that will be spent nationally. It is therefore worthwhile to assess restoration priorities nationally and within ecosystems of concern such as grasslands.

My restoration prioritization approach could add value to existing planning and conservation initiatives. For example, (Comer et al., 2018) identified potential conservation areas in the Great Plains (including Kansas) based on grassland representativeness and intactness, level of historical loss, and input from grassland experts. These areas do not define specific conservation actions, but rather highlight places where conservation attention could be focused. Such analyses could be augmented by my modeling approach, which specifically considers where restoration could be beneficial, and incorporates costs in addition to conservation benefits. For example, my priority tallgrass, mixed-grass, and shortgrass prairie selections could be overlaid with the potential conservation areas to further prioritize restoration sites.

For my cost estimation, I focused on acquisition costs, but acquisition costs and management or restoration costs are not always correlated (Armsworth et al., 2011). Restoration costs include expenses like habitat management, purchasing equipment, administrative costs, and staff time. Estimating conservation and restoration costs beyond acquisition is challenging. Cost reporting is limited and inconstant, resulting in huge variation in estimated restoration costs (Iacona et al., 2018; Knight & Overbeck, 2021). For example, a survey of practitioners found that grassland restoration costs varied from USD 13/ha to 79,255/ha, with a median of \$2,543/ha (Knight & Overbeck, 2021). Differences were driven by project duration and different concepts of what was considered grassland restoration. For example, restoring some native plants on the landscape is easier and less expensive than trying to fully restore native biodiversity. Land use intensity and level of degradation affect project costs and success. Throughout the Great Plains, tallgrass prairies are typically more degraded, and thus likely more difficult to restore than shortgrass and mixed-grass prairie (Comer et al., 2018). Kansas may be the exception – the Flint Hills region is one of the largest remaining tallgrass prairies (With et al., 2008), and thus restoration may be easier here than in other places. One near-term next step would be to use a measure of land use intensity as a proxy of restoration effort (e.g., (Suraci et al., 2023)). This assumes that more intensively used landscapes cost more to restore. Future work that improves our understanding of restoration costs would improve the costs estimates in my analysis.

One challenge for restoration in Kansas and the Great Plains is that much of the land is privately owned (Augustine et al., 2021). However, there are programs to promote conservation and restoration on agricultural lands. For example, the Conservation

Reserve Program (CRP) allows agricultural producers to voluntarily take land out of production and improve it for conservation in exchange for rental payments (USDA Farm Service Agency, 2022). The CRP has benefitted grassland species like the lesser prairie chicken, bobolinks (*Dolichonyx oryzivorus*), and dickcissels (*Spiza americana*), but CRP enrollment in the Great Plains has declined, with ~3.2% of the Great Plains enrolled in the program in 2017 compared to 5.5% in 2007 (Augustine et al., 2021; Herkert, 2009).

Despite the benefits of existing conservation programs, conservation needs far exceed available restoration budgets. The CRP annual budget was \$2.4 billion in 2023 for the entire (U.S. Department of Agriculture USDA, 2022). Although there are other sources of restoration funding (e.g., America the Beautiful program restoration funds), it is not feasible to purchase and restore all of the priority sites selected here. Efficiently choosing restoration sites, as well as developing more biodiverse working landscapes and partnerships with landowners may be needed to meet conservation goals. Additionally, even as croplands are pulled out of production and restored through programs like the CRP, additional grasslands continue to be converted. Over a quarter of converted grasslands between 2008 and 2012 came from long-standing prairie locations (Lark et al., 2015). Thus, preventing the conversion of intact grasslands will also be important.

My model assumes that restored pixels will eventually become habitat for my indicator species. I made this assumption for all three dispersal scenarios. That is, while I used dispersal distance as a weighting factor to calculate benefits for the natural dispersal and intermediate scenarios, I still included the final habitat selection in the extinction risk calculation. I did this because the species area relationship considers long-term (i.e., in

the coming decades), not near-term extinction risk, and ultimately these places may become habitat for the species and contribute to the species survival. However, many factors affect restoration success, and definitions of success or what constitutes a biodiverse restoration can vary across projects (Andres et al., 2022). For example, it is much easier and cheaper to restore a subset of plants back on the landscape than to fully restore native plant diversity (Martin et al., 2005). Restoration feasibility also depends on the level of degradation and the amount of time since land conversion. A recently converted agricultural site may still have a native seedbank, whereas places with a longer history of cultivation may require seeding (Bakker & Berendse, 1999; G. Wang et al., 2017). Seeds for some prairie species are difficult to collect, which can make it challenging to include all remnant species in seed mixes (Newbold et al., 2020). Seed-limited grasslands that are restored with more species and managed for biodiversity recovered faster than other restored grasslands (Klopf et al., 2017; Martin & Wilsey, 2006). Grazing can also have benefits for restoration success (Martin & Wilsey, 2006). Bison reintroductions in tallgrass prairies can increase native plant species richness, and cattle grazing can increase plant richness to a lesser extent (Ratajczak et al., 2022).

Future model applications

My modeling approach can be modified or scaled up depending on management needs. For example, indicator species could be adjusted or added depending on the target ecosystem and management goals. If I expand the analysis to the entire Great Plains Region, for example, I may wish to add wetland species to capture benefits of restoration in the Prairie Pothole region (Dixon et al., 2019). Here, I only included species for which

I have an estimated historical range so that I could account for extinction risk from historical habitat loss. To incorporate species where data are lacking, users could estimate historical ranges using preferred habitat types, species distribution models, or expert opinions on the amount of historical range loss. Ideally, it would be useful to estimate current potential ranges as well, which may differ from historical ranges due to climate or other ecosystem changes. I also used a map of historical Great Plains grassland types to select potential restoration area. Estimates of historical land cover also exist for other ecosystems, e.g. eastern U.S. grasslands (Hanberry & Noss, 2022).

My model could also be modified to include other ecosystem services that are improved through ecological restoration. For example, grassland restoration can have large benefits for carbon storage and for cultural services like access to nature (Bengtsson et al., 2019; Samson & Knopf, 1994). Global analyses have incorporated carbon storage as an additional restoration benefit that can be modeled (e.g., (Strassburg et al., 2020)). In the future, it may be possible to add other metrics such as distance to population centers to approximate how restoration could affect equity of access to native ecosystems.

Finally, users may wish to account for other aspects of landscape configuration or future threats such as climate change. For example, Henslow's sparrow (*Ammodramus henslowii*) populations increased more in areas with high local CRP enrollment (Herkert, 2007). On the other hand, high turnover of prairie plant species across space means that protecting multiple small remnant patches rather than a few large patches can be important for conserving plant diversity (Wilsey, Martin, et al., 2005). Thus, depending on conservation goals, clusters of restored pixels may be more beneficial than a single restored pixel. One way to do this could be to start with a map of current intact habitat,

and weight conservation benefits based on distance to between pixels. Using an iterative approach, pixels selected for restoration could be added to the current habitat map, and thus pixels would be more likely to be selected if they were close to other selected pixels. Weighting could be based on species dispersal distances. That is, species that can disperse farther would benefit more from pixels that are farther from current habitat, while those with smaller dispersal distances would benefit more from clumping of restoration pixels since they are less likely to reach areas that are too far away. Climate change could also be incorporated by weighting. As temperatures rise, species are expected to move poleward and upward in elevation to maintain their temperature niches (Rubenstein et al., 2023). Therefore, poleward edges of a species range may be more beneficial in the long-term than equatorial range edges, and benefit weighting could be updated to reflect this.

CONCLUSION

Given limited budgets, deciding where to restore habitat will be an important need in the coming decade. Here, I developed a model that can be used to maximize conservation benefit to cost ratios. My approach is flexible and can be updated for different ecosystems, species, and conservation priorities. I also outlined potential alterations that can be made in future analyses, depending on desired restoration goals.

