BIOTIC AND ABIOTIC DRIVERS OF AVIAN COMMUNITY DYNAMICS

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Abstract: Birds are an imperiled taxon in North America and have experienced rapid and widespread decline in the most recent century. Here, we use both basic and applied approaches to better understand how bird communities function at regional and continental scales. Specifically, we used a half-century of continental-scale bird community data to quantify avian community variability across diverse biomes in North America, and compared the relative contributions of climate (both mean conditions and weather extremes) and species richness to avian community stability. Our results indicate that—despite disproportionately high attention to the diversity-stability concept in the literature—environmental conditions better explained community stability than the species richness of the community itself. Specifically, extreme heat and extremely low precipitation are associated with low community stability. Next, we investigated the spatial and temporal scaling relationships of a hypothesized mechanism of ecological stability, compensatory dynamics. Results indicate that community-level compensatory dynamics are generally rare, but also highly spatially scale-dependent (more prevalent at small scales). We also found strong evidence of synchronous bird species at large (decadal) temporal scales—that is, areas of long-term bird abundance declines of some species are less likely to experience concomitant abundance increases of other species. We also evaluated the response of northern bobwhite to drought conditions across two biomes. We found that bobwhite abundance significantly decreased in both biomes, but decline was more than twice as sharp in the Eastern Forest as it was the Great Plains. We also found that bobwhite declined with drought conditions in the Great Plains but had a positive association with drought in the Eastern Temperate Forest. Finally, we investigated the response of northern bobwhite to woody cover across two, proximal study areas and found markedly different resource selection patterns. Specifically, whether bobwhite selected for shrub cover and whether they strongly avoided trees, depended on the study site in focus. Additionally, the spatial scale of selection was nearly an order of magnitude different between the cover types. All four chapters highlight an important pattern: complexity appears to be the rule rather the exception in natural systems.

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CHAPTER I

WEATHER EXTREMES EXPLAIN AVIAN COMMUNITY VARIABILITY BETTER THAN SPECIES RICHNESS

ABSTRACT

Understanding a general relationship between biodiversity and ecological stability has become increasingly urgent as rapid species extinction is occurring and anticipated to continue. Though evidence of a positive diversity-stability relationship is accumulating, empirical results are inconsistent and effect sizes tend to be small. This raises questions about the relative contributions of biotic (i.e., species composition and their interactions) and abiotic (i.e., environmental conditions) drivers of community stability. Though theory predicts that environmental conditions at a particular site may be a stronger determinant of community stability than the diversity of the community itself, few studies have directly compared the relative importance of diversity and environmental factors regulating community stability. Here, we use a half-century of continental-scale bird community data to quantify avian community variability at 1,379 sites, across diverse biomes in North America and compare the relative contributions of climate (both mean conditions as well as weather extremes) and species richness. Our results indicate that—despite disproportionately high attention to the diversity-stability concept in the literature—environmental conditions better explained community stability than the species richness of the community itself. Specifically, we found that extreme heat and extremely low precipitation are associated with low community stability. This provides large-scale, empirical support for the theoretical concept that environmental conditions play a larger role determining community stability than diversity in North American avian communities. Additionally, on a more applied level, our findings add to the growing list of diverse ecological responses to weather extremes.

INRODUCTION

The decades-long focus on identifying a general relationship between biodiversity and ecological stability has become increasingly urgent as rapid species extinction is occurring and anticipated to continue (Loreau *et al.*, 2001; Dirzo *et al.*, 2014). Research has explored the conceptual basis of the diversity-stability relationship (Loreau, 1998; Ives and Carpenter, 2007), tested empirical data (e.g., Tilman, Reich and Knops, 2006; Bezemer and Van Der Putten, 2007; Yang *et al.*, 2012), and suggested mechanisms behind the observed patterns in diversity-stability relationships (e.g., Yachi and Loreau, 1999; Bezemer and Van Der Putten, 2007; Yang *et al.*, 2012; Loreau and de Mazancourt, 2013). Though evidence of a positive diversity-stability relationship is accumulating (Tilman and Downing, 1994; Mccann, 2000; Cottingham, Brown and Lennon, 2001; Ives and Carpenter, 2007; Chen *et al.*, 2021), empirical results are inconsistent (Schmid and Pfisterer, 2002; Houlahan *et al.*, 2018) and this pattern is not always straightforward. For example, the diversity-stability relationship can change along environmental gradients such as latitude (Shurin *et al.*, 2007), nutrient concentration (Li *et al.*, 2018), or patch size (Dunstan and Johnson, 2006), and can simultaneously depend on multiple components of biodiversity, such as species richness, functional diversity, and phylogenetic diversity (Craven *et al.*, 2018). Importantly, because effect sizes tend to be small (Houlahan *et al.*, 2018, global quantitative review), it raises questions about the relative contributions of biotic (i.e., species composition and their interactions) and abiotic (i.e., environmental conditions) drivers of community stability.

Theory predicts that environmental conditions at a particular site may be a stronger determinant of community stability than the diversity of the community itself (Loreau, 1998; Loreau and de Mazancourt, 2013); however, despite a broad and prolific focus on diversity-stability relationships in the literature, few studies have directly compared the relative importance of diversity and environmental factors regulating community stability. Though there is some empirical evidence of abiotic factors outweighing the influence of diversity on community stability in experimentally manipulated plant communities (Zhang *et al.*, 2018), the relative importance of diversity and environmental drivers in naturally variable communities (i.e., not experimentally manipulated) encompassing large (i.e., near-continental) spatial extents is not well understood. Filling this knowledge gap has both applied and basic implications. At the theory level, the question of abiotic vs. biotic factors is central to the equilibrium vs. non-equilibrium debate. Under an equilibrium perspective (i.e., "the balance of nature" in which communities are self-regulating), species interactions (biotic factors) are considered the dominant force driving community dynamics. Under a non-equilibrium paradigm, abiotic (i.e., external to the community) factors dynamically control the state of a system. Understanding the relative contributions of abiotic vs. biotic factors in regulating community dynamics may also contribute to conservation. If a management goals include long-term stability, understanding which forces best promote stability is an important first step.

It is plausible that climatic factors influence community stability, especially for organisms that are especially sensitive to weather extremes or changes in long-term climatic conditions. For example, bird communities have experienced shifts (Princé and Zuckerberg, 2015) or even complete collapse (e.g., Iknayan & Beissinger, 2018) as a result of climate change. Additionally, because weather extremes can cause distributional changes (Bateman *et al.*, 2015; Cohen, Fink and Zuckerberg, 2021) and changes in local occupancy (Cady *et al.*, 2019), it is plausible that areas with more weather variability may also have disproportionately variable bird communities. In other words, a variable climatic environment may simply beget a variable community. As anthropogenic climate change continues (IPCC, 2014), honing our understanding of the varied ways climatic conditions shape and influence ecological communities will become increasingly important.

Ecological stability is multi-dimensional and can include variability, resilience, resistance, invasibility, persistence, and compositional turnover (Pimm, 1984; Donohue *et al.*, 2013). Here, were we focus on a straightforward metric commonly used in empirical studies, dynamic variability (the variation of community-level abundance over time), such that higher variability is related to reduced stability (e.g., Houlahan *et al.*, 2018). Though this approach is not a comprehensive assessment of community stability (Arnoldi, Loreau and Haegeman, 2019), it is sufficient to meet our objectives because variability is can be directly related to other, resilience-based metrics (i.e., variability can be conceptualized as a system's response to continuous pulse disturbances; Arnoldi, Loreau and Haegeman, 2016), is comparable across large scales (Wang and Loreau, 2014), and may immediately precede critical transitions (Carpenter and Brock, 2006; Guttal and Jayaprakash, 2009; Scheffer *et al.*, 2009; *but see* Hillebrand *et al.*, 2020). The broad purpose of this study is to examine and compare potential abiotic and biotic drivers of community variability using a continental-scale bird survey dataset that includes a half-century of systematically collected data. Specifically, we quantify avian community variability across diverse biomes in North America and compare the relative contributions of climate (both mean conditions and weather extremes) and species richness on community variability.

METHODS

Avian Data and Pre-Processing

Ideal for monitoring long-term change, the North American Breeding Bird Survey (BBS) includes over 50 years of annually-surveyed avian community data collected at ~5,000 routes in North America (Sauer *et al.*, 2017). Point count data are collected along approximately 41-km, roadside routes where a trained observer stops at 50 established locations and records all birds detected in a 3-minute time period. We used nearly the full spatial and temporal extent of the BBS. To better ensure data quality and reduce error, we removed species, route-years, or entire routes based on the following *a priori* decisions. First, we removed all route-years that did not meet the BBS quality standard (i.e., incomplete surveys or surveys that were completed during unfavorable weather or outside the breeding season window). Additionally, to reduce the novice effect (Kendall, Peterjohn and Sauer, 1996), all route-years surveyed by observers during their first survey year were excluded. We omitted all bird species unlikely to be accurately and systematically detected in point counts such as raptors, owls, vultures, waterbirds, seabirds, and shorebirds and aggregated subspecies up to the species level.

BBS routes were sampled unevenly (i.e., most routes were not surveyed all 50 years, and many were only sampled once or twice). To ensure long-term data at all locations, we only included routes that were surveyed across a timespan of at least 26 years and sampled at least 70% of those years (resulting in 19-year minimum years of data for each included route). Due to concerns that uneven sampling would cause species richness measurements to be incomparable across routes, we constructed a species accumulation curve at each route to determine the proportion of species detected by nineteenth survey year (the minimum number of years required for inclusion in our analysis). Encouragingly, the mean number of species captured by the nineteenth survey year was 94.7% (SD=2.6%), indicating high confidence that species richness measurements were not meaningfully biased by uneven route sampling (Supplementary Figure 1.S1). To match the spatial extent of the climate data, we only included routes located in the contiguous United States. The final dataset included 367 species surveyed at 1,379 routes between 1967 and 2018.

Analysis

We calculated a site variability index at each BBS route location, which measures the observed abundance variability of a bird community across the entire length of its sampling (resulting in one index for each route; Houlahan *et al.*, 2018). First, we fit a linear mixed model including variance (bird abundance variability of each species at each route over time) as a function of mean abundance (mean count of each species at each route) on the whole, pre-processed BBS dataset (Equation 1.1). A random slope and intercept for species were included in the model to allow each species to have a unique relationship between variance and abundance.

Equation 1.1 $log(variance) \sim log(mean\ abundance) + log(mean\ abundance)|species$

Using the linear mixed model, we compiled the residuals for each species at each route. The residuals are a measure of how variable a species is at a particular route, relative to the expected variance given the model (the observed species variance minus the expected variance, given the mean abundance at each route). We then aggregated the residuals for each species at each route (each route has a number of residuals equal to the number of species at that route) and standardized by dividing by the total route-level species richness. This yields a route variability index where negative numbers indicate bird communities that are more stable than expected (given the abundance of each species) and positive numbers indicate highly variable communities. A benefit to using regression residuals rather than compiling each species' raw variance is that residuals are based on least squares estimation and average to zero. Therefore, each species at each route has the opportunity to contribute negatively or positively to the community-wise variability estimate (or not influence it at all in the case of a zero residual). Alternatively, using a metric where variances are summed directly may create an inherent, positive relationship between species richness and community-wise variability (i.e., increasing the total number of species increases community variability simply by nature of adding positive numbers).

We characterized climatic conditions at each route location using PRISM data from 1967-2018. Variables were selected to capture precipitation and temperature (1) averages, (2) within-year variability, and (3) extremes (Table 1.1). Additionally, we determined avian species richness (i.e., the count of total species detected within the temporal extent of the study) at each route location. Many studies testing the richness-stability concept have examined strictly linear relationships between species richness and stability (e.g., Houlahan et al., 2018; Mikkelson et al., 2011; Steiner, 2005; Valencia et al., 2020; Yang et al., 2012). A central assumption of this approach is that diversity influences stability similarly across all levels of diversity (i.e., both species poor and species rich communities). Because ecological dynamics can be complex and non-linear (Gunderson, 2000), we hypothesize that imposing a linear model is potentially oversimplifying the relationship between diversity and community stability and therefore included cubic and quadratic forms of species richness.

For analysis, we set route variability index as the only response variable in a series of linear models. Each model was structured with only one explanatory variable, though we also tested for quadratic and cubic relationships of species richness. A total of 10 models were ranked using Akaike information criterion (AIC; Table 1.1). Models with delta AIC less than 2.0 and 95% confidence intervals that did not overlap zero were considered competitive models. Due to concerns of spatial autocorrelation (i.e., spatially non-independent sampling), we considered formally including a spatial component in the models (such as a random effect for biome or latitude + longitude). However, we opted against this approach because both competitive models had low residual spatial autocorrelation (global Moran's I coefficients were 0.12 and 0.15, where 1.0 indicates perfect autocorrelation and zero is random arrangement).

RESULTS

Bird community variability was spatially heterogeneous at a continental scale (Figure 1.1) and was best explained by maximum temperature of the hottest month and minimum precipitation of the driest month (Table 1.2; Figure 1.2). Specifically, hot and dry conditions are associated with highly variable bird communities. Minimum precipitation and maximum temperature each explained approximately 5% of the variation in the data (adjusted R-squared = 0.05). Considering that we used a single-variable model to explain variation across the entire spatial and temporal extent of the BBS, an R-squared of 5% is encouraging. For comparison, Houlahan et al. (2018), found an average R-squared of 0.005 when modeling species richness-stability relationships across 91 datasets.

DISCUSSION

The stability-diversity hypothesis is a traditional concept of ecology and improving our understanding of it has increased urgency as species extinction continues to accelerate (Dirzo *et al.*, 2014). However, empirical evidence of a universally positive diversity-stability relationship is inconsistent (Houlahan et al., 2018), indicating a high probability of additional, possibly more significant, factors regulating community stability. Here, we use a half-century of subcontinental-scale community data to add context to the diversity-stability debate by investigating other plausible contributors. Our results indicate that—despite disproportionately high attention to the diversity-stability concept in the literature—environmental conditions better explained community stability than the species richness of the community itself. Specifically, we found that extreme heat and extremely low precipitation are associated with low community stability. Our findings not only contribute to our understanding of the diversity-stability concept, but also add to the growing list of diverse ecological responses to climate change.

Community variability is an expected characteristic of ecological systems. Communities are never static over long time frames, and variability does not necessarily indicate a concerning lack of resilience or stability *per se* (Arnoldi, Loreau and Haegeman, 2019; Roberts *et al.*, 2019). However, in some cases severe abundance fluctuations can indicate more than a benign community characteristic, and may be a warning signal of an imminent conservation concern. For example, ecological theory predicts that the variability of a system may increase the probability of extinction (Pimm, Jones and Diamond, 1988; Lande, 1993, *but see* Schoener and Spiller, 1992), and may immediately precede abrupt regime shifts or critical transitions (Carpenter and Brock, 2006; Guttal and Jayaprakash, 2009; Scheffer *et al.*, 2009; *but see* Hillebrand *et al.*, 2020). We speculate that our results (high community variability associated with hot, dry locations) are unlikely to be artifacts of expected baseline community variability because extreme heat and lack of precipitation are known to be physiologically difficult conditions for birds (Riddell *et al.*, 2019), and have caused definitive avian community collapse in recent decades (Iknayan and Beissinger, 2018). As climate change increases temperature and precipitation extremes (IPCC, 2014) and contributes to biodiversity loss (Dirzo *et al.*, 2014; Johnson *et al.*, 2017), we anticipate a synergistic relationship between weather extremes, diversity, and community stability. That is, extreme heat and drought may act on community variability both directly (through the mechanisms described below), and indirectly through increasing diversity loss (which theory predicts will also increase community variability).

