SPATIOTEMPORAL DYNAMICS OF WILD POPULATIONS IN HUMAN-DOMINATED LANDSCAPES AND AQUASCAPES: MULTIPLE SCALES AND MODES FOR INFERENCE

By

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ABSTRACT

SPATIOTEMPORAL DYNAMICS OF WILD POPULATIONS IN HUMAN-DOMINATED LANDSCAPES AND AQUASCAPES: MULTIPLE SCALES AND MODES FOR INFERENCE

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In this dissertation, I characterize the spatiotemporal dynamics of wild animal populations and communities via literature synthesis and three empirical studies. In Chapter 1, I review how historic foundations of macroecology and the theory of island biogeography inform ecology, restoration, and conservation across in the 21st Century. I conclude that restoration efforts should focus on evaluating and understanding the historical and recent ecological context of areas targeted for restoration, particularly on multiple spatiotemporal scales.

In Chapter 2, I investigate historic dynamics of freshwater fish populations and communities inhabiting Ontario, CAN jurisdictional waters of Lake Huron. I apply a multivariate hierarchical model to relative counts of multiple fish species to estimate fine- and broad-scale effects of environmental and anthropogenic factors associated with species dynamics over time. I conclude that conservation efforts should focus on ecosystem-level governance of Lake Huron fisheries, including expanded ectoparasite control as well as enhanced structural-climatic conditions to maintain stationary water temperatures and nutrient cycling over time.

In Chapter 3, I evaluate historic dynamics of grassland bird populations and communities inhabiting Conservation Reserve Enhancement Program (CREP) lands in eastern Michigan, USA. I apply a multivariate hierarchical model to relative detections and non-detections of multiple species to estimate fine- and broad-scale effects of environmental and anthropogenic factors associated with species occupancy dynamics over time. I conclude that conservation

efforts should focus on increasing the area, frequency, diversity, and distribution of CREP planting practices as well as implement new studies over numerous locations and for extended time periods throughout the Upper Midwest and Great Plains of North America to help ensure the persistence of remnant grasslands and their rarest bird species.

In Chapter 4, I assess how mass-scaling (allometric) relationships can be used to estimate the abundance of wild bird populations across continental North America. I apply a univariate hierarchical model to relative counts of a common forest bird to estimate fine- and broad-scale masseffects of environmental and anthropogenic factors associated with species dynamics over time. I conclude that conservation should focus on expanding the spatiotemporal coverage of banding sites for measuring species body-size characteristics as well as require multiple (geolocated) site visits (e.g., ≥ 3 times per season) in broad-scale monitoring programs, particularly such that allometric-scaling relationships may be better evaluated with hierarchical models investigating indices of species abundance and occupancy status.

I conclude this dissertation with a discussion of the major findings, lessons learned, and implications and recommendations for future population and community research in ecology. Future studies that critically investigate ecological phenomena at various scales, including explicit accounts for ecological data hierarchies, will likely be most useful for separating statistical signal from noise and identifying the scales at which phenomena manifest. Such research will improve basic theory as well as help facilitate improved conservation of biodiversity via increasingly more certain descriptions of ecological patterns and processes, including the scales at which each can be influenced or managed.

Co-dedicated to the love of my life, Amanda Catherine, and to our loving and supportive families, the Dennhardts and Dolinskis, as well as to the beloved memory and legacy of Brian Alan Maurer; rest in peace and power, my friend.

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I also thank staff of the Center for Statistical Training and Consulting for additional training, mentorship, collegiality, friendship, and financial support over the years, including B. Maurer, M. Huebner, S. Pierce, S. Hession, D. Sharma, W. Ma, F. Lawrence, J. Villarreal, K. Hull, H. Akaeze, C. Banerjee, D. Pak, B. Tong, N. Jess, T. Le, S. Wang, S. Jantre, and B. Hui, among many others. I also thank R. Moll, R. Cain, and V. Frans whose abundant generosity in lending their expertise, as well as technological resources and spiritual and emotional support, is sincerely cherished. Without the kindness and guidance of all of the aforementioned individuals and organizations, among numerous others, this dissertation could not have been completed successfully. I am also grateful for undergraduate mentoring opportunities provided by D. Hayes, A. Boike and D. Heit. I also thank colleagues of the Applied Forest and Wildlife Ecology Laboratory at Michigan State University: E. Clark, T. Dokes, S. Sultaire, S. Gray, M. Starking, T. Melvin, E. Raifsnider, A. Baier, J. Gregorini, B. Silet, T. Brockman, J. Sterman, A. Archer, and G. Knowlton whose valued suggestions for improving the seminars, reports, manuscripts, and conduct of research borne out of this dissertation is truly respected and appreciated.