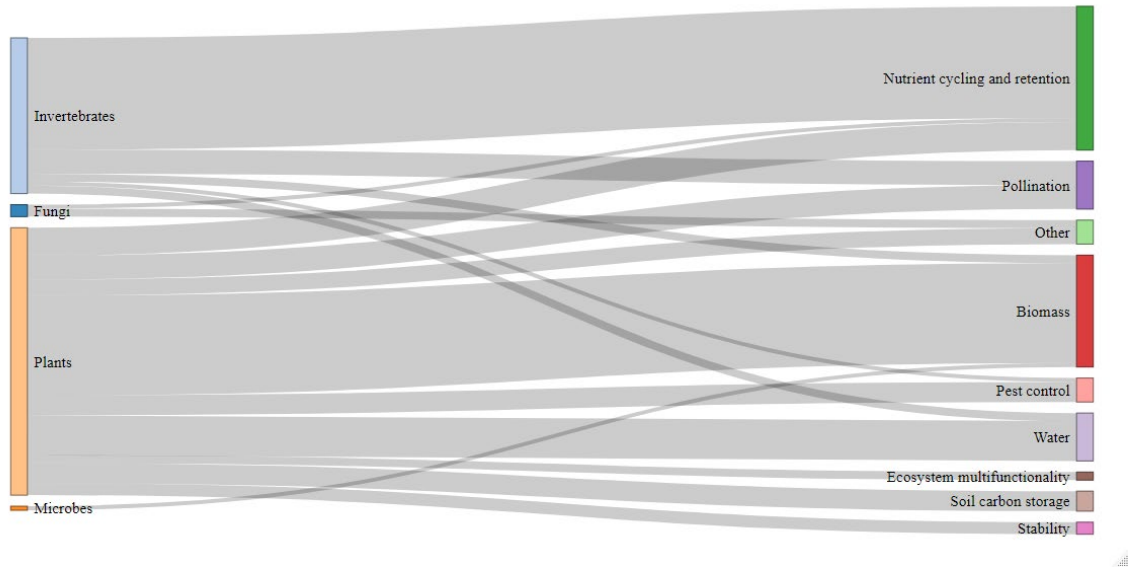
Global and domestic conservation targets highlight the growing recognition that ecological restoration will be needed to meet biodiversity conservation goals. Ecological restoration improves biodiversity and ecosystem services compared to degraded landscapes, but restored areas remain consistently less diverse and provide fewer benefits than unaltered reference ecosystems (Benayas et al., 2009; Martin & Wilsey, 2006;

Newbold et al., 2020). Improving restoration techniques will thus be a critical challenge in the coming years, especially for ecosystems like grasslands that have little remaining intact habitat.

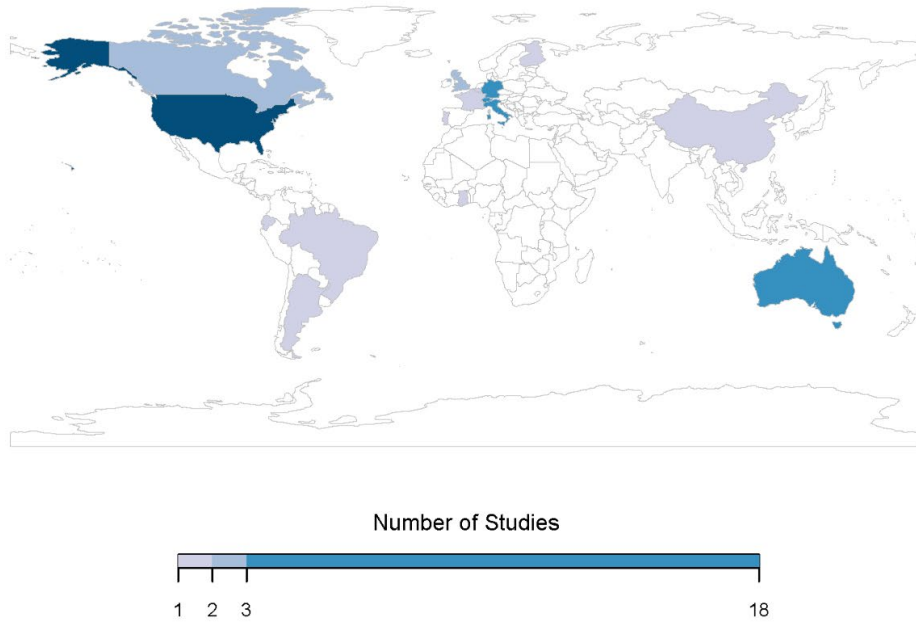
APPENDICES

APPENDIX A

SUPPLEMENTAL FIGURES AND TABLES FOR CHAPTER 1



Supplemental Figure 1.1: A comparison of proportion of positive, negative, neutral, and mixed responses of biodiversity-ecosystem functioning relationships by ecosystem function in urban (this study, n=109 cases) vs non-urban systems (data drawn from (van der Plas 2019), n=1,219 cases).



Supplemental Figure 1.2: A comparison of proportion of positive, negative, neutral, and mixed responses of biodiversity-ecosystem functioning relationships by ecosystem function in urban (this study, n=109 cases) vs non-urban systems (data drawn from (van der Plas 2019), n=1,219 cases).

Supplemental Table 1.1: List of variables and description of data extracted from the papers included in my systematic review.

Study Information and methodology	
Paper ID	Unique numeric ID to identify each paper
Hemisphere	Study area hemisphere
Country	Study area country
City	Study area city
Ecosystem Type	Description of study ecosystem type (i.e., terrestrial, freshwater, marine)
Habitat	Free text description of habitat type (e.g., urban garden, green roof)
Spatial Scale Grain	Study area plot size
Spatial Scale Extent	Extent of inference of BEF relationship
Study Type 1	Was the study observational, experimental (i.e., level of biodiversity explicitly manipulated), or modeled?
Inference Type	Did the study 1) simply consider spatial covariation/correlation between biodiversity and EF or (2) statistically or experimentally consider the causal effects of changes in biodiversity after controlling for other abiotic (e.g., soil fertility or fertilizer or pesticide inputs) or biotic (e.g., composition) factors that are also known to affect EF?
Study Type 2	Describe study location (e.g., lab, mesocosm, field)
Sample Size	How many treatments x replicates were included in the study?
Years	Length of study (number of years). Several studies conducted short experiments that were repeated in more than one year. In these cases, I reported the length of the shorter experiment, rather than total number of years, as my intent was to assess whether BEF relationships grow stronger over time.
Biodiversity-Ecosystem Functioning Relationship	
Ecosystem Function Assessed	Ecosystem function assessed
Ecosystem Function description	Free text description of ecosystem function (or service if applicable)
Focal Taxonomic Group	Group of organisms whose biodiversity levels are related to ecosystem functioning
Biodiversity Metric	Biodiversity metric assessed (e.g., species richness, species evenness, functional traits)
Impact	Impact of diversity metric on ecosystem function (e.g., positive, negative, no effect)
Species Identity	Was species identity considered?

Species Identity Impact	Did species identity have an impact on ecosystem function?
Invasives	Did the authors investigate the impact of invasive vs. native species for ecosystem function?

Supplemental Table 1.2: χ^2 -goodness of fit tests results to assess whether positive biodiversity-ecosystem functioning relationships were more likely than negative ones.

Test	Test statistic (χ^2)	Degrees of Freedom	P-value
All cases combined	25	1	<0.0001
All ecosystem functions with spatial correlation cases removed	27.524	1	<0.0001
Biomass only, all cases	0	1	1
Nutrient cycling and retention, all cases	15.211	1	<0.0001
Pollination, all cases	7.364	1	0.007
Pollination, spatial correlation cases removed	7.364	1	0.007

APPENDIX B

EQUATIONS USED IN THE BILBI MODEL

For additional details, see (Di Marco et al., 2019; Hoskins et al., 2020)

BILBI is a macroecological model that uses generalized dissimilarity modeling (GDM) to map beta diversity over space and time, meaning that it predicts species turnover based on environmental differences (e.g., climate and habitat variables) and spatial distance between sites (Hoskins et al., 2020). Beta diversity estimates can then be coupled with a modified form of species-area analysis to predict the proportion of species expected to persist within a region of interest (e.g., an ecoregion) under different climate and land-use scenarios (Di Marco et al., 2019). To estimate beta diversity, the model evaluates the probability that a random draw of two species from two sites are the same, which is then converted to a Sorensen dissimilarity index and provides continuous predictions of beta diversity on a 0-1 scale across the area being modeled (Di Marco et al., 2019; Hoskins et al., 2020).