Multiple factors are likely contributing to the causal mechanism(s) between climatic extremes and community variability. If conditions are harsh enough to exceed a species' physiological tolerance or influence its habitat resources, populations may temporarily experience increased mortality or decreased breeding success (and the opposite may occur when conditions are favorable). For example, northern bobwhite (*Colinus virginianus*), a broadly distributed North American quail species, notoriously experiences lower survival and reproduction during drought periods, resulting in boom-bust population fluctuations in the semi-arid portion of their range (Hernández *et al.*, 2005). Highly mobile species can also chase favorable conditions by adapting through distributional changes (Bellard *et al.*, 2012). This can include a disproportionate use of species range margins (Bateman *et al.*, 2015), elevational range shifts (Tingley *et al.*, 2012; McCain and Garfinkel, 2021), and species-specific fluctuations in abundance distributions (Cohen, Fink and Zuckerberg, 2021). At the individual scale, heat waves and limited water availability may also prompt changes in bird behavior and daily activity (Wolf, 2000), potentially resulting in reduced species abundance detections (e.g., physiologically stressed birds may suppress their activity levels and be less likely to sing on their territories).

As a variety of causes work in tandem, avian community variability may be reflecting the tendency of some populations to experience abundance swings in response to extreme weather, along with others undergoing distributional shifts and/or behavioral changes. Though there is ample evidence that extreme weather forces dynamic population changes, it is also plausible that variable communities (i.e., communities containing a large proportion of species able to move in response to unfavorable conditions) are simply better adapted to extreme weather and therefore more likely to persist when conditions are harsh. Our results open the door to other important avenues of study. We focused entirely on aggregate community variability, where all species are considered in combination (Micheli *et al.*, 1999). However, future studies examining species tunover, shifts in community composition, and other facets of stability may provide additional context and possible insight into which areas of variabilty are "normal" fluctuations, and which are cause for concern. It is also worth emphasizing that the purpose of this study was not to identify all of the variables that predict community variability. Rather, our central objective was to evaluate whether community variability could be better explained by the community composition itself (i.e., species richness), or by abiotic environmental conditions. It is highly likely that other environmental conditions, such as land cover composition/change, or biome-specific global changes (i.e., woody plant encroachment in the south-central semi-arid Great Plains of North America; Archer *et al.*, 2017) may also play an important role in community stability. Because many of these variables are likely to be correlated with temperature and precipitation metrics (e.g., biomes are largely delineated using climatic patterns), it is important to interpret our results in context.

Our results have implications for the fields of community ecology, theoretical ecology, and conservation biology. We found large-scale, empirical support for the theoretical concept that environmental conditions play a larger role determining community stability than diversity in North American avian communities (Loreau, 1998; Loreau and de Mazancourt, 2013). Even more broadly than the diversity-stability concept, our results contribute to our understanding of the relative roles of abiotic and biotic factors governing community dynamics (Dunson and Travis, 1991). Additionally, on a practical level, this study highlights the importance of accounting for environmental factors when evaluating the relationship between diversity and stability (Zhang *et al.*, 2018). In other words, if abiotic conditions are a more impactful determinant of ecological stability than diversity, diversity-stability signals might be difficult to detect if samples are taken across an environmental gradient.

<u>TABLES</u>

Table 1.1 Model structure and variable descriptions for all linear models used in analysis. "Variability" refers to site variability index calculated at each route (i.e., the quantified variability of the bird community) and is the response variable for all models. All explanatory variables are calculated at each route location.

Model Structure	**Explanatory Variable Description**
CLIMATE AVERAGES	
Variability ~ Mean Temperature	Annual mean temperature (averaged across all years from 1967-2018)
Variability ~ Mean Precipitation	Annual total precipitation (averaged across all years from 1967-2018)
CLIMATE EXTREMES	
Variability ~ Max Temperature	Annual maximum temperature of the warmest month (averaged across all months from 1967-2018)
Variability ~ Min Temperature	Annual minimum temperature of the coldest month (averaged across all years from 1967-2018)
Variability ~ Minimum Precipitation	Minimum precipitation of the driest month (averaged across all years from 1967-2018)
CLIMATE VARIABILITY	
Variability ~ Temperature Variability	Variability of yearly mean temperature (standard deviation of yearly mean temperature 1967-2018)
Variability ~ Precipitation Variability	Variability of yearly precipitation (standard deviation of total yearly precipitation 1967-2018)

SPECIES RICHNESS	
Variability ~ Richness	Species richness
Variability ~ Richness + Richness^2	Quadratic relationship between variability and species richness
Variability ~ Richness + Richness^2 + Richness^3	Cubic relationship between variability and species richness

Table 1.2 Bird community variability models ranked by AIC. All models were linear and had route variability index as the response variable. A positive relationship between variability and the explanatory variable (beta) indicates an increase in variability with increasing explanatory variable. Models in bold were considered competitive.

Model (explanatory variable)	ΔAIC	Weight	β	95% CI
Minimum precipitation of driest month	**0**	**0.56**	**-0.003**	**-0.004, -0.002**
Maximum temperature of the hottest month	**0.4**	**0.44**	**+0.01**	**+0.01, +0.02**
Species richness + species richness^2 + species richness^3	29.3	<0.001		
Species richness	33.0	<0.001		
Species richness + species richness^2	34.3	<0.001		
Mean temperature	42.1	<0.001		
Total precipitation	50.6	<0.001		
Minimum temperature of the coldest month	57.3	<0.001		
Null	70.4	<0.001		
Between-year precipitation variability	70.9	<0.001		
Between-year average temperature variability	72.2	<0.001		

FIGURES

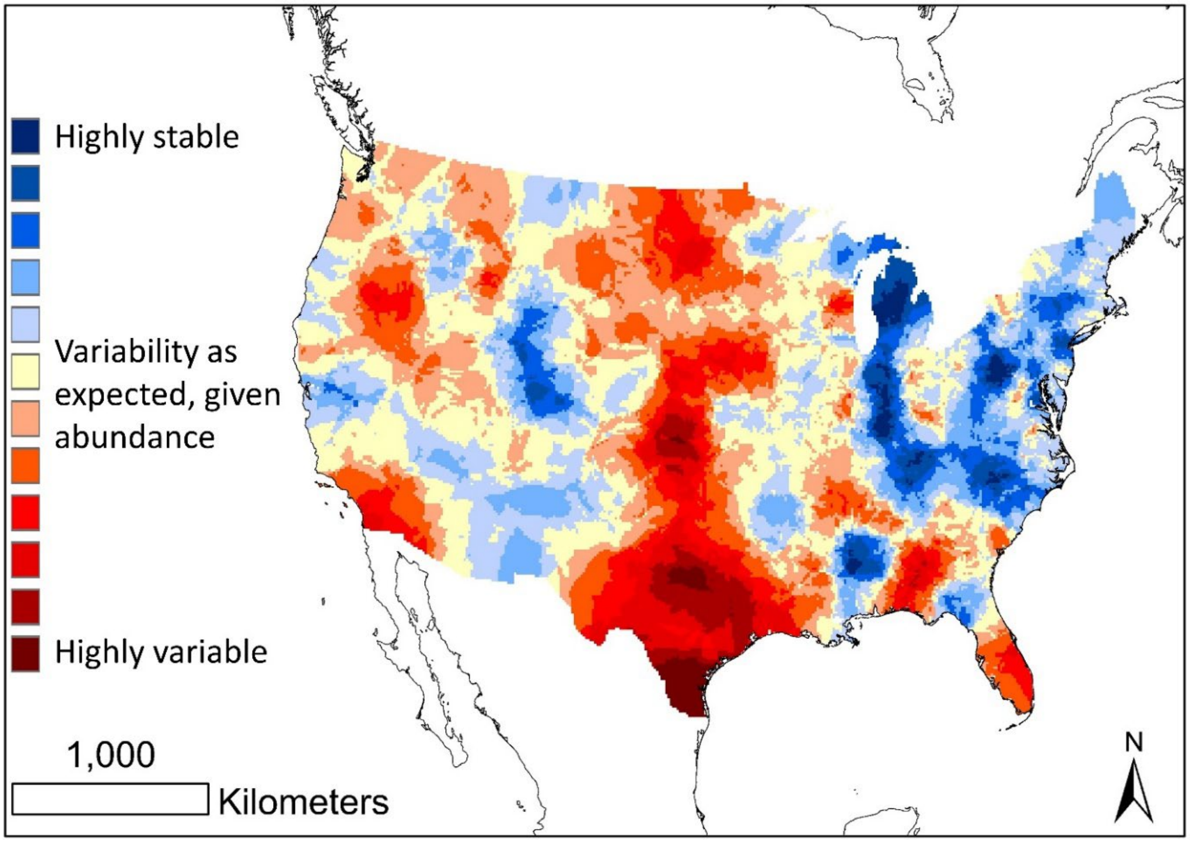

Figure 1.1 Interpolated and smoothed avian community variability of North American breeding bird communities.

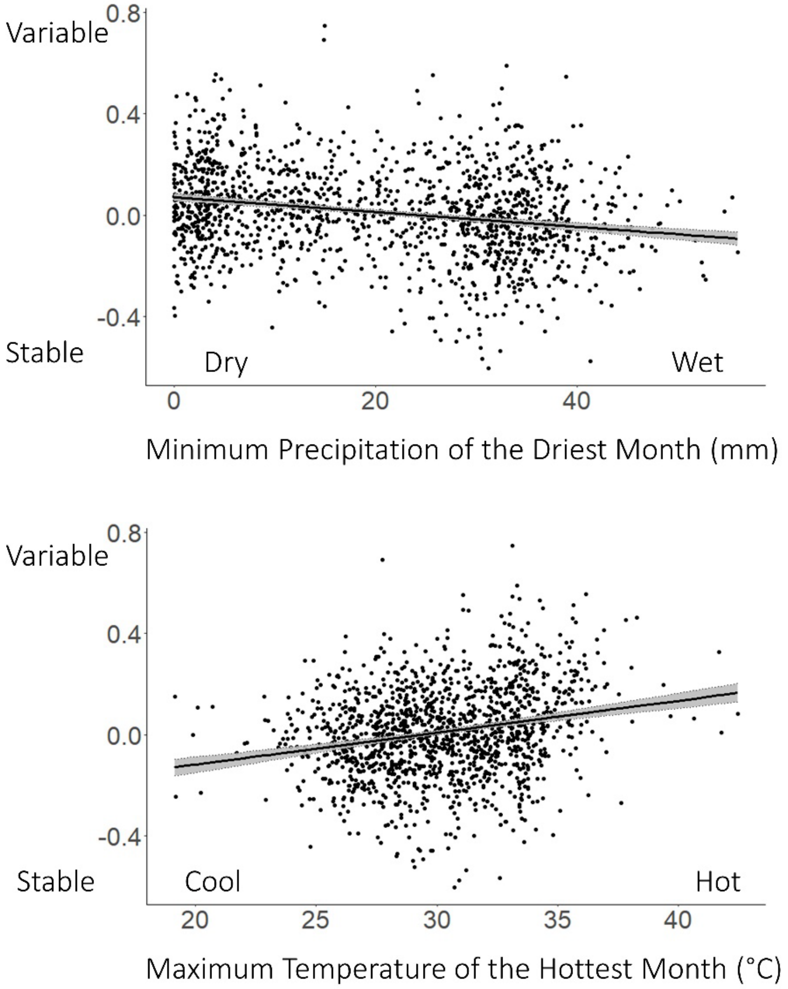

Figure 1.2 The relationship between avian community variability and climatic extremes, as represented by the best performing models (with 95% confidence intervals) overlaid on the raw data.

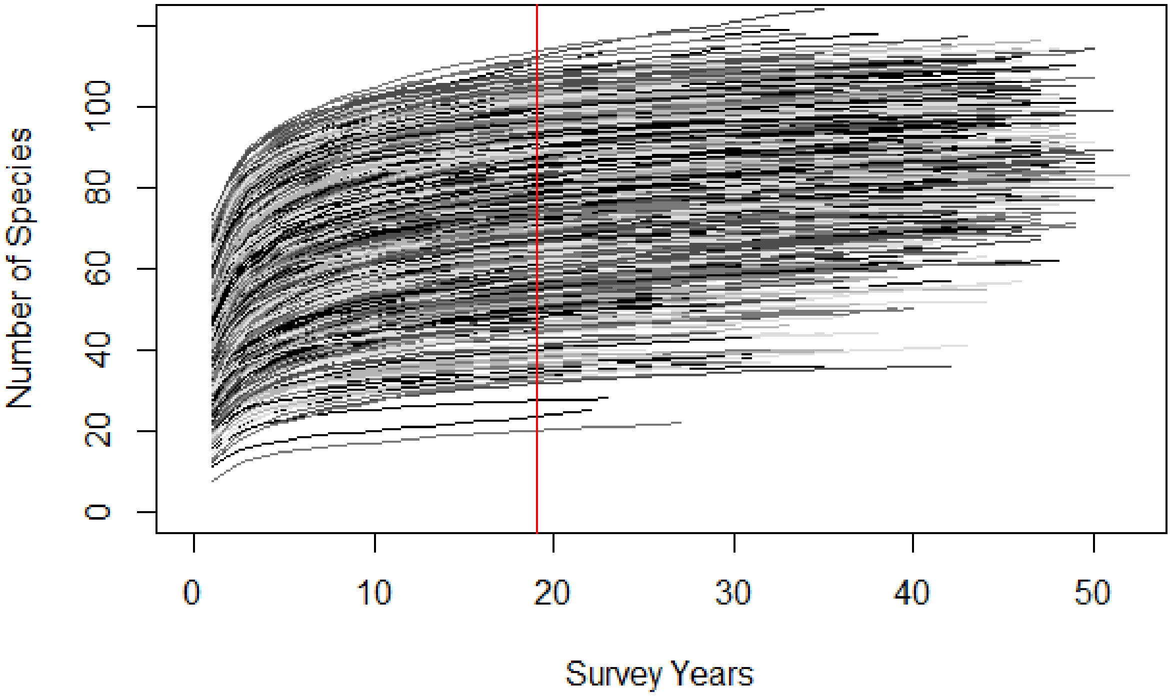

Figure 1.S1 Species accumulation curves for each of 1379 routes included in analysis. The red line represents the minimum number of survey-years included in analysis.

CHAPTER II

COMPENSATORY DYNAMICS ARE MOST PREVALENT AT SMALL SPATIAL SCALES

ABSTRACT

Compensatory dynamics are hypothesized to be a principal mechanism of community stability—as an environmental perturbation drives poorly-adapted species abundances down, they are replaced by better-adapted species, resulting in a roughly "zero-sum game" and apparent community stability. Despite long-standing ecological theory, empirical examples of negative species covariance are rare in ecological systems. Short term compensation may not adequately curtail long-term decline, yet relatively little is known about the influence of temporal scale on compensatory dynamics at large extents. Additionally, though there is some evidence that weak, negative species covariance may be spatially scale-dependent, a formal systematic scale analysis has not been done. Here, we used long-term, continental scale, bird community abundance data (the North American Breeding Bird Survey) to assess the influence of temporal and spatial scales on compensatory dynamics. We evaluated whether short-term (annual

scale) negative covariance is scale-dependent and compared empirical results to a simulated null model. Additionally, we held spatial scale constant and evaluated compensatory dynamics at a large (multi-decadal) temporal scale. Our results indicate that community-level compensatory dynamics are generally rare (less than 10% of communities display compensatory dynamics across most scales), but also highly spatially scale-dependent (more prevalent at small scales). Though this scale-dependent pattern also weakly appears in the simulated community data, it is much more pronounced in the natural bird community data, plausibly indicating a biological signal in addition to a relatively small mathematical pattern in the data. We also found strong evidence of synchronous bird species at large (decadal) temporal scales—that is, areas of long-term bird abundance declines of some species are less likely to experience concomitant abundance increases of other species. Our finding of an overall lack of compensatory dynamics at small and large temporal scales, as well as across nearly all spatial scales, may be indicative of widespread and consistent long-term abundance decline of many bird species without compensation.

INRODUCTION

Ecologists have been honing our understanding of ecological stability since the inception of the field of community ecology (Kéfi *et al.*, 2019). The concept of stability has spanned basic and applied science, donned over 160 definitions, and is rooted in at least 70 conceptual frameworks (Grimm and Wissel, 1997); its study has even generated entire new domains of ecological research (e.g., the body of literature stemming from resilience theory; Holling, 1973). In recent decades, ecological stability is emerging as an important topic in environmental conservation (Donohue *et al.*, 2016) because the concept of stability is closely related to environmental change and an ecological system's response (Kéfi *et al.*, 2019). In the face of novel global change pressures associated with the Anthropocene (Crutzen, 2006), it is increasingly important to continue to develop our understanding of ecological stability and its underlying mechanisms.