The following equations are used to predict the proportion of species originally associated with a given grid cell (30 arc-seconds globally, ~1 km² at the equator) which are expected to persist (i.e. avoid extinction) over the long term, anywhere within their range (Di Marco et al., 2019):

Calculate the total area of similar ecological environments relative to a given cell i by summing the predicted similarity (under the present baseline climate) to all other cells j :

$$A_{i_{baseline}} = \sum_{j=1}^{j=n} S_{i_{present}j_{present}} \quad (1)$$

where $A_{i_{baseline}}$ = the effective area (# of grid cells) of similar ecological environments relative to cell i in the baseline period, n =the total number of cells for which compositional similarity with cell i was modeled, $s_{i_{present}j_{present}}$ = the GDM-predicted compositional similarity between cells i and j (i.e., pairwise beta diversity on a 0-1 scale) under present climatic conditions. Thus, cells that have completely similar composition would be counted as a full grid cell, while less similar cells would count less towards potential area.

Calculate the potential area of similar ecological environments under a future scenario ($A_{i_{scenario}}$):

$$A_{i_{scenario}} = \sum_{j=1}^{j=n} s_{i_{present}j_{future}} h_{j_{scenario}} \quad (2)$$

where $s_{i_{present}j_{future}}$ = the predicted similarity between cell i under the present climate and cell j under the future climate associated with this scenario (using standard space-for-time substitution), and $h_{j_{scenario}}$ is the habitat condition score of cell j under the scenario.

Use the species-area relationship to translate the amount of habitat remaining across similar ecological environments under the scenario (expressed as a proportion of the total area of similar environments prior to climate and land-use change) into the proportion of species (originally associated with cell i) expected to persist over the long term ($p_{i_{scenario}}$):

$$p_{i_{scenario}} = \left[\frac{A_{i_{scenario}}}{A_{i_{baseline}}} \right]^z \quad (3)$$

where z is the exponent of the species-area relationship, which determines how loss of species scales with loss of habitat area. A z value of 0.25 is widely used in other studies predicting the proportion of species remaining over time in fragmented habitats. However, intact habitats also experience species relaxation (i.e., long-term loss of species as the community approaches equilibrium species richness (Diamond, 1972)), commonly estimated at $z=0.15$. To estimate the additional loss of species due to climate and land-use change, I can subtract these two estimates of z to obtain a lower bound of $z=0.1$ (Gonzalez, 2009; Isbell, Tilman, et al., 2015). Other metapopulation models estimate that extinction debts could be higher (Isbell, Tilman, et al., 2015). Thus, I use a range of z values between 0.1 and 0.65, similar to Isbell et al. (2015), to capture some of the uncertainty around the magnitude of species extinction debts.

I used two scenarios: SSP1/RCP 2.6, a low land-use change and low climate change scenario (“global sustainability”²), and SSP5/RCP8.5, a high climate change and intermediate land-use change scenario (“fossil-fueled development”) (Kriegler et al., 2017; van Vuuren et al., 2017). I estimated the collective proportion of those species originally associated with each ecoregion which are expected to persist over the long term as a weighted geometric mean of the p_i values for all cells in the ecoregion. The contribution of each cell was weighted by how unique it is within the context of the biome where the ecoregion is found (i.e., regionally rare environments have a higher weight, since these areas are likely to have more unique species and thus may contribute

² Note that SSP1/RCP2.6 still entails a significant amount of land use change due to bioenergy production and increased food demand (Ciais et al., 2013).

more to regional species loss). See (Di Marco et al., 2019) for further explanation of this approach.

The proportion of species persisting at the ecoregion level (p_{region}) was therefore calculated as:

$$p_{region} = \exp\left(\frac{\sum_{i=1}^m w_i \ln(p_i)}{\sum_{i=1}^m w_i}\right) \quad (4)$$

where m is the number of cells in the ecoregion of interest, and w_i is the weight applied to each cell:

$$w_i = \frac{1}{\sum_{j=1}^{j=n} S_{i_{present}j_{present}}}$$

These ecoregional aggregations were performed using the raster package (Hijmans 2020) in R version 4.0.4 (R Core Team 2021).

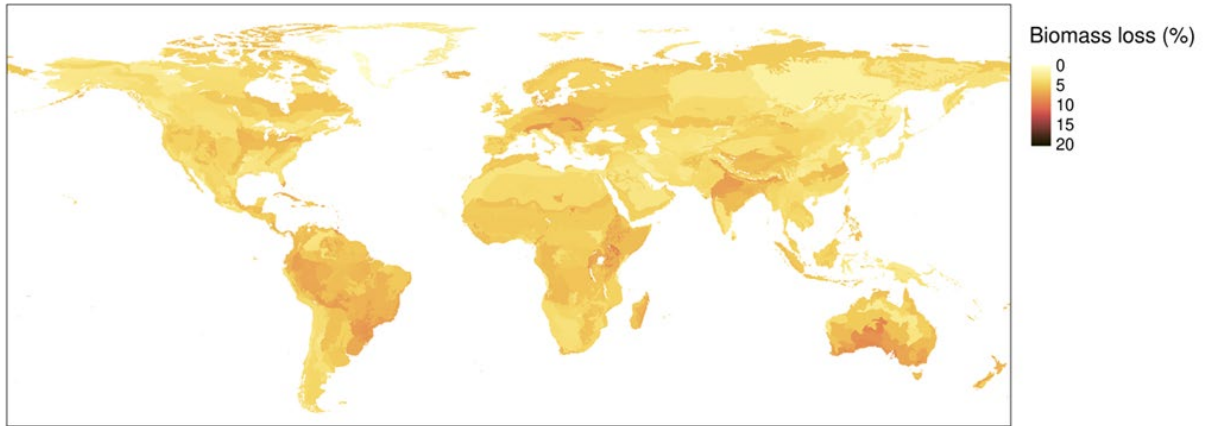
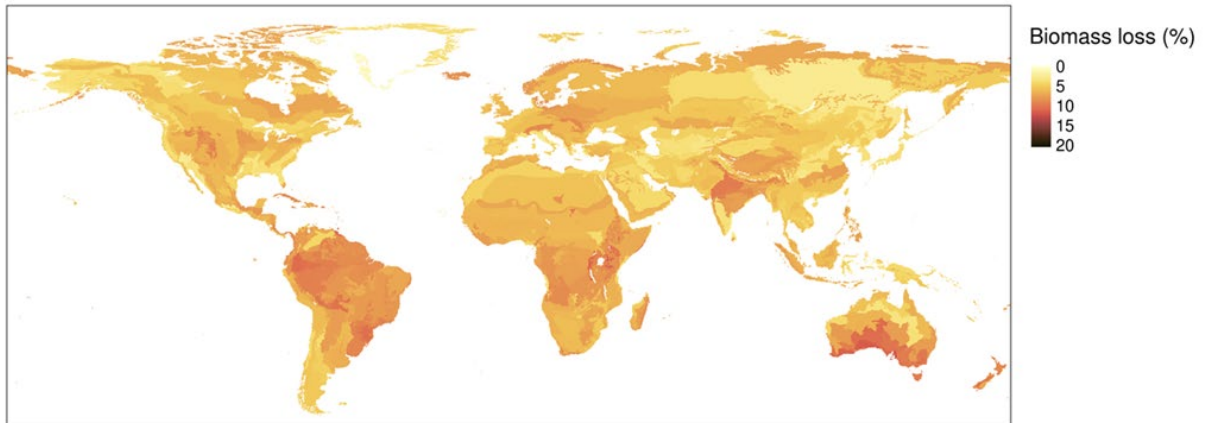
APPENDIX C

SUPPLEMENTAL FIGURES AND TABLES FOR CHAPTER 2

Supplemental Table 2.1: Projected carbon loss from various sources under global sustainability (SSP1/RCP3.6) and fossil-fueled development (SSP5/RCP8) scenarios.