Compensatory dynamics are hypothesized to be a principal mechanism (or suite of mechanisms; Gonzalez and Loreau, 2009) of community stability (Holling, 1973; Patten, 1975). The concept is intuitive—as an environmental perturbation drives poorly-adapted species abundances down, they are replaced by increasing abundances of better-adapted species (Morgan Ernest and Brown, 2001; Ives and Cardinale, 2004; Gonzalez and Loreau, 2009), resulting in a roughly "zero-sum game" and apparent community stability. This pattern can be driven directly by environmental conditions (i.e., no species can be a top-performer under all conditions) or by species interactions (e.g., competition) (Gonzalez and Loreau, 2009). However, despite long-standing ecological theory, empirical examples of negative species covariance are rare in ecological systems (Houlahan *et al.*, 2007; global quantitative review).

Theory predicts that compensatory dynamics may act profoundly differently across multiple temporal scales of observation (Gonzalez and Loreau, 2009). Importantly, if we examine pairwise covariance at a single temporal scale we could possibly fail to detect patterns occurring at other temporal scales (Vasseur, Gaedke and McCann, 2005). Presumably, the lack of inferential power when evaluating one temporal scale may partially explain the relative lack of empirical data supporting compensatory dynamics in natural systems. For example, two species may consistently compensate at short timescales, but when considered at larger temporal scales, the aggregate community composition may be unstable (Vasseur and Gaedke, 2007). This disparity can manifest as short-term oscillations coupled with sustained decline, plausibly caused by a variety of environmental pressures acting similarly on multiple species (Gonzalez and Loreau, 2009). In other words, short term compensation may not adequately curtail long-term decline. For lakes and experimentally manipulated aquatic mesocosm studies (where most studies have taken place), there does not seem to be a clear, universal relationship between temporal scale and compensatory dynamics. For some taxa, compensatory dynamics may be detectible at small temporal scales, but absent at large scales (Vasseur and Gaedke, 2007) or the reverse—present at large scales but not detected at small scales (Keitt and Fischer, 2006). Little is known about the influence of temporal scale on compensatory dynamics at large (i.e., continental) extents, especially for terrestrial taxa, which are understudied in this context.

Just as scale is a central feature of all observed ecological patterns (Wiens, 1989), there is some evidence that weak, negative species covariance may be spatially scale-dependent (Houlahan *et al.*, 2007). However, to our knowledge a formal, systematic scale analysis has not been done and our understanding of whether compensatory dynamics may increase or decrease with increasing scale is not immediately obvious. On one hand, the spatial insurance hypothesis predicts that large scales may be more likely to display stability driven by compensatory dynamics (Loreau, Mouquet and Gonzalez, 2003). Under this conceptual framework, large-scale meta-communities remain stable through dispersal-related compensation (Loreau, Mouquet and Gonzalez, 2003; Leibold and Norberg, 2004; Mougi and Kondoh, 2016). However, a global-scale review found some support for the opposite pattern (i.e., generally decreasing compensatory dynamics with increasing spatial scale; Houlahan *et al.*, 2007). Though the mechanism behind this pattern is not clear, it is possible that between-species interactions may disproportionally drive abundance at local scales (i.e., scales relevant to individual home ranges) and manifest as compensatory community trends, but environmental conditions may simultaneously act on many species in similar ways at large scales (e.g., widespread drought causing overall faunal abundance declines; Iknayan and Beissinger, 2018).

Birds are an ideal study taxa to assess change across multiple temporal and spatial scales because they are highly mobile and respond quickly to changes in their environment. Additionally, it is plausible to expect compensatory patterns in bird communities because the two major classes of mechanisms, intrinsic (i.e., within-community species interactions such as competition) and extrinsic (i.e., abiotic factors), both act on birds. Specifically, competition within bird communities is likely because we assess species on the same (or similar) trophic levels and because many species are territorial during breeding season, and compete for food and nesting habitat. Additionally, extrinsic environmental pressures such as habitat loss and direct mortality from anthropogenic sources, are influencing bird communities at broad and local scales, causing significant long-term loss in North America (Brennan and Kuvlesky, 2005; Loss, Will and Marra, 2015; Rosenberg *et al.*, 2019). Here, we leveraged a half-century of continental scale, bird community abundance data to assess the influence of temporal and spatial scales on compensatory dynamics. We evaluated whether short-term (annual scale) negative covariance is scale-dependent and compared empirical results to a simulated null model. Additionally, we held spatial scale constant and evaluated compensatory dynamics at a large (multi-decadal) temporal scale.

METHODS

The North American Breeding bird survey is a nearly continental-scale dataset spanning multiple decades of bird abundance data (Pardieck *et al.*, 2020). Point count data are collected annually during the breeding season (May, June, and July) along thousands of established, 41-km routes. At each route, a skilled observer stops at 800-meter intervals and conducts a timed, three-minute point count of all birds detected within a 400-meter radius (resulting in 50 point counts along each route). We used nearly the entire spatial and temporal extent of the data, but for each objective we subset the data in such a way as to optimize each objective (explained in detail below). For all analyses, we began by applying standard BBS cleaning methods, which included removing (1) data that did not meet the BBS quality standards (i.e., surveys that were incomplete or completed under substandard weather conditions likely to make detection abnormally difficult), (2) data collected by observers in their first year (Kendall, Peterjohn and Sauer, 1996), (3) bird detections with uncertain species identification and species unlikely to be detected reliably by point count methodology (i.e., removed owls, raptors, vultures, waterfowl, ducks, and shorebirds) and (4) subspecies by reclassifying them into their respective species.

Compensatory dynamics across spatial scales

For this objective, we prioritized keeping sample sizes equal across all scales to minimize bias and maximize confidence that inferences were a result of scale-dependency. We limited analysis to routes surveyed after 1996 (when point-level data became available) so we could systematically adjust bird abundance data across spatial scale by combining point-level data. We aggregated each route's bird abundance data into 50 spatial scales using the point-level count data (Jenkins, White and Hurlbert, 2018; e.g., the smallest scale included only the first point of bird count data for each species, the second smallest scale included the first and second point of bird count data summed by each species. . . and the largest scale included all 50 points of bird point count data summed by each species). To further reduce potential confounding factors, we limited analysis to routes surveyed between 21-23 years to minimize some routes with small yearly samples being compared to routes with many years sampled. The resulting dataset included a sample size of 733 routes for all scales and 395 species detected from 1997-2019 (Figure 2.1).

We used a derivation of the variance of the sum equation to generate a community-level covariance estimate for each route at each spatial scale. Specifically, this estimate describes the sum of all pairwise species covariances in abundance over time at each spatial scale, resulting in 50 covariance estimates per route. According to probability theory, the variance of the sum can be expressed as the sum of the species abundance variances in a community plus twice the sum of all pairwise covariances (Schluter, 1984). Algebraically solving for the sum of pairwise covariances yields a straightforward approach to test association (covariance) between species abundances at the community level (equation 2.1, where n is the number of species in a community and x is a species-level abundance; Schluter, 1984; Houlahan *et al.*, 2007).

Equation 2.1 $$\sum_{i=1}^{n} \sum_{i<j}^{n} \sigma^2(x_j, x_i) = \frac{\sigma^2(\sum_i^n x_i) - \sum_i^n \sigma^2(x_i)}{2}$$

We also simulated point count data to provide a baseline for comparison, and to ensure that any scale-dependent trends were not an artifact of aggregation (i.e., to increase confidence that results were not somehow pre-determined by the process of increasing bird counts over large spatial scales). Using parameters estimated from the original data, we generated artificial point count data with a negative binomial distribution because the real data were over-dispersed. Specifically, we calculated the estimated species means counts for all 395 species in the dataset as well as their dispersion parameters (a measure of spread relative to the mean) to simulate count data for each species using a negative binomial distribution. We generated a total of 60 simulated datasets, each of which approximated the real data in terms of sample size, number of species, and their associated mean/dispersion. Our goal was to keep simulations as true to reality as possible to allow us to evaluate what results would have been if bird species counts were entirely independent of each other but remained the same in all other respects.

It is important to note that a mathematical constraint requires the overall probability of negative pairwise covariances to decrease as the number of species pairs increases (Brown *et al.*, 2004). For example, if we assessed two species (one pair), they could show perfect negative covariance (Pearson correlation coefficient = -1) without constraint. However, if we assessed three species in the same analysis, it is not possible for all three to perfectly negatively covary (i.e., if two species negatively covary, the third species must positively covary with one of the others; Brown *et al.*, 2004). We were concerned that the positive semidefinite constraint could appear as scale-dependence because the species-area concept predicts an increase in number of species detected at large spatial scales, and therefore, more pairwise species covariances at large scales. To investigate, we re-ran the scale analysis on the bird community data, while keeping number of species even across scales (i.e., we only included species present at the first point at each route for all scales).

Covariance of long-term common species loss and gain

For this objective, we were interested in correlations between species' consistent, multi-decadal trends. Specifically, our goal was to evaluate whether species in long-term decline are associated with species in long-term abundance increases. We therefore prioritized large sample sizes in order to confidently fit linear regressions to each species' abundance over time at each route and, as such, constrained our analysis to focus on common and widespread species as a model guild. Specifically, we limited analysis to species found on at least 70 routes (widespread), with at least 30 detected individuals at each route over the temporal extent of the study (common). We held spatial scale constant at the route-level scale, (i.e., used bird survey data aggregated over all 50 stops) to maximize counts and therefore the number of usable route-species for analysis. We constrained analysis to routes with at least 30 years of sampling (including at least a 38 year span with 80% survey years covered) to ensure a multi-decadal timescale at all locations. BBS routes often have multiple observers over time, which can influence data quality (Sauer, Peterjohn and Link, 1994). To mitigate, we limited analysis to routes with five or fewer observers across the temporal extent of the study. The final, preprocessed dataset resulted in 627 routes across North America and included 129 common and widespread species.

To quantify long-term trends in abundance, we constructed generalized linear models at each route location and for each species (32,589 models total). We selected a Poisson error distribution in favor of a negative binomial distribution to improve computation time and because Poisson models consistently fit the data (negative binomial models often did not). For each route, we aggregated positive and negative slopes separately (if a model was not statistically significant at alpha=0.05, beta was set to zero) and standardized by the total number of common/widespread species at the route. This resulted in two variables for each route: “defaunation” or the standardized sum of all negative slopes (long-term abundance decline) and “afaunation”, the standardized sum of all positive slopes (long-term abundance increase). Though we used a frequentist approach across many models, we do not anticipate Type I error (false positives) to be problematic for this application because, though we expect 5% spurious model results, they should be evenly distributed across the data and merely act as a source of random noise rather than systematic bias in any particular direction. To assess the relationship between afaunation and defaunation, we used a generalized linear model with a gamma error distribution (alpha=0.05). If compensatory dynamics are occurring at large temporal scales, defaunation and afaunation should be positively related (i.e., routes experiencing common species abundance loss should also be experiencing common species abundance gains). All analyses were completed in R version 4.1.1 (R Core Team, 2021).

RESULTS

Compensatory dynamics across spatial scales

The proportion of negative species abundance covariance was approximately 0.5 at the smallest spatial scale, yet dropped rapidly to nearly zero at large spatial scales (Figure 2.2). The randomly simulated communities showed a similar trend of decreasing proportion negative covariance with increasing spatial scale, but a much weaker magnitude of effect. Due to concerns of bias arising from increasing species pairs at increasing spatial scales (due to the species area concept and positive semidefinite constraint; Brown *et al.*, 2004), we held species richness constant across scales and ran the same analysis. Results were nearly identical to the original analysis, indicating that the positive semidefinite constraint has very weak influence on our results (Figure 2.S1).

Covariance of long-term common species loss and gain

We found a significant, negative association between long-term bird community defaunation and afaunation ($\beta=-43.0$, $p<0.001$). That is, bird communities that were experiencing high rates of abundance loss in some species were less likely to experience concomitant increases in other species, suggesting minimal support for compensatory dynamics (Figure 2.3).

DISCUSSION

We used decades of continental-scale bird community data to systematically investigate temporal and spatial scaling tendencies of compensatory dynamics in North American bird communities. Our results indicate that community-level compensatory dynamics are generally rare (less than 10% of communities display compensatory dynamics across most scales), but highly spatially scale-dependent (Figure 2.2). That is, we are much more likely to observe evidence of between-species compensating abundance changes at small scales than we are at large scales. Though this pattern also weakly appears in the simulated community data, it is much more pronounced in the natural bird community data, plausibly indicating a biological signal in addition to a relatively small mathematical pattern in the data. We also found strong evidence of synchronous bird species at large (decadal) temporal scales—that is, areas of long-term bird abundance declines of some species are less likely to experience concomitant abundance increases of other species.

The two major classes of mechanisms driving compensatory dynamics are intrinsic (factors relating to species interactions; sometimes referred to as "biotic factors") and extrinsic (environmental factors outside the community; sometimes referred to as "abiotic factors") (Gonzalez and Loreau, 2009). It is plausible that extrinsic environmental variables are a major driver behind the observed relative lack of compensatory dynamics at most spatial scales. Most bird taxa have been experiencing large-scale population loss during the past century as a result of anthropogenic global changes at a continental scale (Dirzo *et al.*, 2014; Rosenberg *et al.*, 2019), and this steady decline may be reflected by synchronous (and often downward) population trajectories among species. However, because environmental changes can influence the nature of competition (e.g., synergistic effect of competition and environmental stress on population loss; Young *et al.*, 2017; changing environmental conditions altering the relative competitive abilities of species; Napier, Mordecai and Heckman, 2016; or, changes in disturbance frequency and scale causing entire ecological regime shifts; Archer *et al.*, 2017), it is plausible that anthropogenic global change related pressures may also be indirectly influencing species interactions. This complexity makes it difficult to isolate the central mechanisms driving compensatory dynamics (or lack of compensatory dynamics). Additionally, it is important to note that we assumed that species increases occur simultaneously with decreases (i.e., we did not investigate lagged effects). However, not only can species interactions exhibit lagged responses (e.g., the Lotka-Volterra model), environmental conditions can also influence different species at different times (e.g., drought-related cross-ecosystem trophic cascade in a pelagic seabird; Thomsen and Green, 2019). It is plausible that compensatory dynamics may be detected in more natural systems if multiple temporal windows and lag effects are investigated. This caveat opens the door to further research.

The mechanism driving the observed, weak mathematical relationship between spatial scale and compensatory dynamics in our simulated communities is not immediately clear. We speculate that as species richness increases with scale (i.e., the species-area concept; Connor and McCoy, 1979), the positive semi-definite constraint increasingly limits negative covariance (Brown *et al.*, 2004). In other words, as spatial scale increases, the number of species detected increases, as does the number of species pairs considered in a covariance matrix, which mathematically constrains the magnitude of negative relationships. However, the effect of species richness appears small, as we found only a slightly dampened response when species richness was held constant (Figure 2.S1). Regardless of the exact mathematical relationship, importantly, we found evidence that negative covariance-scale relationships may arise solely by nature of their calculation, especially at small spatial scales. Whether these calculation-related effects should be considered biologically relevant or an artifact may be a matter of perspective, however, our results highlight the importance of using appropriate null models to better understand the sources of patterns in the data. And in our case, the simulated null models showed bird communities are much less likely to display negative covariance than would be expected given pure chance across nearly all scales.

Our large temporal scale analysis indicated not only a lack of compensatory dynamics at large (decadal) temporal scales—importantly, we found that areas experiencing disproportionate bird declines of some species are significantly less likely to experience concomitant abundance increases of other species (Figure 2.3). In other words, where birds are declining long-term, they are not being replaced by other birds. This finding is not only theoretically interesting, but has immediate conservation implications. Birds are an imperiled taxa in North America and have experienced rapid and widespread decline in the most recent century (Rosenberg *et al.*, 2019). Bird populations have been influenced by direct and indirect sources of mortality, including land cover change (e.g., Brennan and Kuvlesky, Jr., 2005), climate change (e.g., Iknayan and Beissinger, 2018), predation by free-ranging cats (on the order of billions of birds lost annually in North America; Loss, Will and Marra, 2015), human-made structure collisions (hundreds of millions of birds lost annually in North America; Loss, Will and Marra, 2015), overexploitation (e.g., Cannon, 1996), chemical contamination (e.g., Plaza and Lambertucci, 2019), and novel pressures due to invasive species (e.g., Whitworth, Carter and Gress, 2013). Our finding of an overall lack of compensatory dynamics at short and long temporal scales as well as across nearly all spatial scales may be indicative of concerning, widespread, and consistent long-term abundance decline of many bird species without compensation.