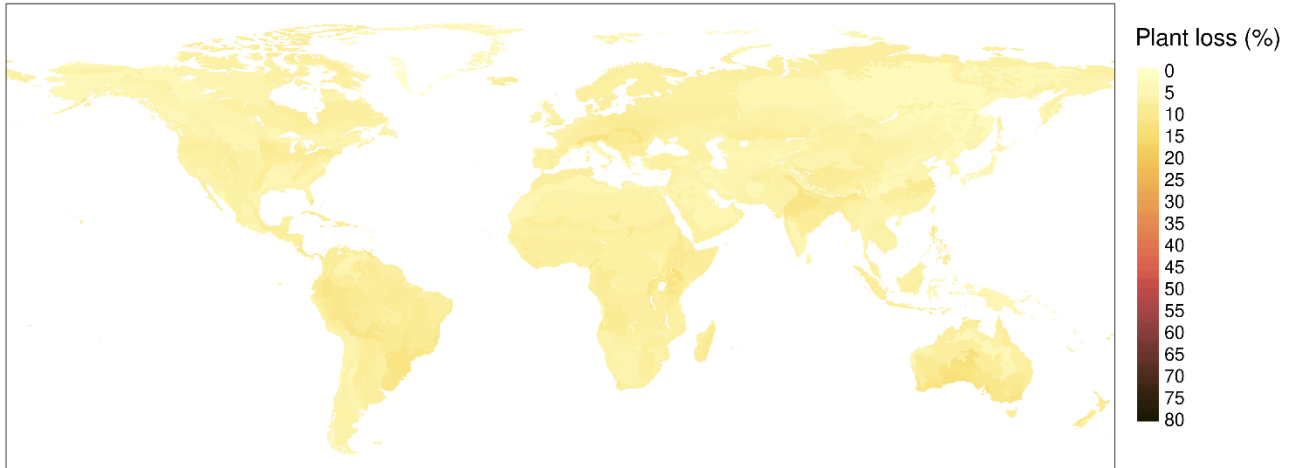
Source	Timeframe of C emissions	C loss		Other	Citation
		SSP1/RCP2.6	SSP5/RCP8		
Long-term vegetation carbon loss associated with biodiversity loss	Over the long term (the coming decades) based on cumulative biodiversity loss projected from climate and land-use conditions in 2050.	7.44-103.14 PgC	10.87-145.95 PgC		This analysis
Long-term vegetation and soil carbon loss associated with biodiversity loss	Unclear, but over the long term based on cumulative biodiversity loss projected from climate and land-use conditions in 2050.	18.87 – 262.09 PgC	26.49 – 356.71 PgC		This analysis
Land-use CO ₂ emissions estimated from integrated assessment models (IAMs) 2006-2100	Cumulative emissions from 2006-2100	61.1 PgC	53.8 PgC		(Ciais et al., 2013) Extracted using WebPlot digitizer from figure 6.23
Emissions from melting permafrost based on IPCC AR6 model	2100	20-58 PgC	92±17 PgC	3-41 PgC per 1°C warming	(Canadell et al., 2021; Meredith et al., 2019; Schneider Von

ensembles (low confidence)					Deimling et al., 2015)
LPJ-GUESS	2100		10% increase in ecosystem carbon storage		(Smith et al., 2014)

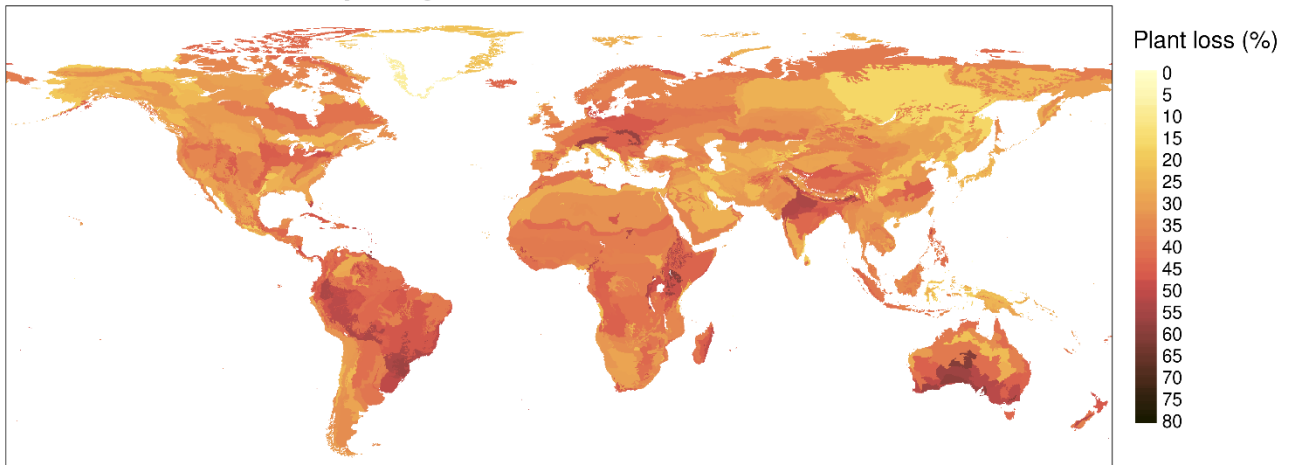
A**B**

Supplemental Figure 2.1: Biomass loss - Percent change in biomass by ecoregion under a global sustainability (SSP1/RCP2.6, panel A) and fossil-fueled development (SSP5/RCP8.5, panel B) scenario using the mean b value of 0.26 and a species-area relationship of $z=0.25$. Darker areas indicate greater loss of plant biomass. This biomass loss is from within remaining vegetation as a result of biodiversity loss, over and above any biomass loss resulting from the direct impact of land-use change under a given scenario.

Global sustainability, Low z value

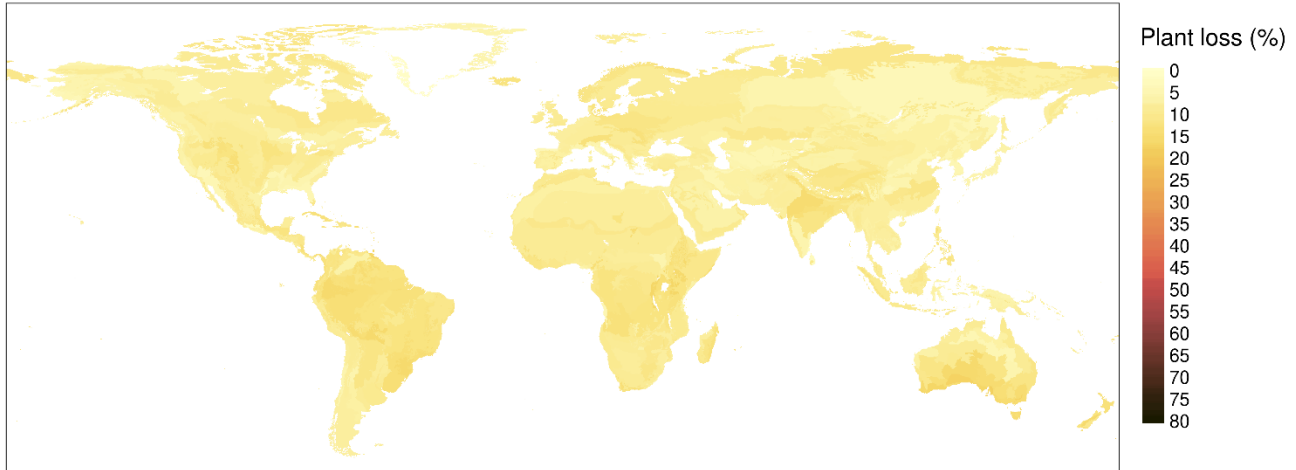


Global sustainability, High z value

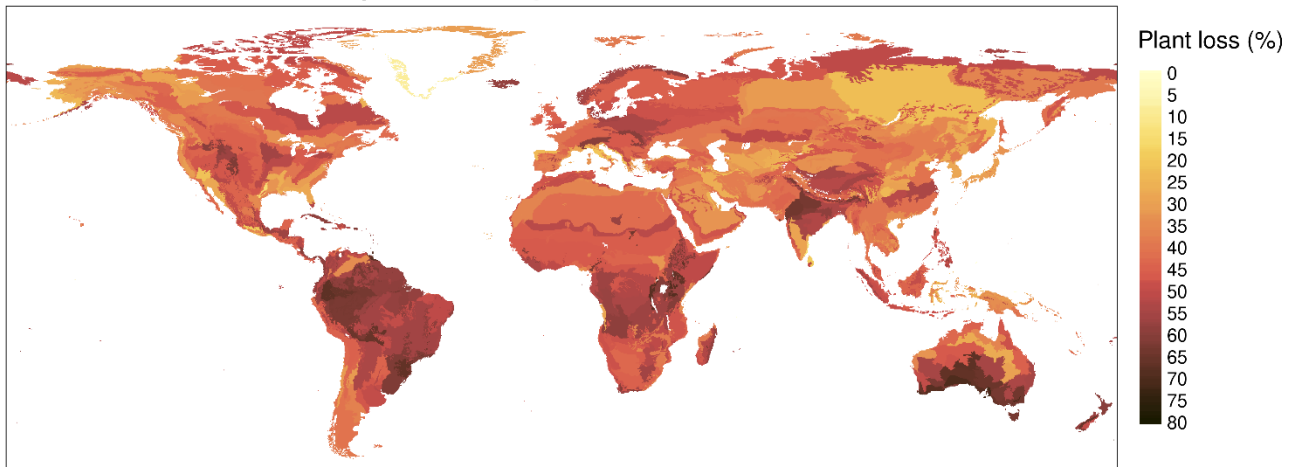


Supplemental Figure 2.2: The full range of plant species loss by ecoregion projected by the BILBI model under a global sustainability (SSP1/RCP2.6) scenario. Darker areas indicate greater plant species loss. The top figure shows plant species loss using the lowest species-area relationship value, while the bottom figure shows the highest species-area relationship value.

Fossil-fueled development, Low z value

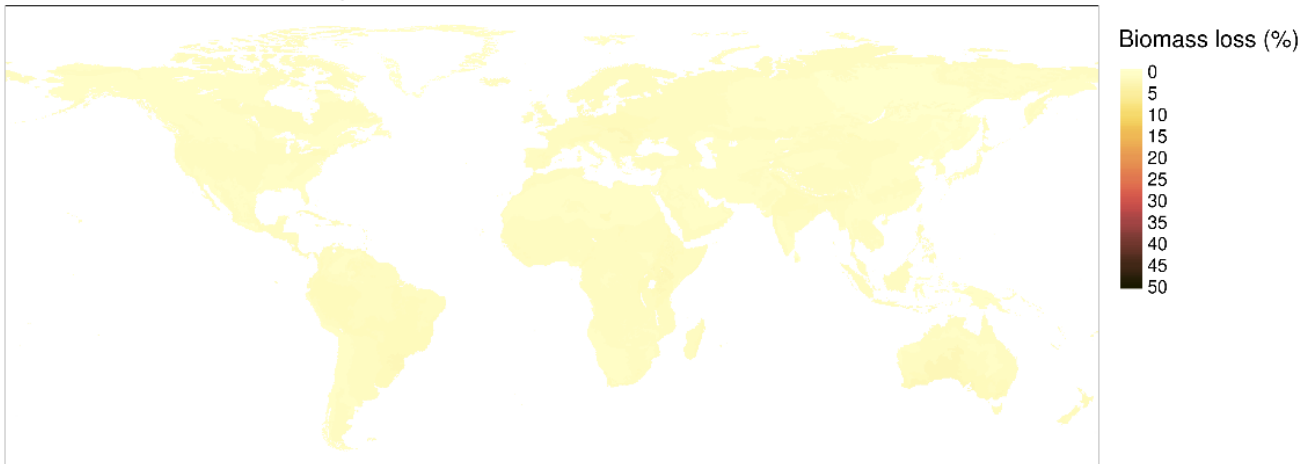


Fossil-fueled development, High z value

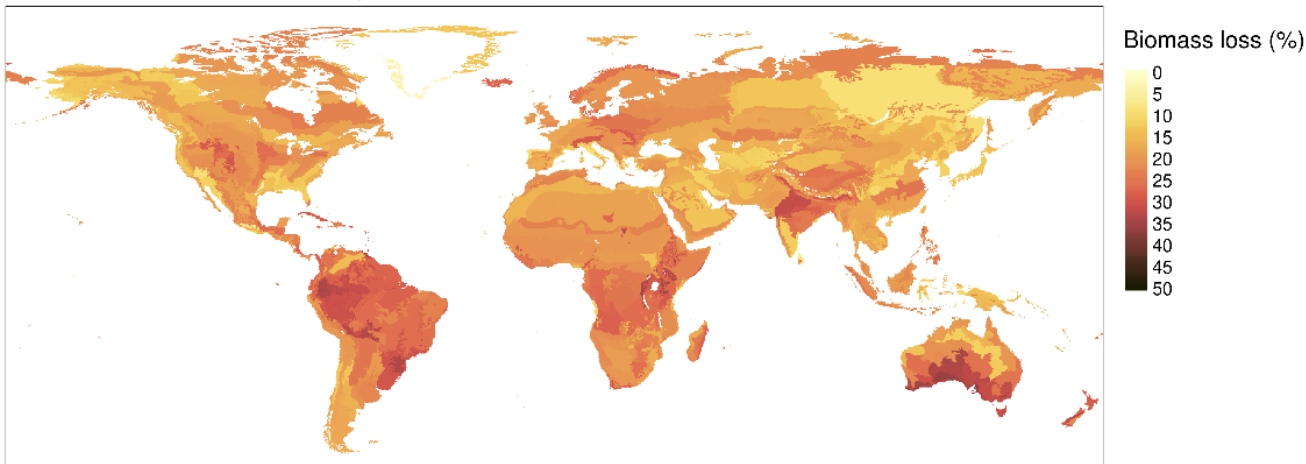


Supplemental Figure 2.3: The full range of plant species loss by ecoregion projected by the BILBI model under a fossil-fueled development (SSP5/RCP8.5) scenario. Darker areas indicate greater plant species loss. The top figure shows plant species loss using the lowest species-area relationship value, while the bottom figure shows the highest species-area relationship value.

Global sustainability, Low z value, Low b value

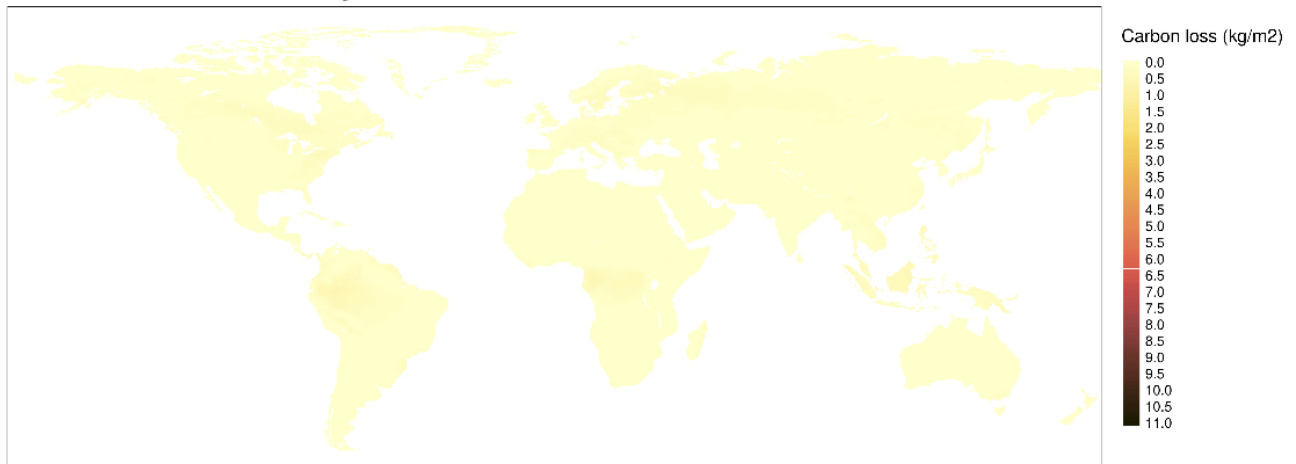


Fossil-fueled development, High z value, High b value

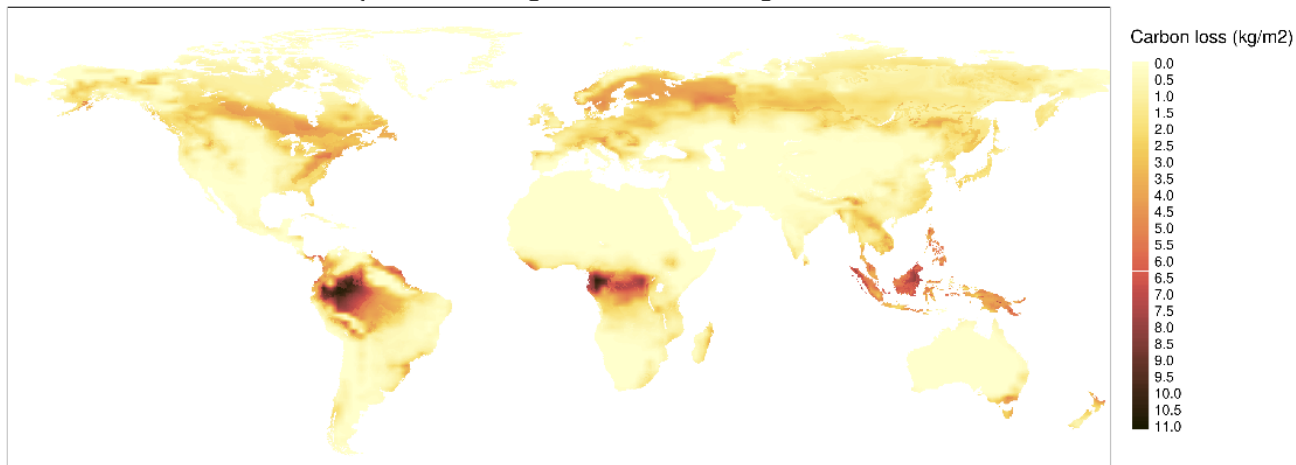


Supplemental Figure 2.4: The full range of uncertainty for percent change in biomass by ecoregion. Darker areas indicate greater percent biomass loss. The top figure shows percent biomass loss under a global sustainability scenario using the lowest species-area relationship value and the lowest biodiversity-biomass relationship value, while the bottom figure shows the highest of both values under the fossil-fueled development scenario.