FIGURES

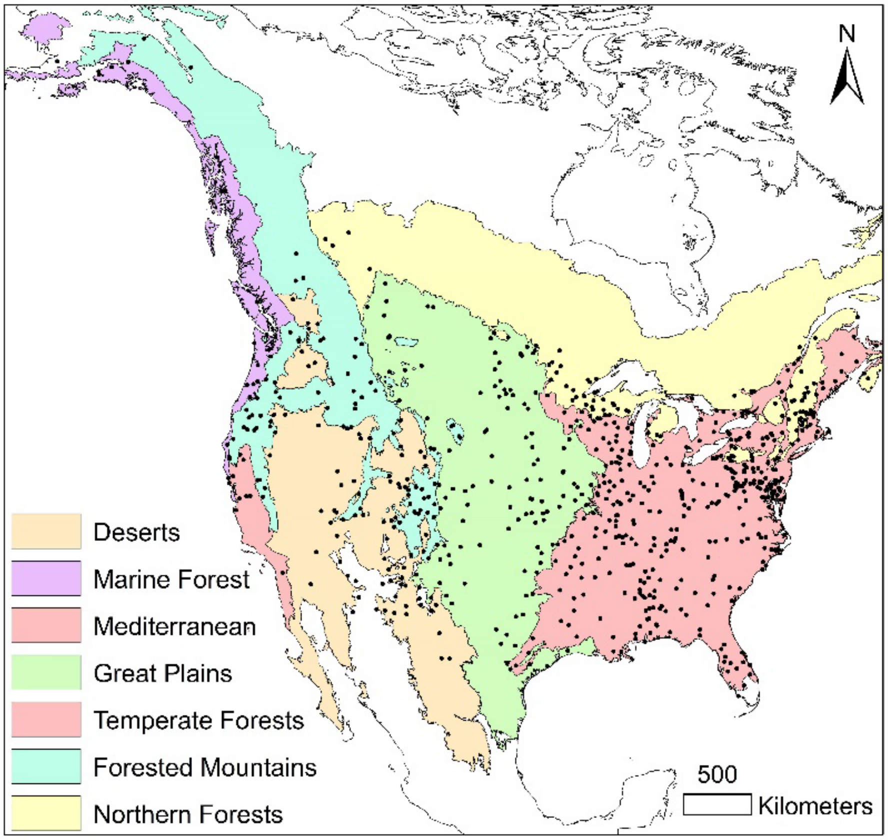

Figure 2.1. Map of all routes used in compensatory dynamics across spatial scales analysis.

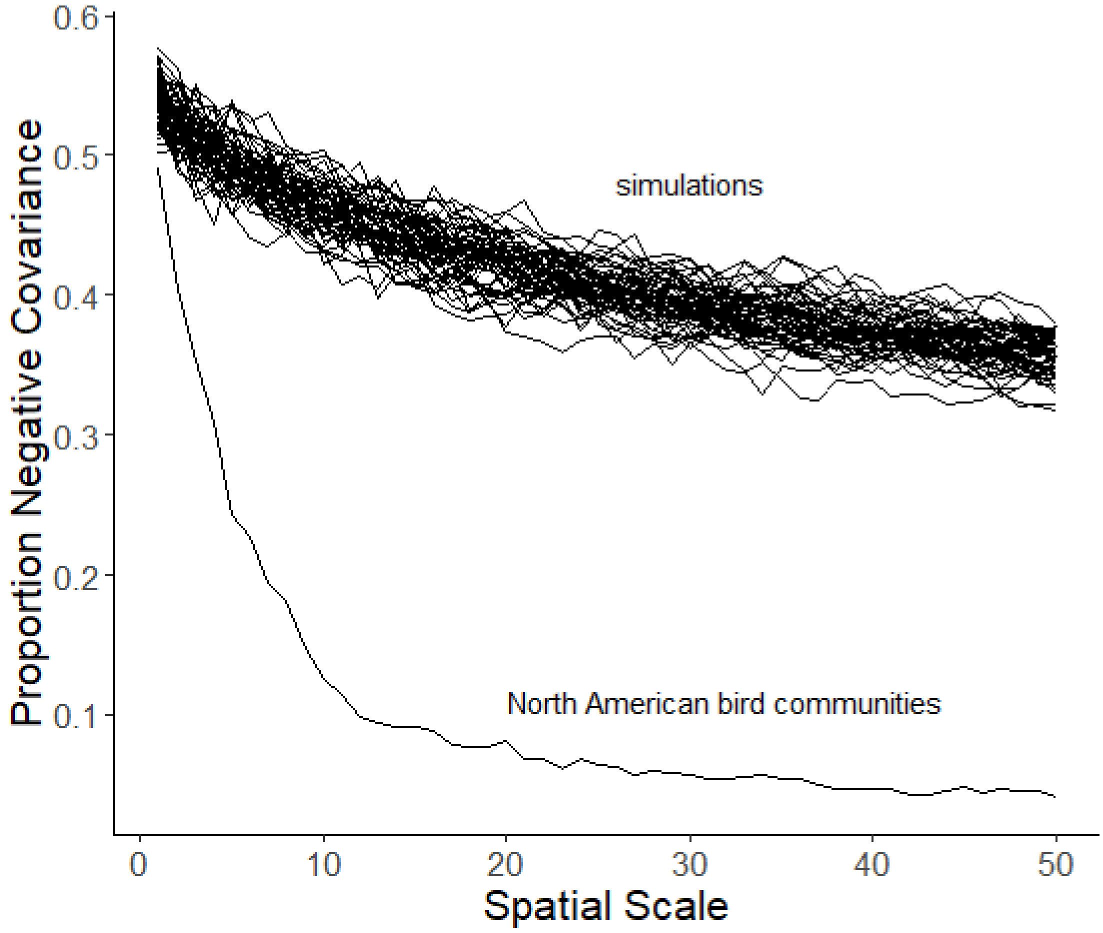

Figure 2.2 Proportion of North American bird communities with community-level negative covariance (indicating compensatory dynamics) across spatial scales and compared to randomly generated bird community data. Sample size is 733 communities (BBS routes) for all scales.

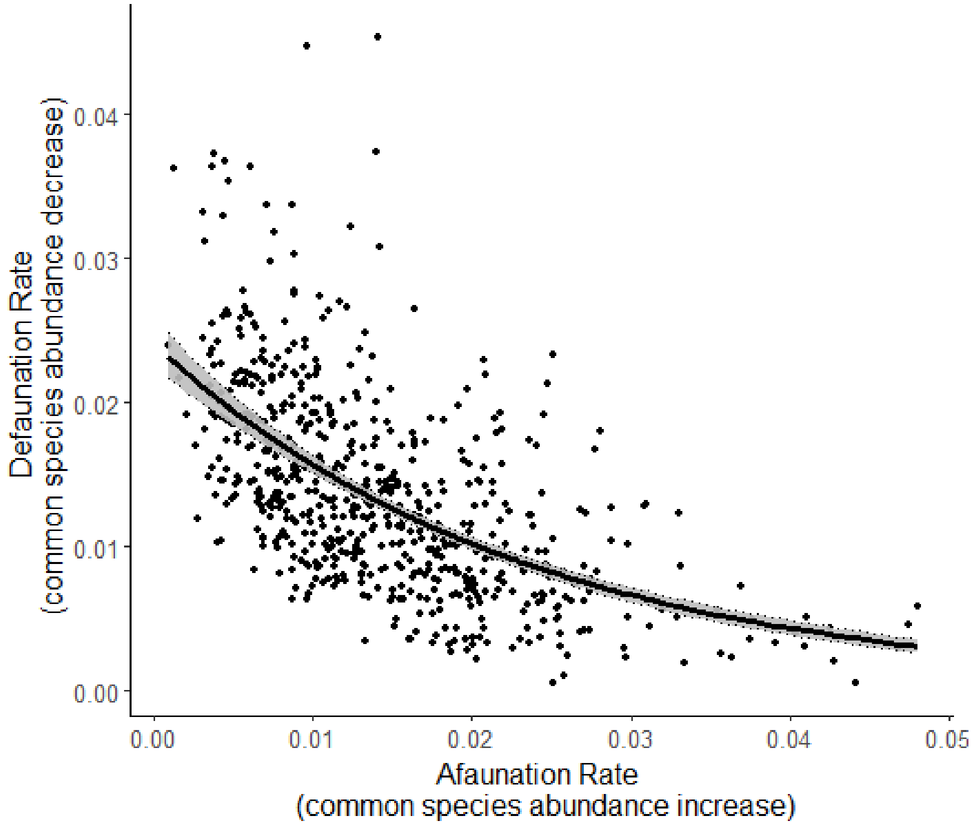

Figure 2.3 Relationship between long-term (30+ year) North American breeding bird abundance decreases (defaunation, or negative model slope) and increases (afaunation, or positive model slope) among common and widespread species at a 50ha spatial scale. Model fitted using a generalized linear model with a gamma error distribution with 95% confidence intervals (n=627 routes).

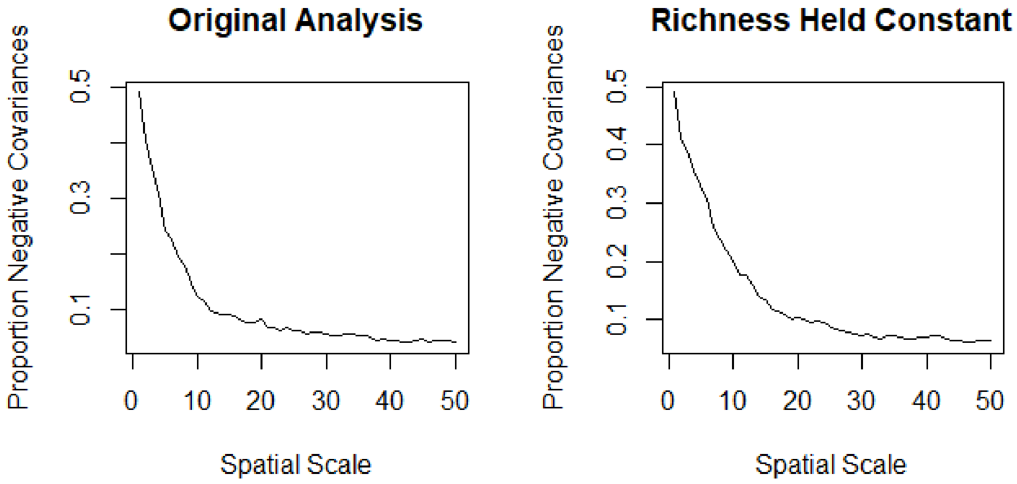

Figure 2.S1 Proportion of North American bird communities with community-level negative covariance (indicating compensatory dynamics) in (1) the original results, and (2) results when species richness is held constant (i.e., routes have the same number of species across all scales).

CHAPTER III

NORTHERN BOBWHITE RESPONSE TO DROUGHT IS BIOME-DEPENDENT

ABSTRACT

Weather extremes are increasing in frequency and magnitude as a result of anthropogenic climate change, and can include protracted increases in severe and prolonged drought as well as anomalously heavy rainfall. Though many studies have evaluated wildlife responses to precipitation variability, less is known about possible biome-specific responses within a single species, especially a non-migratory species unlikely to disperse large distances in response to unfavorable conditions. Using a half-century of systematically collected avian abundance data (the North American Breeding Bird Survey), we investigated biome-specific responses of Northern bobwhite (*Colinus virginianus*) to drought conditions at a sub-continental scale. Specifically, we (1) evaluated biome-specific, multi-decadal bobwhite abundance trends and (2) bobwhite response to drought (and anomalously wet) conditions in the central Great Plains and Eastern Hardwood Forest biomes of North America. We used generalized linear mixed models to fit bobwhite abundance as a function of drought (12-month scale Standardized Precipitation Evapotranspiration Index) or year (to assess abundance over time) at 1,503 survey locations in the Eastern Temperate Forest biome and 453 survey locations in the Great Plains biome. Bobwhite abundance decreased in both biomes, but decline was more than twice as sharp in the Eastern Forest ($\beta = -0.05$, $p < 0.0001$) than it was the Great Plains ($\beta = -0.018$, $p < 0.0001$). We also found that bobwhite declined with drought conditions in the Great Plains ($\beta = +0.065$, $p < 0.0001$) but had a positive association with drought in the Eastern Temperate Forest ($\beta = -0.08$, $p < 0.0001$). Though the Great Plains bobwhite population is more stable than the Eastern Forest population, if drying trends continue in the Great Plains, our data suggest that the holdout populations in the arid west may become increasingly imperiled. Because we found evidence of a dynamic interaction between biome and the influence of weather extremes on a generalist species, our results emphasize the importance of understanding regional differences in species responses to landscape factors or environmental change for effective management.

INTRODUCTION

It is well-known that weather extremes are already increasing in frequency and magnitude, and this trend is projected to continue as anthropogenic climate change progresses (Coumou & Rahmstorf, 2012; IPCC, 2014). These extremes can include protracted increases in severe and prolonged drought as well as anomalously heavy rainfall (Armal et al., 2018; IPCC, 2014; Strzepek et al., 2010). Drought conditions can have varied and severe implications for avian populations and communities. For example, drought can cause changes in local occupancy (Cady et al., 2019), short-term dispersal

(Bateman et al., 2015), dynamic range shifts (Cohen et al., 2020), abundance changes (Gorzo et al., 2016; Selwood et al., 2015), and reductions in species richness (Albright et al., 2010). Perhaps most concerning, consistent and long-term decreases in precipitation have caused entire avian community collapse within the past century (Iknayan & Beissinger, 2018). In contrast, anomalously heavy rain can also influence bird communities by reducing reproductive success (Öberg et al., 2015; Schöll & Hille, 2020) and possibly directly causing mortality during migration (Diehl et al., 2014). As birds continue to face novel climatic pressures, as well as frequent, record-setting extremes, the need to hone our understanding of the complexities of their (often complex) responses to drought is becoming increasingly urgent.

It is plausible to observe differential responses to variable precipitation across different landscapes because extreme drought is more likely to exceed an organism's physiological tolerance in already dry biomes. This response may be reflected in unusual dispersal patterns during drought. For example, when dickcissel (*Spiza americana*) experience drought conditions, they disperse, causing an increase in abundance at their range margins and a decrease at their core (Bateman et al., 2015). In addition to different precipitation regimes, some biomes may be better suited to buffer extreme conditions than others. For example, in montane ecoregions of North America, some bird guilds have experienced increased abundance during drought conditions, presumably due at least in part to the dominate plant community being comprised mostly of evergreen trees, which are less immediately responsive to drought conditions than deciduous trees (Albright et al., 2010). Though many studies have evaluated wildlife responses to precipitation variability, less is known about possible biome-specific responses within a single species, especially a non-migratory species unlikely to disperse large distances in response to unfavorable conditions. It is important to better understand the response of resident species, because, in some cases, results have suggested that residents tend to be more sensitive to short term extreme heat events (Cohen et al., 2020). Additionally, evaluating drought responses across biomes allows a level of nuance that has value for generating detailed management recommendations in the face of climate change, because species responses can be complex and site-specific (Cady et al., 2021; Shirk et al., 2014; Wan et al., 2017).

Using a half-century of systematically collected avian abundance data, we investigate biome-specific responses of a single avian species to drought conditions at a sub-continental scale. Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite), a common and widespread Galliform, is well-suited as a model species to investigate long-term wildlife responses to drought because they are exceptionally well-studied (i.e., much is known about their life history requirements) and their extensive range spans diverse biomes. Additionally, understanding the dynamic responses to extreme conditions exhibited by generalist species such as bobwhite is increasingly important as communities are predicted to favor generalists as global changes continue (Davey et al., 2012; Mckinney & Lockwood, 1999; Viol et al., 2012). Finally, bobwhite are known to be a drought-sensitive species (Hernández et al., 2005; Lusk et al., 2001) and are therefore appropriate to investigate precipitation response patterns. Here, we (1) evaluate biome-specific, multi-decadal bobwhite abundance trends and (2) bobwhite response to drought (and anomalously wet) conditions in the central Great Plains and Eastern Hardwood Forest biomes of North America.

METHODS

The North American Breeding Bird Survey (BBS) is a continental-scale dataset of annually-collected bird community abundance data (Pardieck et al., 2020). Data are collected during breeding season (mostly in June), by skilled observers along thousands of 41km routes in North America. Every 800m, the observer stops and records all birds seen or heard within 400 meters for 3 minutes. To optimize confidence in analysis, we cleaned the data by (1) removing any surveys completed by observers in their first year (Kendall et al., 1996), (2) removing surveys that did not meet the United States Geological Survey quality control standards (e.g., surveys completed during weather conditions that limit detection ability or completed outside the optimal survey window), and (3) excluding routes without a bobwhite detection within the study period (to limit our analysis to routes within bobwhite's range). We limited analysis to routes within the continental United States to match the spatial availability of the climate data we used. We delineated biomes using the United States Environmental Protection Agency Level 1 ecoregion classification (coarsest scale; Figure 3.1) and included the Eastern Temperate Forest (hereafter, Temperate Forest) and Great Plains. We used data from 1,956 routes in North America (including 1,503 routes in the Temperate Forest biome and 453 routes in the Great Plains biome).

We used the Standardized Precipitation Evapotranspiration Index (SPEI) to quantify drought (R package, "SPEI"; Beguería and Vicente-Serrano, 2017). SPEI is well-suited to our objectives because the index is calculated units of standard deviation from normal conditions at each location (BBS route, in this case), allowing for direct comparison across biomes, and because it is highly flexible in terms of temporal scale (Vicente-Serrano et al., 2010). We used PRISM monthly weather variables from 1950-2019 and the Hargreaves evapotranspiration equation to model drought under the SPEI framework (Beguería & Vicente-Serrano, 2017). Wildlife responses to drought can be temporally scale-dependent (Albright et al., 2010; Cady et al., 2019), and bobwhite are known to be responsive to 12-month scale drought, ending in April (i.e., drought calculated by compiling weather data from April and the 12 months preceding it; Cady et al., 2019). Therefore, we elected to use April-ending 12-month drought as the explanatory variable for analysis.

We used generalized linear mixed models with a Poisson error distribution (to fit count data) and a random intercept grouped by BBS route to account for route-level differences in baseline bobwhite abundance (e.g., bobwhite abundance relative to habitat features other than precipitation). We assessed bobwhite abundance trends over time and bobwhite response to drought using separate models and used year or SPEI as an explanatory variable, respectively (Bates et al., 2015). Each biome was modeled separately (alpha=0.05) and 95% confidence intervals were bootstrapped (1,000 iterations).

RESULTS

Bobwhite were detected on 1,956 BBS routes in North America and had a median of 6 birds per route across the temporal and spatial extent of the study. Bobwhite abundance decreased in both biomes (Figure 3.2), but decline was more than twice as sharp in the Eastern Forest (β= -0.05, $p< 0.0001$) than it was the Great Plains (β= -0.018,

$p < 0.0001$). Specifically, both regions averaged approximately 17 birds per route in 1967, but by 2019, the Great Plains population declined to approximately 7 birds per route, while the Eastern Forest population dropped to approximately 1 bird per route.

Both study regions experienced significant drought years as well as significant wet years throughout the study period (Figure 3.3). Specifically, SPEI ranged widely from a minimum of -2.9 and -2.7, to a maximum of +3.4 and +3.0 standard deviations from average precipitation/evapotranspiration in the Eastern Forest and Great Plains, respectively. Bobwhite declined with April-ending, annual-scale drought conditions in the Great Plains ($\beta=+0.065$, where a positive coefficient is indicative of a negative relationship between bobwhite abundance and drought conditions, $p<0.0001$) but had a positive association with drought in the Eastern Forest ($\beta=-0.08$, where a negative coefficient indicates a positive relationship between bobwhite abundance and drought conditions, $p<0.0001$) (Figure 3.4).

DISCUSSION

As anthropogenic climate change continues to accelerate, weather extremes such as drought and anomalously heavy precipitation are becoming increasingly severe and frequent, adding urgency to developing our understanding of the ecological implications. Species responses can be complex (e.g., scale dependent, regional- and species-specific; Albright et al., 2010), and sometimes non-intuitive (e.g., multi-directional range shifts relative to global warming; VanDerWal et al., 2013). Using multi-decadal, continental-scale bird abundance data, we evaluated the response of a non-migratory, generalist bird species to variable drought conditions across two, diverse biomes in North America. Our study demonstrated that, though bobwhite underwent a significant response to precipitation throughout its range, the direction of effect was biome-dependent. Specifically, bobwhite experienced decreased abundance during drought in the Great Plains, but increased during drought in the Eastern Forest. Our results also supported the well-documented widespread bobwhite decline, but we found that decline was more than two times sharper in the Eastern Forest than it was in the Great Plains.

A general and widely recognized prediction of global change is the emergence of "winners and losers" (e.g., Somero, 2010; Wiegmann & Waller, 2006). The theoretical framework is intuitive—species that are better able to adapt to changing conditions will persist, while less-suited species will suffer declines or extirpation (Mckinney & Lockwood, 1999), ultimately resulting in geographic reduction in losers, and proliferation in winners (Baskin, 1998). This study adds complexity to the winners-losers paradigm—our results suggest that a single species can be both a winner and loser to the same environmental pressure. In the case of bobwhite, the answer to the question "is a predicted increase in frequency and intensity of drought good, bad, or neutral?" is not as straightforward as it may appear.

A species' negative response to drought on one landscape and neutral relationship with drought on another is somewhat predictable given that different habitat features may mitigate/buffer against abundance declines in some biomes (e.g., woody cover providing refuge for bobwhite during thermal extremes; Carroll et al., 2015). However, opposing but significant directions of effect is less immediately intuitive. Though we did not directly test mechanisms, we speculate that abundance fluctuations likely reflect decreased reproduction or mortality because, as a resident species with mean dispersal distances of approximately 1-5 km (Fies et al., 2002; Liberati & Gates, 2012), bobwhite are unlikely to disperse long distances to flee unfavorable, short-term weather conditions (i.e., the biome-drought interaction is unlikely to be a result of Great Plains individuals colonizing the Eastern Forest during drought periods). Additionally, we suspect differences in how drought influences vegetation in the Great Plains versus the Eastern Forest is likely to be an important factor driving the observed pattern. It has been suggested that bobwhite need a consistent level of vegetative biomass, but that different environmental conditions may facilitate that biomass in different regions (Guthery, 1997). Under this assumption, in the arid Great Plains, where vegetation is relatively sparse, drought may decrease biomass below optimal levels for bobwhite. Alternatively, in the Eastern Forest, where vegetation is more robust, high precipitation may create an understory too dense for bobwhite to persist. Some support for this pattern has been observed on a smaller scale in southern Texas, where bobwhite density increased with early seral stage in highly productive sites (i.e., high biomass), however, a relationship between bobwhite and seral stage was not observed on unproductive sites (Spears et al., 1993).

The results presented here inform conservation in two key ways. First, and perhaps most straightforward, we found widespread, multi-decadal decline among bobwhite in North America, which is consistent with myriad research describing this trend (Brennan, 1991; Sauer et al., 2013; Williams et al., 2004), largely attributed to habitat loss and fragmentation (Hernández et al., 2013). Specifically, we found that the Eastern Forest bobwhite population is declining more than twice as fast as the Great Plains population (Figure 3.2). Our study contributes to the well-documented, east-to-west nature of bobwhite decline (i.e., severe decline in the east and milder, but still consistent, decline in the west). However, if drying trends continue in the Great Plains (Seager et al., 2018), our data suggest that the holdout populations in the arid west may become increasingly imperiled, supporting previous predicative models forecasting climate-change-driven bobwhite declines in western part of their range in 2050-2070 (Tanner et al., 2017). Second, our findings underline the importance of understanding regional differences in species responses to landscape factors or environmental change (Cady et al., 2021; Shirk et al., 2014; Wan et al., 2017). Here, we found evidence of a dynamic interaction between biome and the influence of weather extremes on a generalist species, emphasizing the complexity of management in the face of climate change.

FIGURES

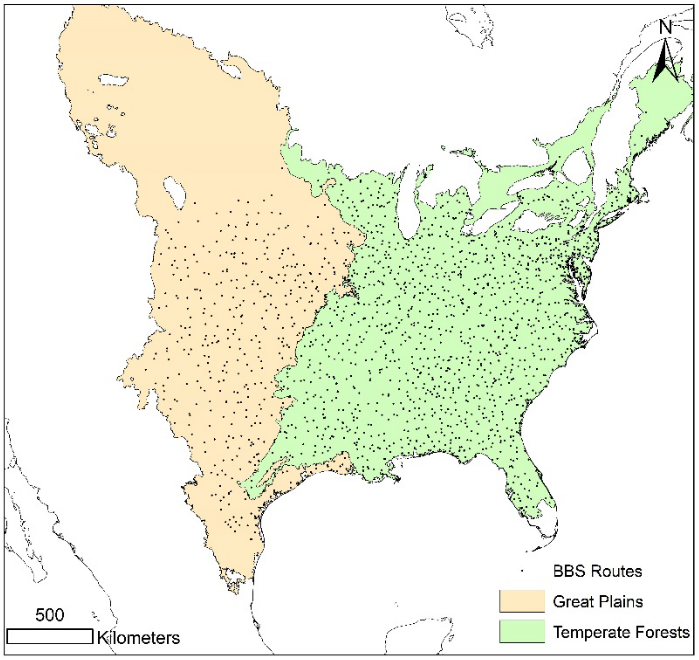

Figure 3.1 Study regions and BBS routes used in analysis.

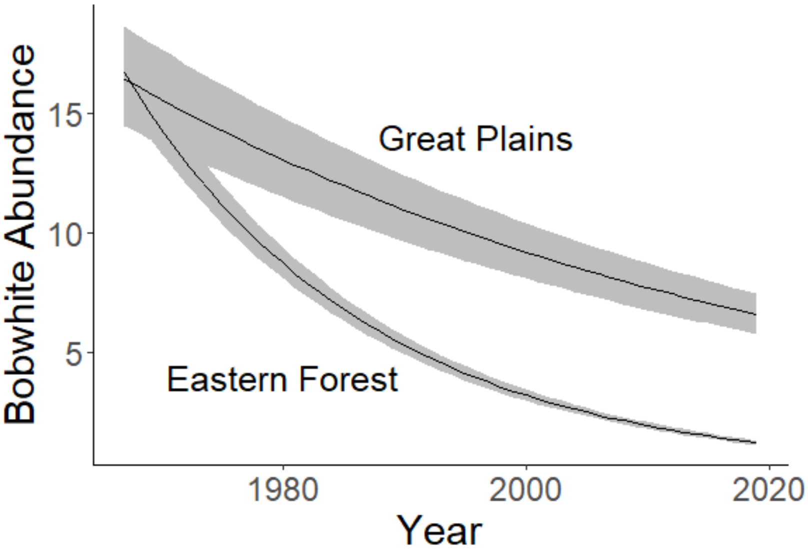

Figure 3.2 Change in northern bobwhite abundance (average count of birds per BBS route) from 1967 to 2019 within the Eastern Hardwood Forest and Great Plains biomes of North America. Trends were predicted using generalized linear mixed models (Poisson error distribution and route included as a random intercept) with 95% bootstrap confidence intervals (1000 iterations).

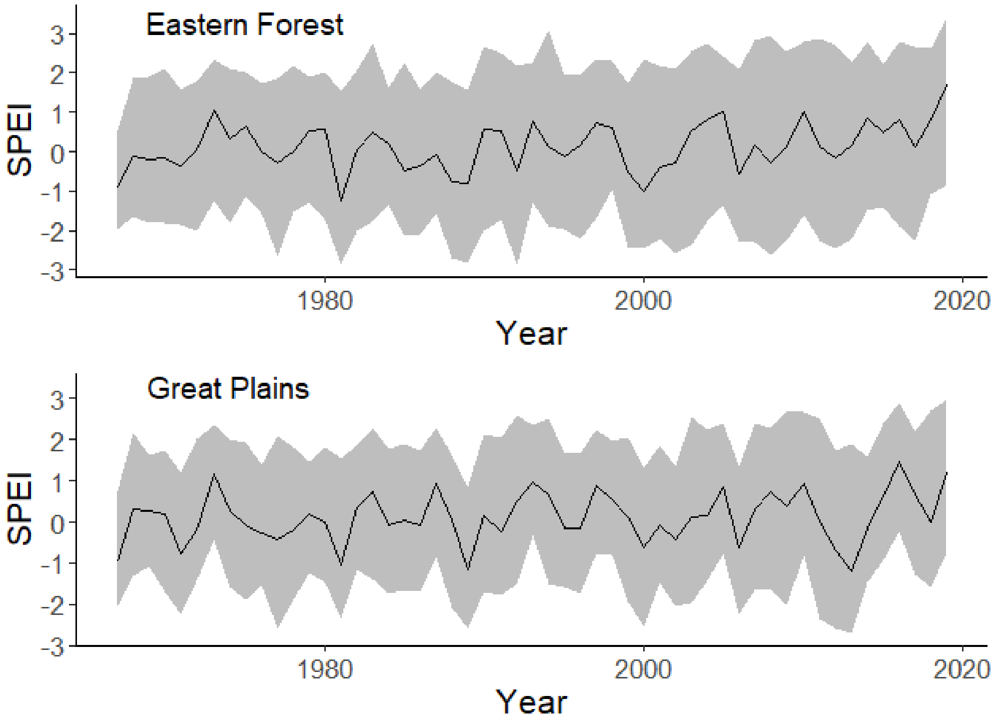

Figure 3.3 Average, annual-scale drought conditions during the study extent by biome. Average SPEI (black line) represents the mean route-level SPEI each year. Gray ribbons represent the minimum and maximum SPEI captured each year.

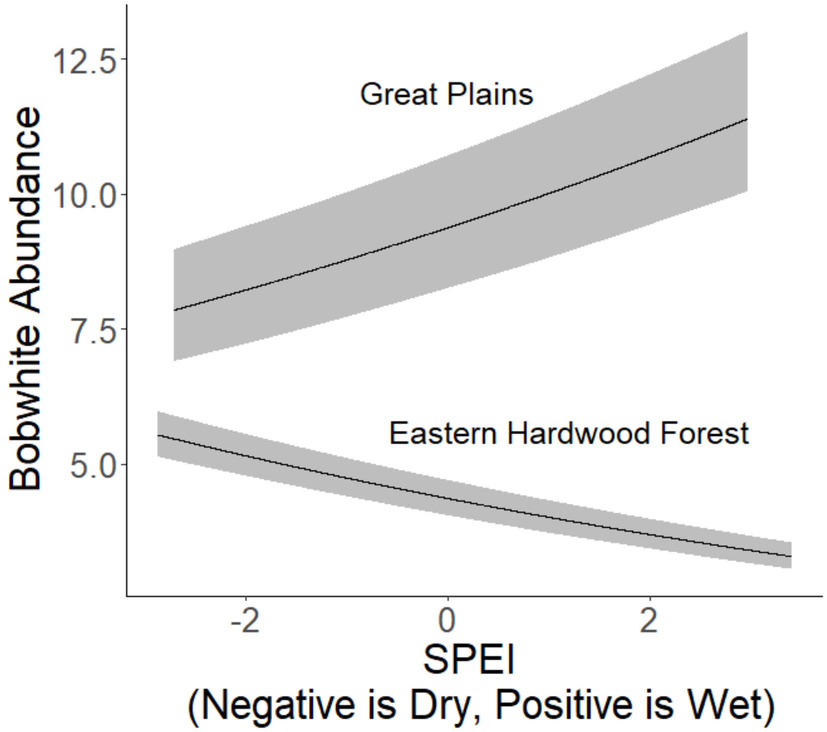

Figure 3.4 Relationship between northern bobwhite abundance (average count of birds per BBS route) and drought (standardized precipitation evapotranspiration index; "SPEI") in the Eastern Hardwood Forest and Great Plains biomes of North America. Trends were predicted using generalized linear mixed models (Poisson error distribution and route included as a random intercept) with 95% bootstrap confidence intervals (1000 iterations).