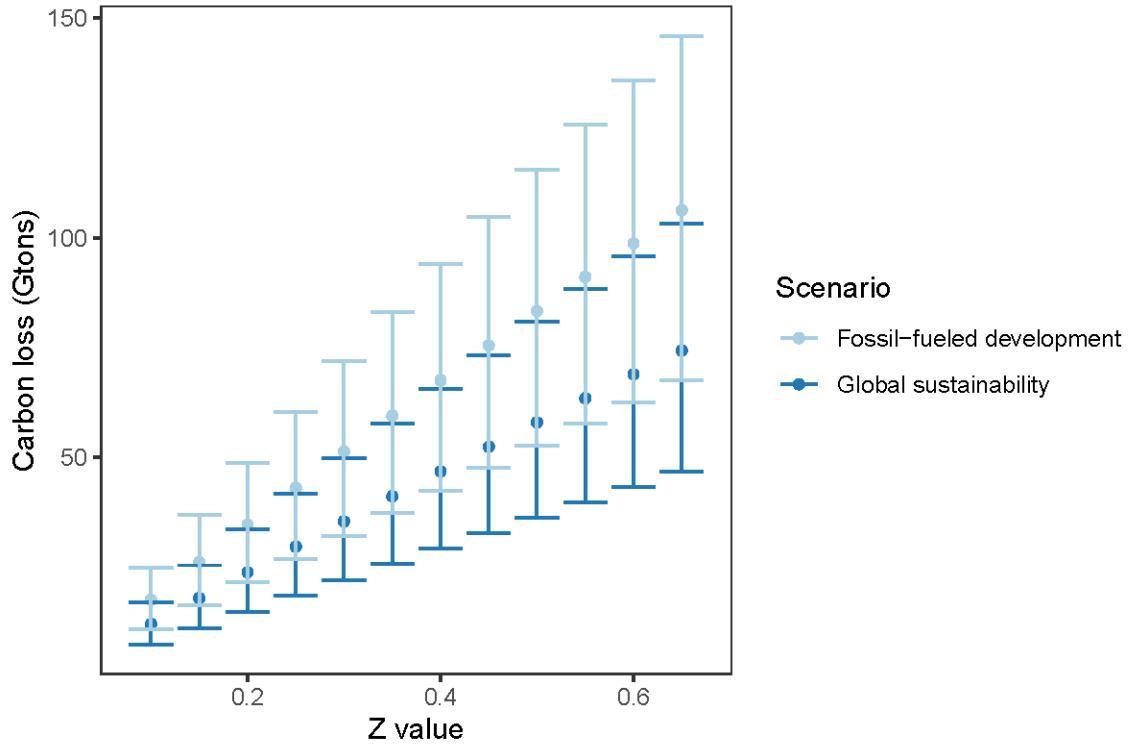
Global sustainability, Low z value, Low b value



Fossil-fueled development, High z value, High b value

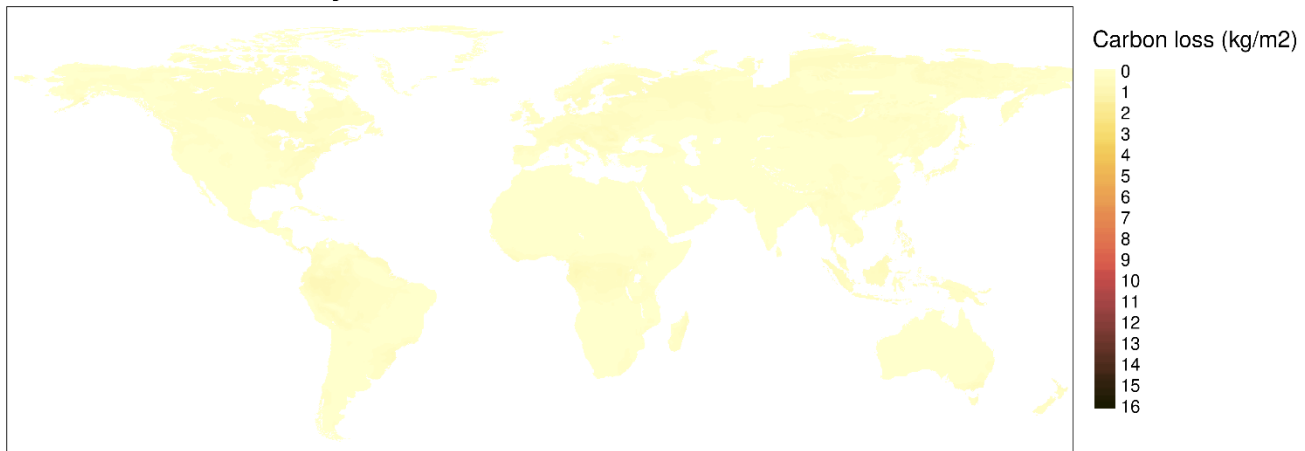


Supplemental Figure 2.5: The full range of uncertainty for vegetation carbon loss from (kg/m²) driven by long-term loss of plant biodiversity by ecoregion. Darker areas indicate greater percent carbon loss. The top figure shows carbon loss under a global sustainability scenario using the lowest species-area relationship value and the lowest biodiversity-biomass relationship value, while the bottom figure shows the highest of both values under the fossil-fueled development scenario.

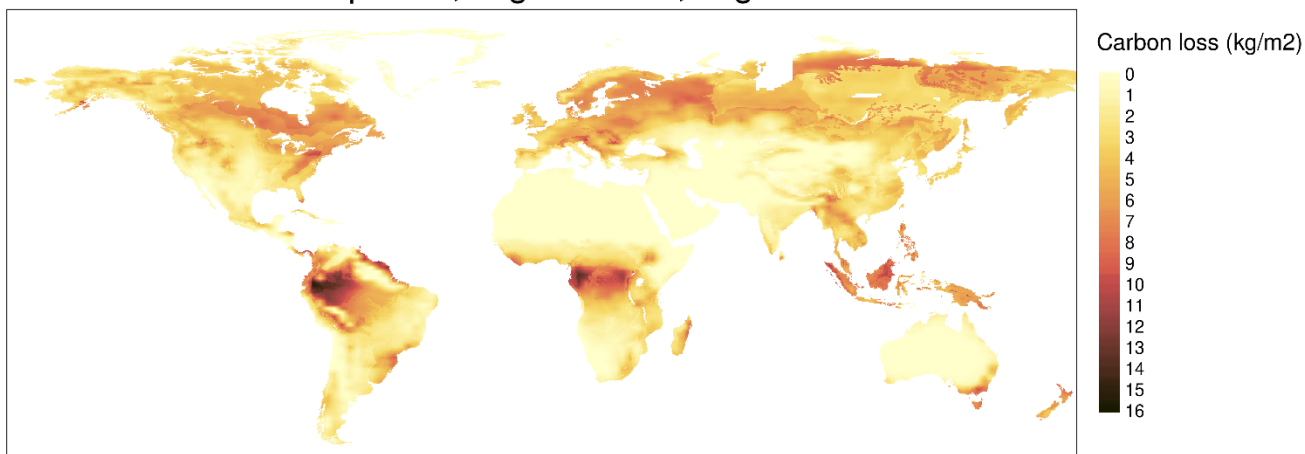


Supplemental Figure 2.6: Uncertainty in vegetation carbon losses with different species-area relationships (Z-values) for different climate and land-use change scenarios. Error bars represent uncertainty across the biodiversity-biomass production relationship.