CHAPTER IV

A GENERALIST BIRD EXHIBITS SITE-DEPENDENT RESOURCE SELECTION

ABSTRACT

Quantifying resource selection (an organism's disproportionate use of available resources) is essential to infer habitat requirements of a species, develop management recommendations, predict species responses to changing conditions, and improve our understanding of the processes that underlie ecological patterns. Because study sites, even within the same region, can differ in both the amount and the arrangement of cover types, our objective was to determine whether proximal sites can yield markedly different resource selection results for a generalist bird, northern bobwhite (*Colinus virginianus*). We used five years of telemetry locations and newly developed land cover data at two, geographically distinct but relatively close sites in the south central semi-arid prairies of North America. We fit a series of generalized linear mixed models and used an information-theoretic model comparison approach to identify and compare resource selection patterns at each site. We determined that the importance of different cover types

to northern bobwhite is site-dependent on relatively similar and nearby sites. Specifically, whether bobwhite selected for shrub cover and whether they strongly avoided trees, depended on the study site in focus. Additionally, the spatial scale of selection was nearly an order of magnitude different between the cover types. Our study demonstrates that—even for one of the most intensively studied species in the world—we may oversimplify resource selection by using a single study site approach. Managing the tradeoffs between practical, generalized conclusions and precise but complex conclusions is one of the central challenges in applied ecology. However, we caution against setting recommendations for broad extents based on information gathered at small extents, even for a generalist species at adjacent sites. Before extrapolating information to areas beyond the data collected, managers should account for local differences in the availability, arrangement, and scaling of resources.

INTRODUCTION

Quantifying resource selection—an organism's disproportionate use of available resources (D. H. Johnson, 1980)—is essential for applied ecologists to infer habitat requirements of a species. For example, an organism's biological requirements can be altered by multiple processes such as thermal variability (e.g., Carroll *et al.*, 2015), food availability (e.g., Gittleman and Harvey, 1982; Dupke *et al.*, 2017), perceived predation risk (e.g., Lagos *et al.*, 1995), and population density (e.g., Benson, Chamberlain and Leopold, 2006), among other factors, leading to spatial and temporal shifts in resource selection. Developing a comprehensive picture of a species' resource requirements allows researchers to create management recommendations based on those needs. However, because resource selection is typically quantified by comparing use vs. available resources, any conclusions drawn are highly conditional on the resources available to the study organism at the time and location of data collection (Beyer et al., 2010; Mysterud & Ims, 1998), and our ability to accurately describe them.

Delineating resource availability is challenging and always somewhat subjective (Beyer et al., 2010), as decisions must be made regarding the scale of availability (e.g., deciding whether areas considered available to an organism are within or outside the individual's home range) and which of these areas are actually accessible to the species. Notably, how a study defines availability can influence resource selection simply by nature of its derivation because the decision directly influences the denominator in a (% use)/(% availability) resource selection function (the class of model generally used to understand an organism or population's resource selection patterns; Manly *et al.*, 2007). This built-in arbitrariness of resource selection functions may lead to erroneous conclusions if availability is delineated inappropriately for the organism or research objective. An added challenge arises because landscapes are, by definition, spatially heterogeneous and patchy (Turner, 1989). Within a species' distribution, the location of a study site (in this case, referring to the location of data collection within the context of a species' range) can determine the amount, quality, and configuration of land cover types available to the organism. Studies explicitly examining the influence of site on resource selection results have largely found evidence of site-dependent selection trends (Mcnew et al., 2013; Shirk et al., 2014; Wan et al., 2017). However, less is known about the influence of close and relatively similar sites on the resource selection patterns of generalist species.

As the Anthropocene continues (Crutzen, 2006), ecologists anticipate a disproportionate representation of generalist species (i.e., species that are widespread and broadly adapted; Mckinney and Lockwood, 1999), a trend which has already been documented in some communities (e.g., Davey *et al.*, 2012; Viol *et al.*, 2012). As a result, it will become increasingly important for managers to understand the habitat needs of generalist species, which can be complex. For example, generalist species have shown differential resource selection patterns in response to variable habitat composition (Roever et al., 2012), food availability (Hansen et al., 2009), and weather conditions (Sunde et al., 2014). Here, we further investigate this pattern by determining whether generalist species may also exhibit functional responses at similar, nearby, study sites. We selected Northern bobwhite (*Colinus virginianus,* hereafter "bobwhite", Figure 4.1), an intensively studied, generalist bird, as a model organism because we already have a strong understanding of their basic habitat requirements. We therefore can select variables already known to influence this species, in this case woody cover (Carroll et al., 2015). Additionally, as a non-migratory species, we have added confidence that environmental variables occurring in regions other than our study areas will not influence the bird and confound results.

It is now widely understood that spatial scale is inherently related to space use (D. H. Johnson, 1980; Mayor et al., 2009; Whittingham et al., 2005)—that is, selection decisions are not necessarily preserved across multiple spatial scales (Mayor et al., 2009). For precision, we note although the term "scale" can refer to spatial, temporal, or organizational grains (unit of resolution) or extents (study area boundary), we use it here as shorthand for spatial grain. In recent decades, there has been increased effort to identify the “proper” scale of resource selection from a species-specific perspective (McGarigal et al., 2016). However, any identified scale of wildlife resource selection can plausibly be different between two landscapes, even if they are nearby—yet, little is known about the influence of proximal study site location on the scaling of resource selection.

A challenge with developing a comprehensive, science-based approach to large-scale resource selection, is that replicating large landscapes is logistically difficult, expensive, and time-intensive. Broadly, we aim to contribute to a more comprehensive model of wildlife resource selection by examining the selection patterns of a common and well-studied, generalist species. Specifically, we use two, nearby study sites (140 km apart, which is arguably close in the context of the species’ entire range) and five years of bobwhite movement data to determine whether proximal sites have the capacity to yield markedly different resource selection results for a generalist species. Additionally, because wildlife select different habitat types at different scales (Anderson et al., 2005; Beatty et al., 2014; Mayor et al., 2009), we investigate whether the scale(s) at which species select their habitat is divergent between sites. Finally, we compare the differences in potential habitat availability at randomly selected landscapes with actual quail resource selection patterns.

METHODS

Resource selection Analysis

i. Study Sites

This study was conducted in the south-central semi-arid prairies of North America, on two Oklahoma wildlife management areas (“WMA”, Figure 4.2) managed by the Oklahoma Department of Wildlife Conservation, mostly for hunting and cattle grazing. Both WMAs are located on the western margin of the bobwhite’s range, and are approximately 140 km apart. A distance of 140km is arguably proximal within the context of the entire species’ continental range, which extends to the east coast of North America and includes diverse ecoregions (Figure 4.2) Beaver River WMA (“Beaver River”, WGS 36.8293, -100.664) includes approximately 7,200 hectares of southwestern tablelands and high plains, dominated by sandsage-grassland and shortgrass prairie (Tyrl et al., 2008). Packsaddle WMA (“Packsaddle”, WGS 35.883, -99.6591) is 8,100 hectares of central Great Plains, where the dominant vegetation includes mixed grass prairie with shinnery-oak grassland (Tyrl et al., 2008).

Vegetation composition and configuration differ between the two sites. Specifically, woody vegetation on Packsaddle is comprised mostly of shinnery oak (*Quercus harvardii*), but also includes sand sagebrush (*Artemisia filifolia*) and sandplum (*Prunus angustifolia;* DeMaso *et al.*, 1997). Tall woody vegetation at Packsaddle is mostly hybrid sand shinnery/post oak (*Quercus havardii x Quercus stellata)* and occasionally cottonwood (*Populus deltoides*), hackberry (*Celtis occidentalis*), soapberry (*Sapindus drummondii*), and black locust (*Robinia pseudoacacia*; Rakowski *et al.*, 2019). Whereas at Beaver River, woody cover is dominated by sand sagebrush (*Artemisia filifolia*) with occasional sandplum (*Prunus angustifolia*) in the uplands, along with salt cedar (*Tamarix* spp), hackberry (*Celtis occidentalis*), American elm (*Ulmus americana*), and sandplum (*Prunus angustifolia*) in the floodplains and river bottom (Atuo &

O'Connell, 2017). Packsaddle and Beaver River have both been subjected to oil and gas development, though well activity is more active and extensive at Packsaddle. Additionally, both sites are managed using cattle grazing and prescribed fire, but Packsaddle is burned much more frequently than Beaver River.

ii. Bird Location Data

Bobwhite movement data were collected from wild birds on both WMAs from 2012-2016. Adult bobwhite were captured using walk-in funnel traps, fitted with a VHF radio-collar, and located using radio-telemetry approximately 4-7 times per week. Trapping effort was high; 2,399 trap locations were established at Packsaddle and 1,382 were established at Beaver River. It is worth noting that trap effort was not uniform across the study sites (Appendix 1) and trapping intensity tended to be higher along roads. Though some bobwhite individuals were tracked year-round, to mitigate confounding factors (e.g., uneven seasonal sampling between sites) and improve inference confidence, we limited analysis to bird locations collected during the breeding season (April-September; e.g., Carroll *et al.*, 2017). To increase sample independence, duplicated locations were removed by (1) including only one bird per covey and (2) including only one point at a nest location. If a bird location did not occur on a pixel with land cover data (i.e., not a rangeland pixel and not associated with Rangeland Analysis Platform data), it was not included in analysis. During the 5-year study period, 35,499 locations were recorded from 1,725 birds across both sites and used in analysis (21,172 locations from 968 birds on Packsaddle, and 14,327 locations from 757 birds on Beaver River). Each telemetry fix (bird GPS location) was considered a "presence" to be compared with “pseudo-absences” (described in more detail in the statistical analysis section). A more comprehensive description of the dataset and field methods is detailed in Davis *et al.*, (2017).

iii. Environmental Variables

Our research objectives require high-resolution, continuous environmental data and the Rangeland Analysis Platform (Jones et al., 2018) is well-suited to meet these needs. The raster dataset contains annual-scale, continuous percent land cover data for multiple plant functional groups at approximately 30m resolution, and is freely available online (https://rangelands.app/). The percent cover data were generated by compiling field-collected data from approximately 60,000 field plots along with over 200 layers of gridded surface data, and a random forest model to predict functional cover types across the western half of the United States (Jones et al., 2018). The predictive accuracy of the Rangeland Analysis Platform (Cover Version 1.0) included 6.9% mean absolute error for the shrub layer and 4.7% for the tree layer. Because our objectives are to identify broad selection trends at medium to large scales (0.81 to 1,739 hectares), and because we are not investigating thresholds or change over time, we are confident that the Rangeland Analysis Platform is appropriate for our purposes. Because it is well-known that woody cover is important for bobwhite (e.g., Carroll *et al.*, 2015), we included both shrub cover and tree cover functional groups in analysis.

iv. Statistical Analysis

We excluded all non-rangeland pixels in the WMAs (e.g., standing water, agriculture, roads) because the Rangeland Analysis Platform algorithm is designed to best predict rangeland cover types. To simultaneously test bobwhite responses to shrub and tree cover at multiple scales, we systematically scaled up both cover classes (i.e., averaged pixel neighborhoods by moving windows). Moving windows sizes (of 30m-resolution pixels) included 3x3, 9x9, 27x27, 81x81, 113x113, and 139x139. This resulted in 30m-resolution percent cover data that was aggregated to incorporate 0.81ha (90m x 90m), 7.29ha (270m x 270m), 65.61ha (810m x 810m), 590ha (2.43km x 2.43km), 1,149ha (3.39km x 3.39km), and 1,739ha (4.17km x 4.17km) of surrounding landscape context (i.e., the grain resolution remained 30m, but included average percent cover at various sized moving windows). In other words, the spatial resolution was preserved at 30m at all spatial scales because we used a moving window rather than scaling up the raster to a lower resolution. We intentionally selected a wide range of scales, encompassing several orders of magnitude (less than one hectare up to 1,739 hectares), to allow bobwhite use to determine the appropriate scale of selection (using the telemetry data and model ranking, explained in more detail below). Percent cover data for all moving window sizes (each size to represent a spatial scale) and cover types were extracted to each bird location in each year (i.e. the telemetry year was matched with the year of the land cover data). For example, a bobwhite telemetry location collected in 2012 would have 12 environmental variables associated with it, including 6 scales of shrub cover and 6 scales of tree cover.

We generated random-point pseudo absences in each given year, and in equal proportion to presence data (i.e., one absence point per presence point) within each study region (Packsaddle and Beaver River, including a 500m buffer around the WMA boundary to include birds that were tracked slightly outside the WMA boundary lines) to function as unused habitat in the models. In other words, 35,499 bobwhite presence locations—each paired with a randomly generated absence location—resulted in a dataset of 70,998 presence/pseudo-absence data points. It is important to note that mitigating trap bias while delineating available, unused habitat is an inherent challenge in space use/resource selection analyses (Millspaugh & Marzluff, 2001). Because our objective was to investigate large-scale resource selection patterns at a population level (comparable to a second-order approach; Johnson, 1980), we defined "available" habitat as the entire buffered WMAs. At Beaver River and Packsaddle, the average long-distance movement of bobwhite (>1000m) was approximately 2,364m and 2,940m, respectively. Because 100.0% of Packsaddle and 99.5% of Beaver River was less than the average long-distance movement from a known bobwhite location, tagged birds could have reasonably dispersed almost anywhere on the buffered WMA. Therefore, trapping intensity and the number of birds tracked were high enough to justify using the entire study area as available habitat.

All parameters were estimated and model comparison was conducted using R v3.6.2 (R Core Team, 2020). For both of the land cover classes (percent cover of trees and shrubs), we created a series of generalized linear mixed models, where bird location/absence was the binary response variable, modeled as a function of percent cover at each spatial scale (0.81ha, 7.29ha, 65.61ha, 590ha, 1,149ha, and 1,739ha) using a binomial error distribution and logit link function in R package "lme4" (Bates et al., 2015). Year was included as a random slope in all models to adjust for variance attributable to yearly differences in bobwhite habitat selection (e.g., birds more likely to use woody cover in hot years). To determine whether site influences scale of resource selection, Beaver River and Packsaddle were modeled separately. We assessed the models using two approaches in order to explore two different facets of resource selection. First, we assessed the overall most important woody cover type for bobwhite at each site using Akaike information criterion (AIC) (i.e., both cover types at all scales ranked in the same AIC), using R package "bbmle" (Bolker & R Development Core Team, 2020). Second, in order to determine the scale of bobwhite resource selection of each environmental variable, we ranked the models using AIC for each site and environmental variable (shrubs and trees at both sites, each ranked in separate AICs). For all models, 95% confidence intervals were estimated via bootstrapping using 1,000 iterations in R package "lme4" (Bates et al., 2015). Models with delta AIC < 2.0 were considered competitive, unless a null model was also competitive or if bootstrapped confidence intervals overlapped zero.

Randomly Selected Site Simulations

Within the South-central semi-arid prairies ecoregion in North America, and using the Rangeland Analysis Platform, we generated 100, randomly located, 10km x 10km, landscapes for each of the three cover types (trees, shrubs, bare ground) and compared resource availability at each landscape to known bobwhite resource selection. We calculated the mean tree cover, shrub cover, and bare ground used by bobwhite on one site (Packsaddle WMA), and compared it to the percent cover available at each simulated landscape in order to determine whether the location of a site determines whether tree cover availability is lower or higher than average use. We also examined the differences in scaling of each environmental variable across the randomly selected landscapes by varying the resolution of each landscape (systematically scaling up each landscape 100 times, while holding the extent at a constant 10km x 10km). The finest resolution was the original RAP data (30m resolution); the coarsest was 3,000m by 3000m. At each resolution, we calculated the overall mean percent cover and the between-cell variance of each cover type.