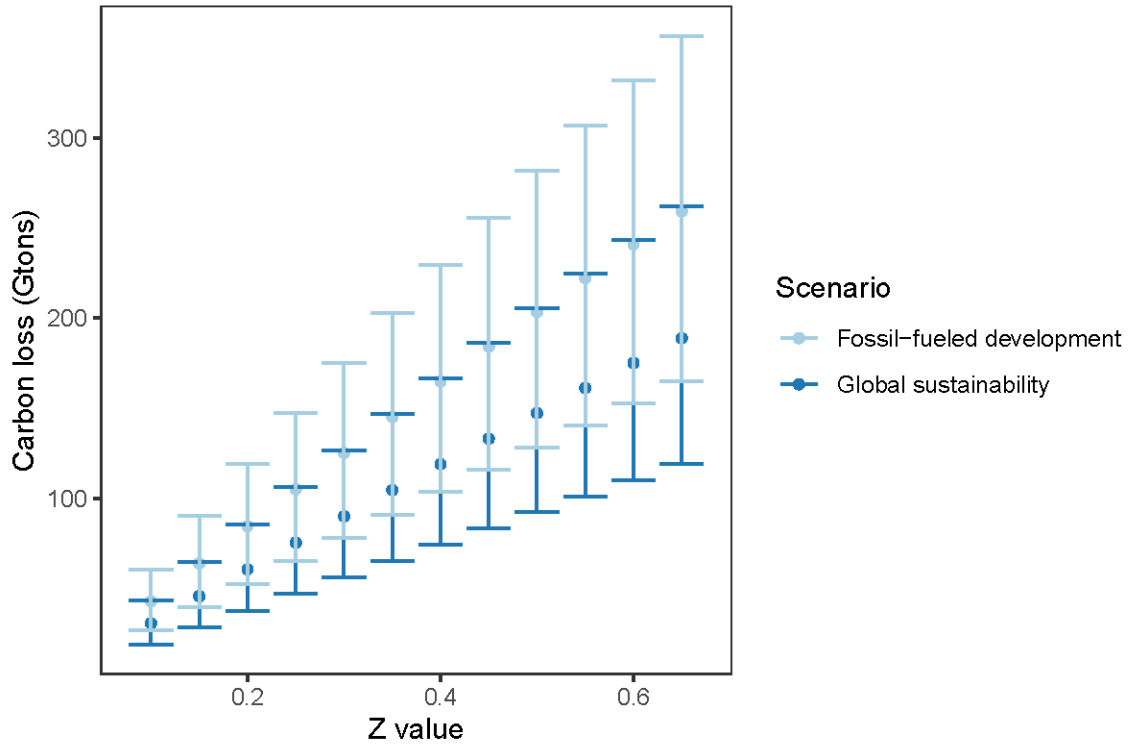
Global sustainability, Low z value, Low b value



Fossil-fueled development, High z value, High b value



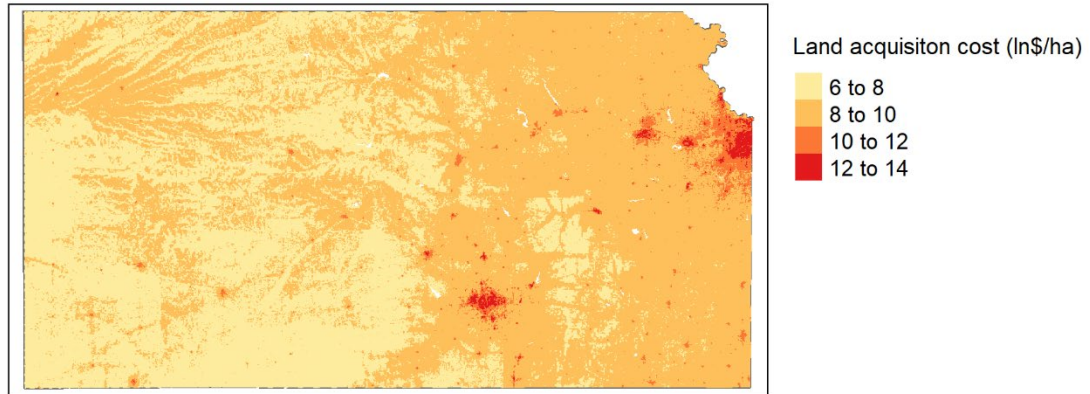
Supplemental Figure 2.7: The full range of uncertainty for carbon loss (kg/m²) driven by long-term loss of plant biodiversity by ecoregion when both vegetation carbon and soil carbon are considered. Darker areas indicate greater percent carbon loss. The top figure shows carbon loss under a global sustainability scenario using the lowest species-area relationship value and the lowest biodiversity-biomass relationship value, while the bottom figure shows the highest of both values under the fossil-fueled development scenario.



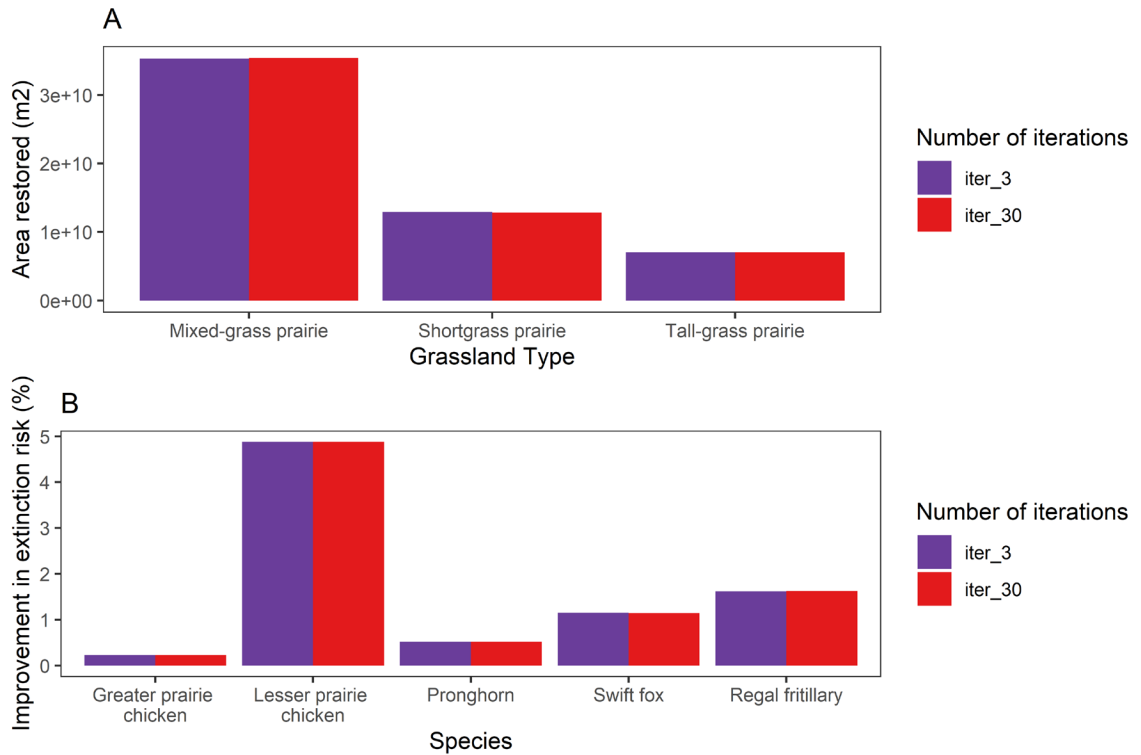
Supplemental Figure 2.8: Uncertainty in carbon losses in vegetation and soil carbon with different species-area relationships (Z-values) for different climate and land-use change scenarios. Error bars represent uncertainty across the biodiversity-biomass production relationship.