RESULTS

Packsaddle had a higher mean density of tree cover than Beaver River, but the WMAs were comparable in terms of average shrub cover (Table 4.1). For both tree cover and shrub cover, measurements were highly correlated across spatial scales (Appendix 2).

Wildlife Resource selection

According to AIC model ranks, bobwhite resource selection varied by study site. That is, we found differences in both the relative importance of cover types across the two sites. The top-performing model for resource selection at Packsaddle WMA included a negative relationship with tree cover (β=-0.19), whereas the top model for Beaver River WMA indicated a positive association with shrub cover (β=+0.40, Table 4.2). Although bobwhite responded strongly and negatively to tree cover at Packsaddle (i.e., bobwhite habitat use was less likely in areas with high tree cover), we found no response to tree cover at Beaver River (Table 4.3, Figure 4.3). Conversely, though bobwhite responded strongly and positively to shrub cover at Beaver River, we found no bobwhite response to shrub cover at Packsaddle (Table 4.3, Figure 4.3). There was considerable between-year variation in shrub selection at Beaver River and trees selection at Packsaddle WMA (Figure 4.4). The comparative direction and strength of effects were similar across all spatial scales, except selection against tree cover was similar between the two sites at small scales and selection for shrub cover was similar between sites at large spatial scales (Appendix 3). There was also variability among the scale of resource selection between environmental variables. Specifically, at Beaver River bobwhite perceived shrub cover at a considerably smaller spatial scale (65.61ha) than they perceived tree cover at Packsaddle (590ha).

Randomly Selected Landscape Comparisons

Across 100, randomly sampled, 10km by 10km landscapes in the South-central Semi-arid Prairies, mean percent cover of each of 6 cover classes ranged widely, yet remained relatively constant across spatial scales (Appendix 4). Further, we found that, although the general trend was between-pixel variance decreasing with increasing scale, the magnitude (slope) varied across landscapes (Appendix 4), indicating substantial scaling differences across landscapes in the same ecoregion. Moreover, the location of a study area determines whether the average percent cover of both cover types available to the bird is within or outside of average bobwhite resource selection (Figure 4.5).

DISCUSSION

Resource selection methods can be applied for many reasons, which include identifying management recommendations that promote optimal habitat (Chandler &

King, 2011; Suárez-Seoane et al., 2002), predicting species responses to changing conditions (e.g, Garcia *et al.*, 2013), and ultimately improving our understanding of the processes that underlie ecological patterns (e.g., Fogarty *et al.*, 2017). Therefore, it is important to understand the limitations of resource selection models to avoid drawing inappropriately generalized conclusions. Because resource selection studies are typically conducted at one study site, and because sites (even within the same region) can differ in the amount, arrangement, and scaling of cover types, we set out to determine whether site location substantially influences the results of a resource selection analysis for a generalist species. Our study demonstrates—even for one of the most intensively studied species in the world—we are may oversimplify resource selection by using a single study site approach. That is, we determined that the importance of different cover types to northern bobwhite is site-dependent, even for proximal study sites.

Previous studies investigating bobwhite resource selection have revealed a range of results and found little evidence of a single "ideal landscape" for the species (Guthery, 1999). For example, bobwhite can select for bare ground (Lusk et al., 2006) or avoid it (Duquette et al., 2019; Tanner et al., 2016). Similarly, we found there is no universally optimal percent cover of trees or shrubs on a landscape because results are dependent on the structure, availability, and arrangement of woody cover. Though the study sites are close to one another in the context of the bird's entire range, there are marked differences in the site-level woody cover composition and management practices, which may be driving the differential responses in results. We found a strong selection for shrubs at Beaver River, but no response to tree cover at Packsaddle. The exact mechanism behind the site-dependent woody cover selection pattern remains speculative and could be related to a number of differences between the two sites. First, Packsaddle undergoes significantly more prescribed fire than Beaver River. Though fire has been shown to have little effect on bobwhite space use (Carroll, Davis, et al., 2017) or density (Ransom et al., 2008), fire likely changes the vegetative functional groups perceived by the Rangeland Analysis Platform, which could partially confound the relationship between bobwhite and shrubs on Packsaddle. In other words, if a shrub-dominated area used by bobwhite is burned, the Rangeland Analysis Platform may show an increase in herbaceous cover and a concomitant decrease in shrub cover, yet bobwhite are likely to remain in the area (possibly resulting in the neutral relationship between bobwhite and shrubs that we found at Packsaddle). The relationship between bobwhite and shrub cover is more straightforward at Beaver River, where fire is rare, shrubs are more diverse, and bobwhite strongly select for them. This positive association between bobwhite and shrubs at Beaver River is unsurprising because shrubs are a critical bobwhite habitat component (Carroll et al., 2015; Wiseman & Lewis, 1981). Finally, we suspect the strong selection against trees at Packsaddle with no response at Beaver River, to be mostly a function of differences in overall tree cover between the two sites. Because bobwhite tend to have decreased survival in closed-canopy areas (Howell et al., 2021; Seckinger et al., 2008), it follows that birds may respond differently to trees at Packsaddle, where trees are more abundant, than they would at Beaver River, where trees are an anomaly on the landscape.

Our results indicate there is no universally correct scale of resource selection for bobwhite. This is in alignment with an extensive body of literature underlining the importance of multi-scale resource selection (Bauder et al., 2018; Mayor et al., 2009; McGarigal et al., 2016; Timm et al., 2016). Specifically, we found evidence that the scale at which bobwhite select their habitat depends on the habitat feature in focus. Specifically, bobwhite select for shrub cover at intermediate spatial scales (65.61ha) but they select against tree cover at larger spatial scales (590ha). The importance of considering scale before drawing conclusions from resource selection studies is well documented in the literature (Bowyer & Kie, 2006; Mayor et al., 2009; McGarigal et al., 2016). For example, mule deer (*Odocoileus hemionus*) in California, USA were found to select (and avoid) different habitat components at different scales (Kie et al., 2002), however, an unexpected scale—much larger than the deer's home range—was found to be the most informative in predicting deer use and ultimately led to the conclusion that heterogeneity is important for deer conservation. Had management recommendations been developed based on any of the smaller scales, inferior habitat may have been promoted, leading to ineffective management strategies for the species.

Though not a central objective of this study, an interesting finding was that correlated scales are not necessarily perceived equivalently by a species. In other words, even though the woody cover variables we investigated were correlated across spatial scales, there was still a preferred scale in terms of bobwhite resource selection for each cover type (i.e., only one competitive model in our set for both environmental variables). This was unexpected because perfectly correlated scales will always yield identical results, so it stands to reason highly correlated scales will yield highly similar results (i.e., many, or no, competitive models). According to Wiens, (1989), ecological phenomena occur along portions of the scale spectrum (spatial grain ranked from small to large), such that they are scale-independent within their scale domain (i.e., the portion of the scale spectrum where processes are similar enough that generalizations are appropriate). We found bobwhite still showed affinities for some spatial scales over others, regardless of high correlations across habitat variable scales, suggesting that ecological domain boundaries may not be detected by the correlation between scaled environmental data. This finding contributes to a more comprehensive understanding of the role of spatial scale in resource selection studies, which is important because scale is the central factor that determines all observed patterns in ecology (Levin, 1992; Wiens, 1989).

Our study suggests using a single study site approach to examine resource selection is unlikely to extrapolate perfectly across a species' distribution—or even across similar sites. Beaver River and Packsaddle are located on the western periphery of northern bobwhite distribution and, although they have differences in habitat composition, both landscapes are in the same ecoregion with similar broad-scale habitat (prairie/grassland). Despite these similarities, we found considerable differences in bobwhite resource selection, highlighting the importance of using caution when using single-site studies to describe resource selection patterns across a species' distribution. However, the difference in resource selection between sites is only one piece of the many sources of variation inherent in ecological systems. Differential selection responses can be found depending on the season (Beck et al., 2013), time of day (e.g., Richter *et al.*, 2020), scale of habitat feature (Mayor et al., 2009), and simply between unique individuals (e.g., Leclerc *et al.*, 2016). One of the central challenges of ecology is managing the tradeoffs between drawing generalized conclusions and maintaining true complexities inherent in nature (A. F. Johnson & Lidström, 2018). Balancing practical, generalized conclusions that are easy to implement with precision (more accurate conclusions, but complex and difficult to apply), has presented challenges across ecological concepts including alien species invasions (A. F. Johnson & Lidström, 2018), defining species (e.g., Hey *et al.*, 2003), and biological conservation in general (e.g., Lewison, Johnson and Verutes, 2018). While we acknowledge that it is expensive and inefficient to directly study every area we plan to manage, we caution against setting recommendations for broad extents based on information gathered at small extents. Before extrapolating information beyond the data collected, managers should account for local differences in the availability, arrangement, quality, and scaling of resources. Because large areas encompass higher variability (Fuhlendorf & Smeins, 1996; Wiens, 1989), we recommend managing for large and variable tracts of land that are resilient towards uncertainty.

TABLES

Table 4.1 Mean and standard deviation of percent land cover per 30m pixel on Packsaddle and Beaver River WMA from 2012-2016

	Packsaddle	**Beaver River**
Tree Cover	9.7 ± 9.2%	3.3 ± 3.9 %
Shrub Cover	10.4 ± 4.3%	9.7 ± 3.5%

Table 4.2 Northern bobwhite resource selection by site. Models with delta AIC < 2.0 were considered competitive, unless a null model was also competitive or if 95% bootstrapped confidence intervals overlapped zero.

	Cover Type	Spatial Scale	ΔAIC	Weight	β	95% CI
Packsaddle WMA	**Tree**	**590ha**	**0.0**	**1**	**-0.19**	**-0.31 -0.08**
	Tree	1,149ha	307.4	<0.001	-0.20	-0.31, -0.08
	Tree	1,739ha	307.7	<0.001	-0.21	-0.32, -0.10
	Tree	65.61ha	851.1	<0.001	-0.13	-0.21, -0.05
	Tree	7.29ha	2074.4	<0.001	-0.07	-0.12, -0.03
	Tree	0.81ha	2766.8	<0.001	-0.04	-0.07, -0.02
	Shrub	1,739ha	2949.3	<0.001	+0.12	-0.06, +0.29
	Shrub	1,149ha	3086.9	<0.001	+0.10	-0.05, +0.25
	Shrub	590ha	3306.0	<0.001	+0.05	-0.04, +0.13
	Shrub	0.81ha	3451.1	<0.001	+0.03	+0.01, +0.05
	Shrub	7.29ha	3465.8	<0.001	+0.01	-0.00, +0.05
	Shrub	65.61ha	3489.2	<0.001	+0.01	-0.03, +0.05
	Null	NA	3538.2	<0.001	NA	NA

Beaver River WMA	**Shrub**	**65.61ha**	**0.0**	**1**	**+0.40**	**+0.05, +0.74**
	Shrub	590ha	372.8	<0.001	+0.45	+0.02, +0.86
	Shrub	7.29ha	556.1	<0.001	+0.28	+0.06, +0.51
	Shrub	0.81ha	826.6	<0.001	+0.21	+0.05, +0.38
	Shrub	1,149ha	908.3	<0.001	+0.42	+0.01, +0.85
	Tree	590ha	1309.1	<0.001	+0.01	-0.22, +0.25
	Shrub	1,739ha	1354.5	<0.001	+0.38	-0.03, +0.79
	Tree	1,739ha	1444.0	<0.001	+0.12	-0.13, +0.38
	Tree	1,149ha	1457.7	<0.001	+0.06	-0.18, +0.31
	Tree	65.61ha	1698.2	<0.001	-0.02	-0.16, +0.12
	Tree	7.29ha	1999.2	<0.001	-0.03	-0.10, +0.05
	Tree	0.81ha	2143.6	<0.001	-0.01	-0.06, +0.04
	Null	NA	2324.8	<0.001	NA	NA

Table 4.3. Spatial scale of bobwhite resource selection by environmental variable and study site. Models with delta AIC < 2.0 were considered competitive, unless a null model was also competitive or if 95% bootstrapped confidence intervals overlapped zero.

	Spatial Scale	ΔAIC	Weight	β	95% CI
Packsaddle					
Tree Cover	**590ha**	**0.0**	**1**	**-0.19**	**-0.31, -0.08**
	1,149ha	307.4	<0.001	-0.20	-0.31, -0.08
	1,739ha	307.7	<0.001	-0.21	-0.32, -0.10
	65.61ha	851.1	<0.001	-0.13	-0.21, -0.05
	7.29ha	2074.4	<0.001	-0.07	-0.12, -0.03
	0.81ha	2766.8	<0.001	-0.04	-0.07, -0.02
	Null	3538.9	<0.001	NA	NA
Shrub Cover	1,739ha	0.0	1	+0.12	-0.06, +0.29
	1,149ha	137.6	<0.001	+0.10	-0.05, +0.25
	590ha	356.7	<0.001	+0.05	-0.04, +0.13
	0.81ha	501.8	<0.001	+0.03	+0.01, +0.05
	7.29ha	516.5	<0.001	+0.01	-0.00, +0.05
	65.61ha	539.9	<0.001	+0.01	-0.03, +0.05
	NULL	589.6	<0.001	NA	NA
Beaver River					
Tree Cover	590ha	0.0	1	+0.01	-0.22, +0.25
	1,739ha	134.9	<0.001	+0.12	-0.13, +0.38
	1,149ha	148.6	<0.001	+0.06	-0.18, +0.31
	65.61ha	389.1	<0.001	-0.02	-0.16, +0.12
	7.29ha	690.4	<0.001	-0.03	-0.10, +0.05
	0.81ha	834.4	<0.001	-0.01	-0.06, +0.04
	NULL	1015.7	<0.001	NA	NA
Shrub Cover	**65.61ha**	**0.0**	**1**	**+0.40**	**+0.05, +0.74**
	590ha	372.8	<0.001	+0.45	+0.02, +0.86
	7.29ha	556.1	<0.001	+0.28	+0.06, +0.51
	0.81ha	826.6	<0.001	+0.21	+0.05, +0.38
	1,149ha	908.3	<0.001	+0.42	+0.01, +0.85
	1,739ha	1354.5	<0.001	+0.38	-0.03, +0.79
	NULL	2324.8	<0.001	NA	NA

FIGURES

Figure 4.1 Northern bobwhite (*Colinus virginianus*). Photo credit: Todd Johnson, Oklahoma Cooperative Extension Service.

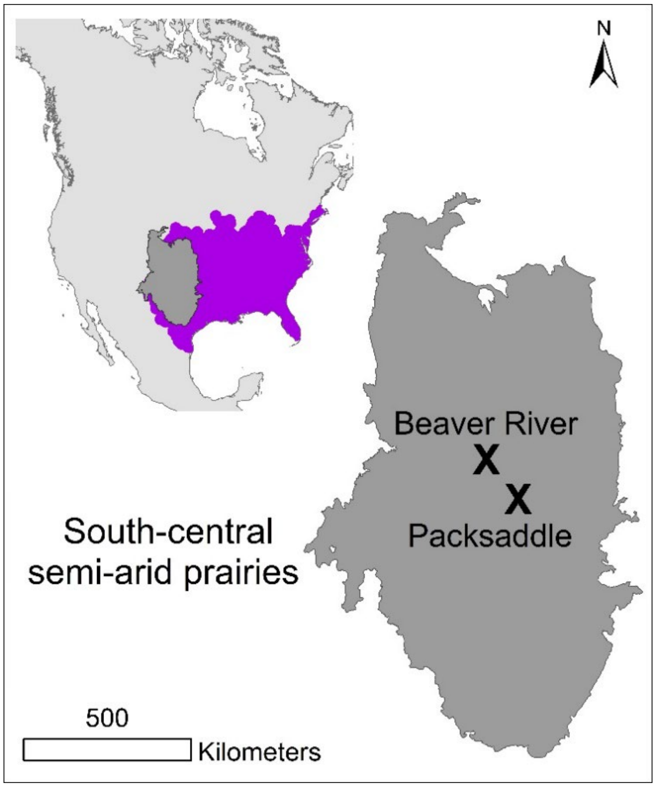

Figure 4.2 Beaver River and Packsaddle WMA in the south-central semi-arid prairies of North America. The purple polygon represents the northern bobwhite's range and was compiled using the North American Breeding Bird Survey data from 1967-2018 (only includes bobwhite in the contiguous United States; Pardieck *et al.*, 2020).