APPENDIX D

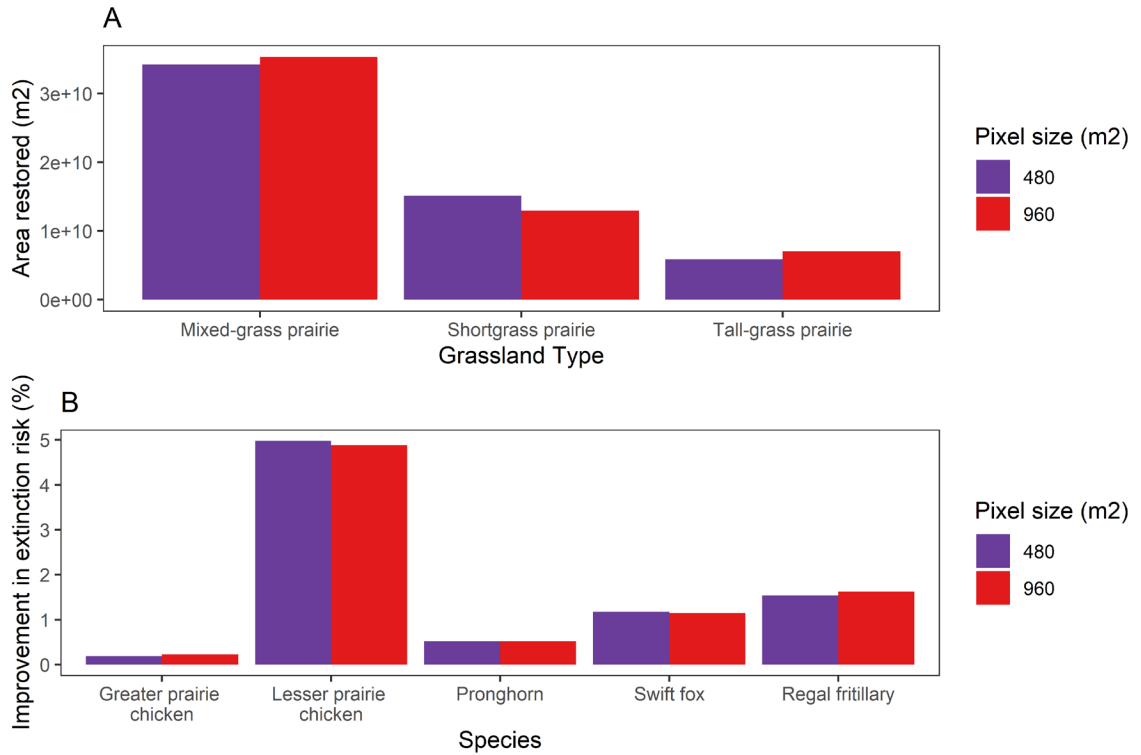
SUPPLEMENTAL FIGURES AND TABLES FOR CHAPTER 3



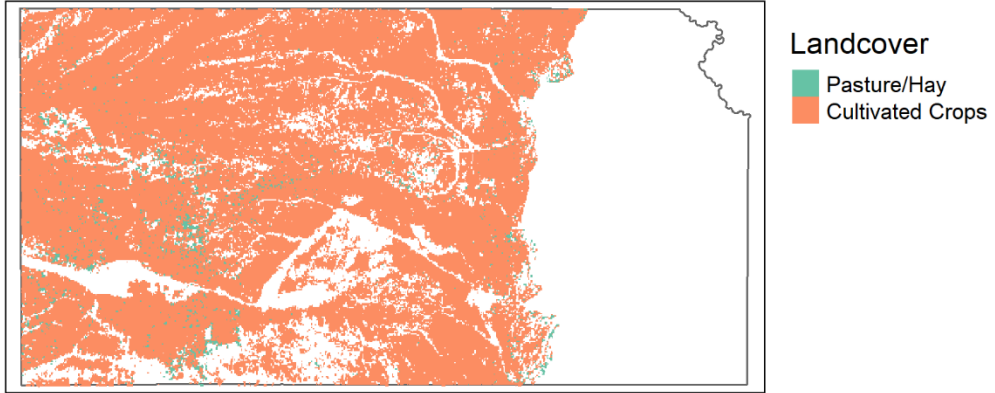
Supplemental figure 3.1: Land acquisition costs across the study area in ln\$/ha. Data comes from (Nolte, 2020)



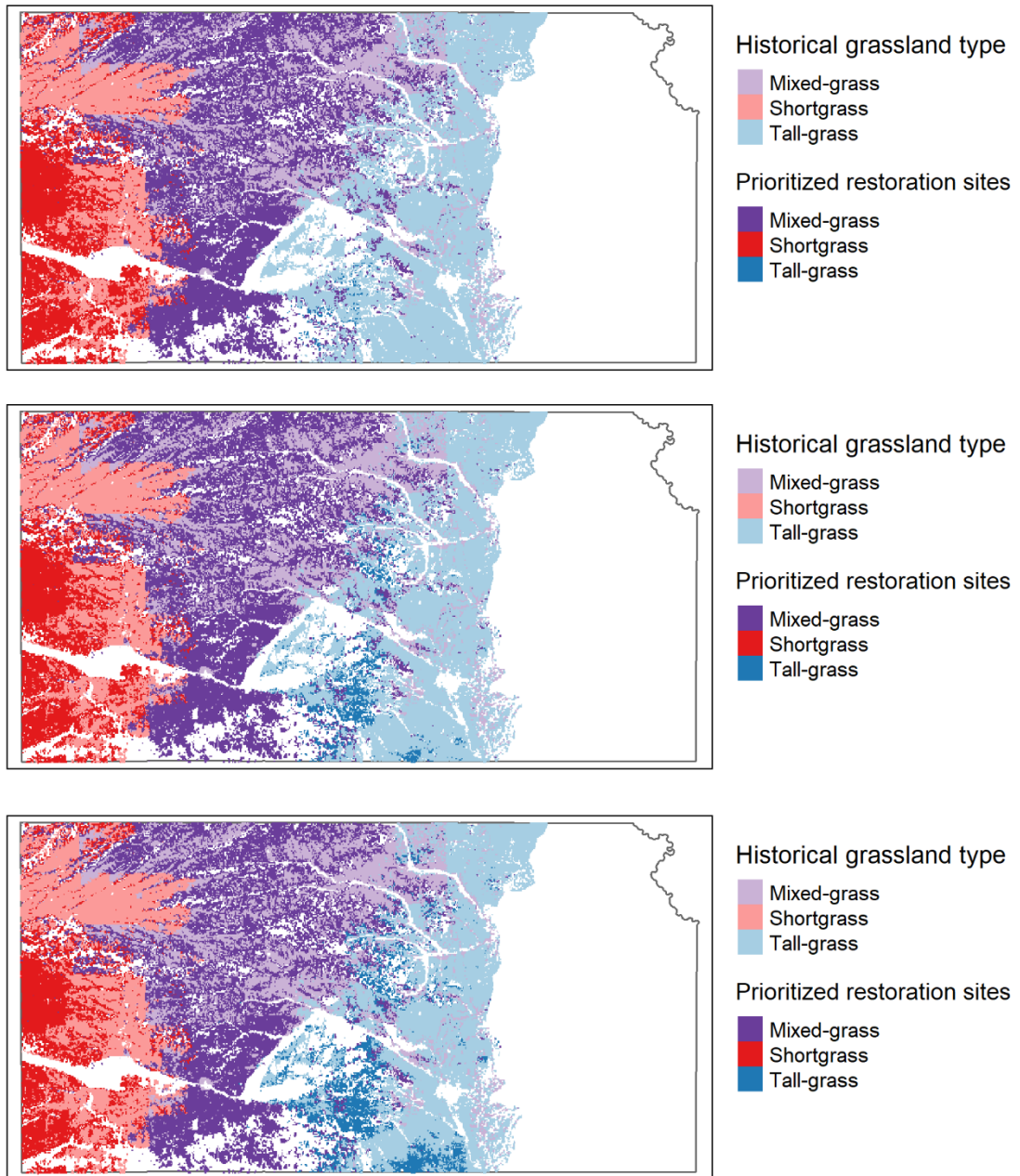
Supplemental figure 3.2: Comparison of how the number of iterations used in the optimization affected area restored by grassland type (A) and improved species' extinction risk (B) under the translocation scenario (i.e., all suitable habitat types were considered equally beneficial for the species regardless of distance to current habitat) and using a 20% minimum restoration threshold per habitat type.



Supplemental figure 3.3: Comparison of how pixel size (resolution) affected area restored by grassland type (A) and improved species' extinction risk (B) under the translocation scenario (i.e., all suitable habitat types were considered equally beneficial for the species regardless of distance to current habitat) and using a 20% minimum restoration threshold per habitat type.



Supplemental figure 3.4: Landcover type of the potential restoration area (960x960 m² resolution).



Supplemental figure 3.5: Priority restoration sites using the translocation scenario when $z = 0.25$, resolution = $960 \times 960 \text{ m}^2$, iterations = 3 for a minimum habitat restoration threshold of 0% (top), 10% (middle) and 20% (bottom).

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