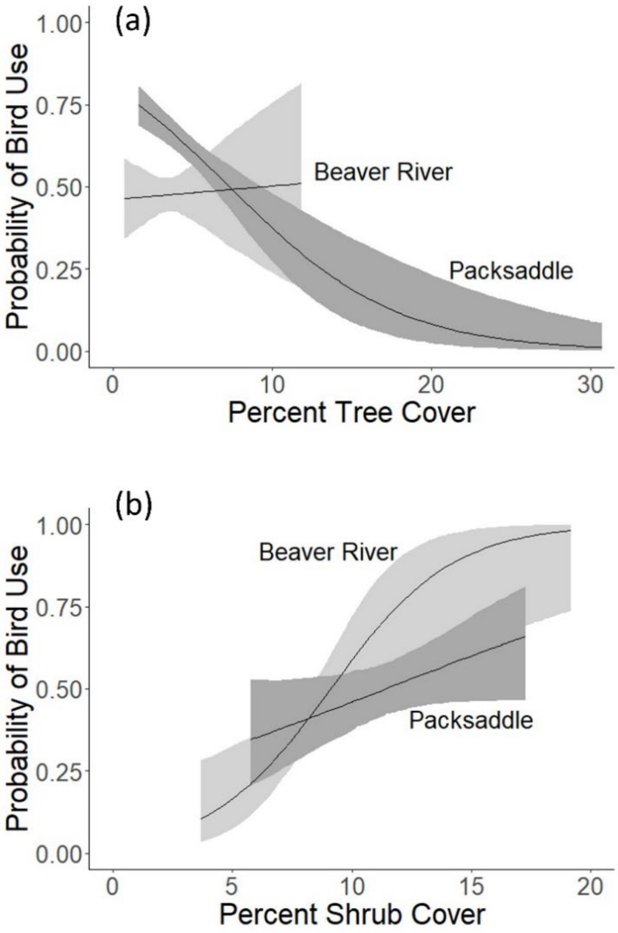

Figure 4.3 Probability of bobwhite resource selection at Packsaddle and Beaver River WMA as a function of (a) percent tree cover, and (b) percent shrub cover. The spatial scale used for each estimation was selected from the top performing model according to AIC.

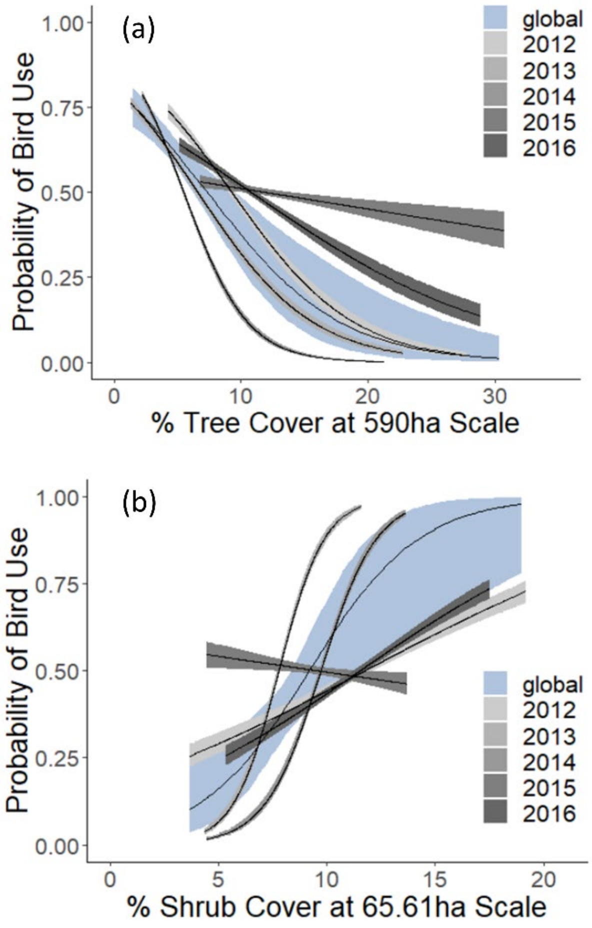

Figure 4.4 Probability of bobwhite resource selection (by year and overall) as a function of (a) percent tree cover at Packsaddle WMA, and (b) percent shrub cover at Beaver River WMA. The spatial scale used for each estimation was selected from the top performing model according to AIC. This figure is to illustrate yearly variation (the spread of random effect groups)—all other inference in this paper refers to the global (averaged) model (blue).

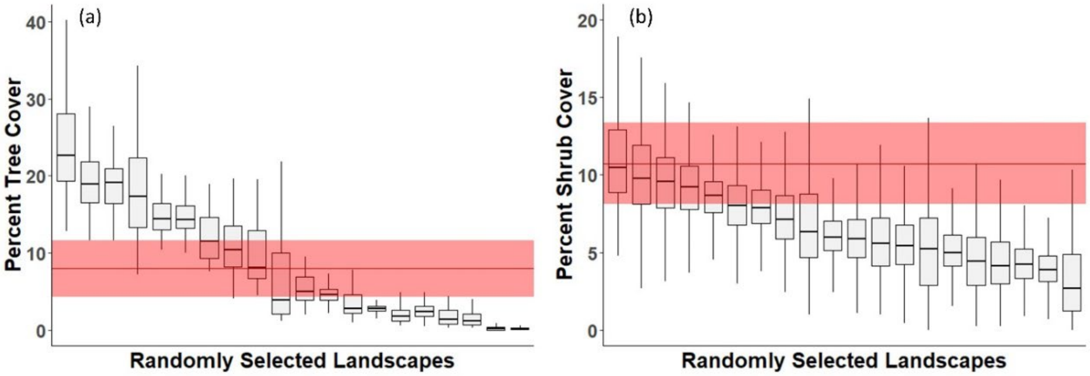

Figure 4.5 Percent woody cover composition of 100 randomly selected, 10km x 10km landscapes in the South-central semi-arid prairies of North America compared with actual bobwhite resource selection. The red ribbon represents mean percent cover (±1 standard deviation) actually used by bobwhite on (a) Packsaddle (trees) or (b) Beaver River (shrubs).

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CHAPTER 4

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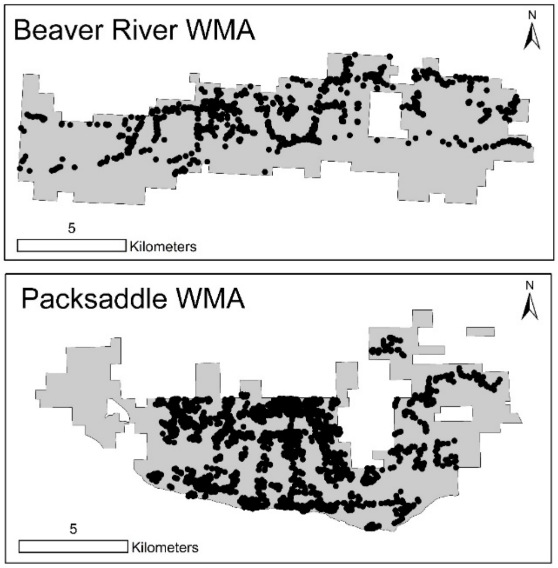
APPENDICES

Appendix 1. Distribution of bobwhite trapping effort at Packsaddle and Beaver River from 2012-2016. Points represent locations where traps were set, not necessarily where birds were caught.



Appendix 2. Pearson's coefficients indicating correlations across spatial scales for three cover types.

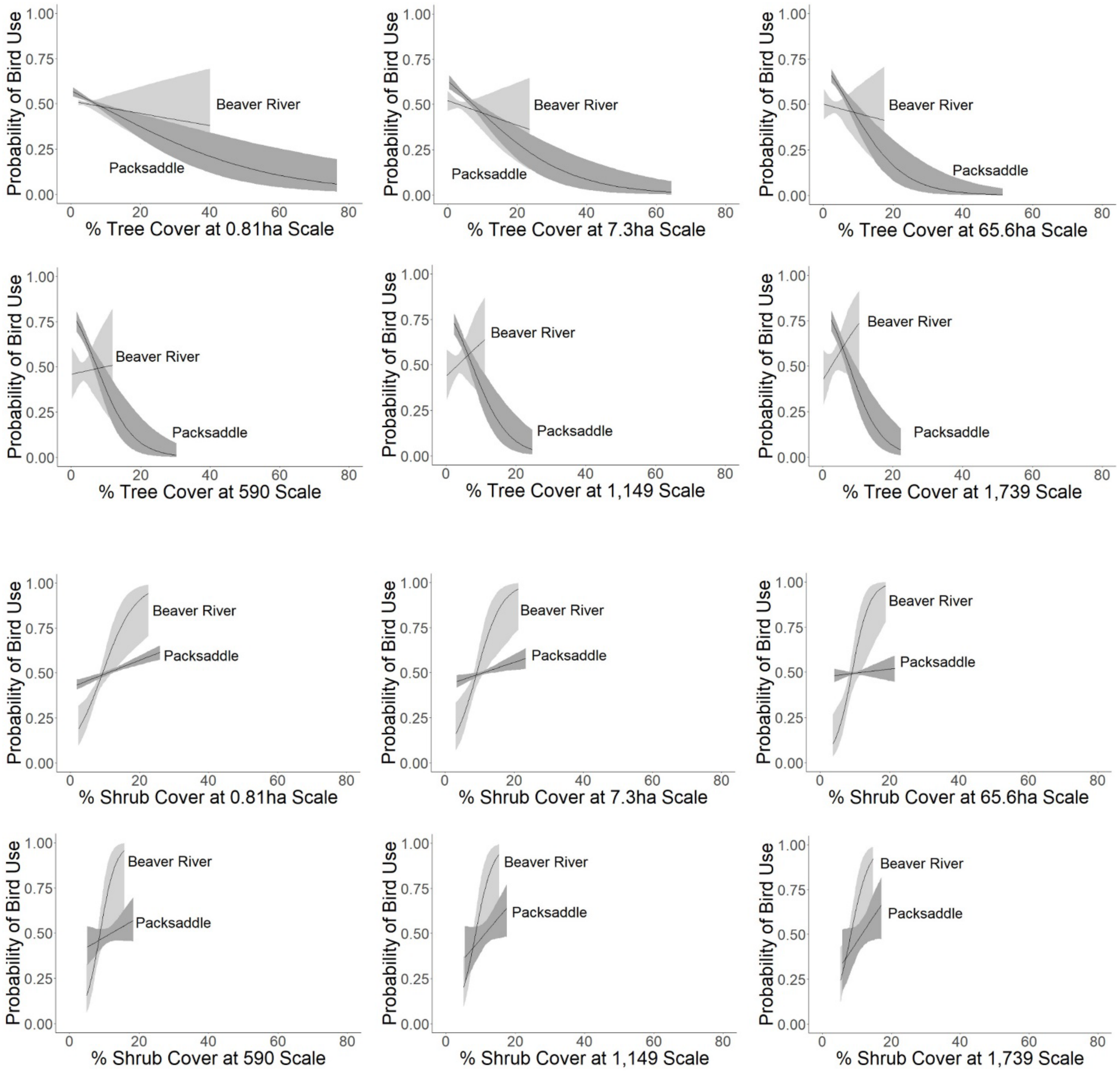
TREE COVER

	7.29ha	**65.61ha**	**590ha**	**1,149ha**	**1,739ha**
0.81ha	0.918	0.798	0.695	0.668	0.657
7.29ha		0.912	0.799	0.768	0.754
65.61ha			0.916	0.882	0.867
590ha				0.988	0.976
1,149ha					0.996

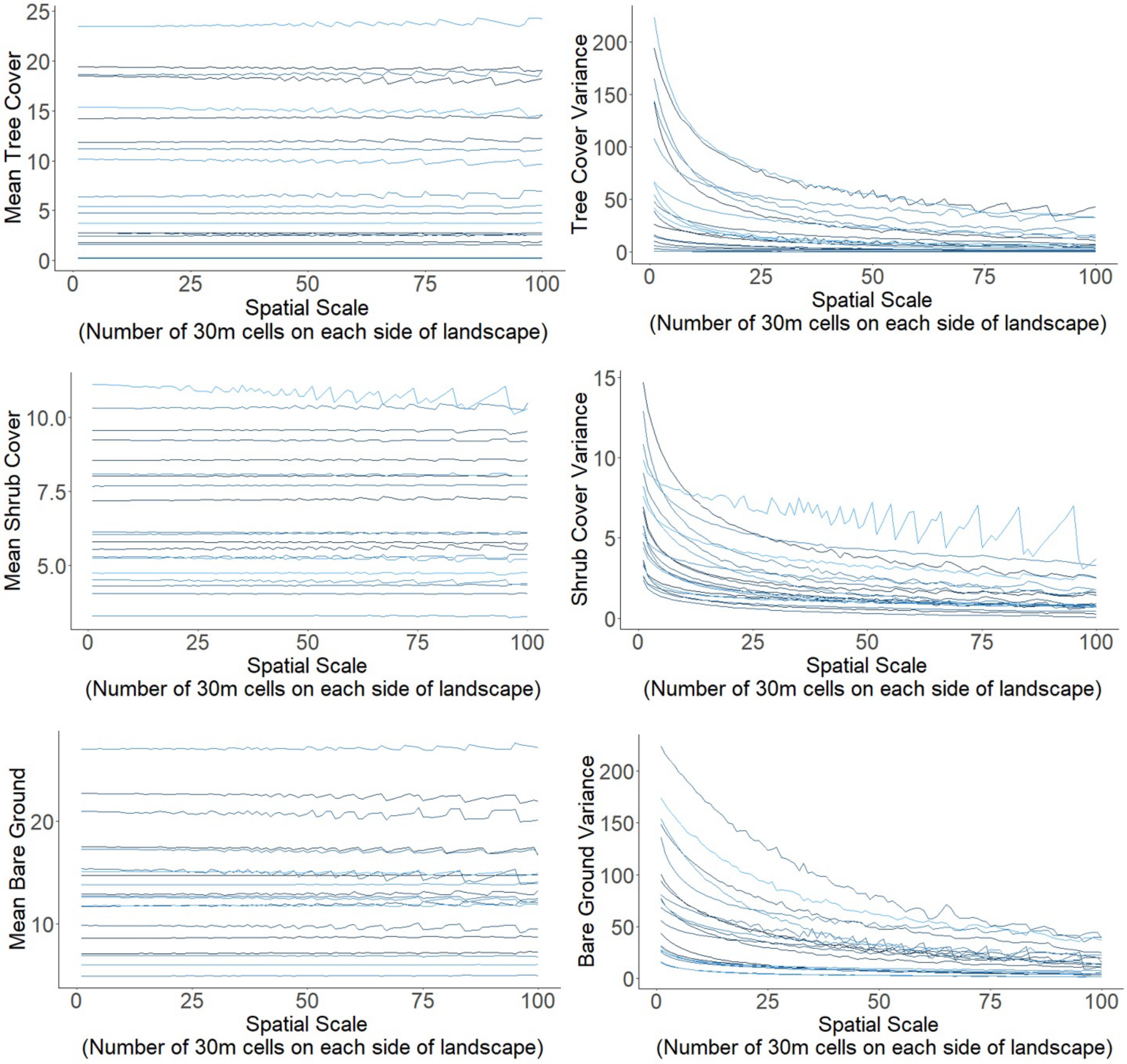
SHRUB COVER

	7.29ha	**65.61ha**	**590ha**	**1,149ha**	**1,739ha**
0.81ha	0.934	0.845	0.762	0.741	0.726
7.29ha		0.936	0.845	0.822	0.805
65.61ha			0.936	0.910	0.893
590ha				0.990	0.976
1,149ha					0.995

Appendix 3. Probability of bobwhite habitat use at Packsaddle and Beaver River WMA as a function of percent tree cover and shrub cover—each across 6 spatial scales.



Appendix 4. Mean percent cover and between-cell variance of percent cover of 3 cover classes within randomly sampled landscapes across 100 spatial grains. Each blue line is a randomly sampled, 10km by 10km landscape in the South-central Semi-arid Prairies.



VITA

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