PREFACE

Excluding the introductory and concluding chapters, the chapters comprising the main body of this dissertation are written using the first plural pronoun “we” to recognize the individual, pertinent contributions of every co-author, colleague, and committee member involved throughout each project’s formulation. Multi-author lists are provided for Chapters 1, 2, and 3, noting shared contributions, and all other chapters were authored by A. Dennhardt. Research was conducted by A. Dennhardt under the primary direction of G. Roloff (2017-2021) and the late B. Maurer (2014-2017) while graduate committee members K. Cheruvelil, P. Zarnetske, and E. Zipkin provided secondary direction and advisement on the scientific methodology, coursework, content, writing, and examinations associated with the projects and degree program.

In addition, one of the four main chapters of this dissertation has been published in a peer-reviewed book with multiple co-authors. With written permission from Island Press (cf. Reference 21-014), the first chapter of this dissertation has been reprinted from Dennhardt et al. (2016). Specifically, we include the original unmodified article as a comprehensive literature review for the three empirical studies that follow it. Also, a figure in the fourth main chapter of this dissertation has been produced and published by an independent team of researchers. With written permission from the Cornell Lab of Ornithology (cf. Data Licensing Agreement), Figure 4.5 has been reprinted from Fink et al. (2020). Specifically, we include the original unmodified figure for comparison with population abundance estimates generated in the fourth chapter of this dissertation.

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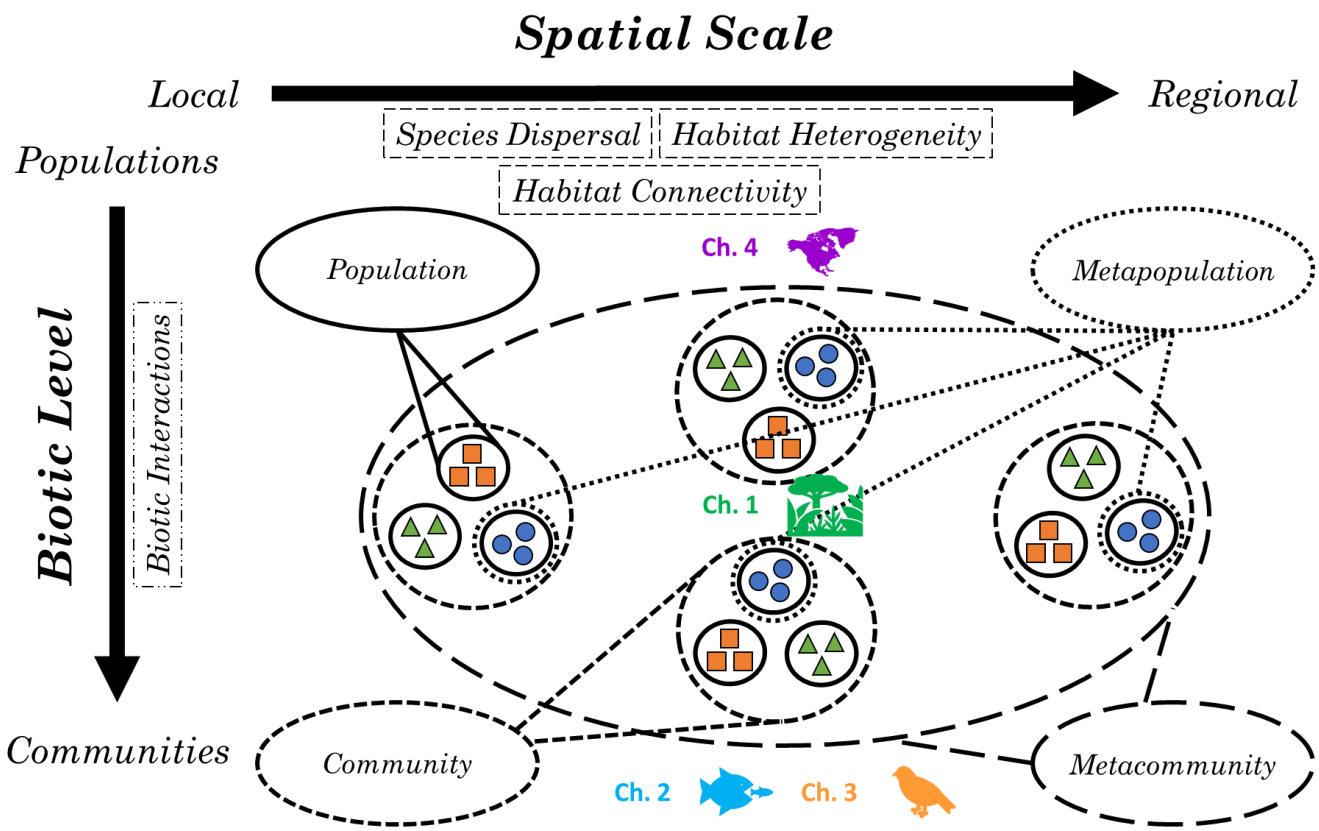
INTRODUCTION

Ecological patterns and processes are inherently hierarchical, continuously varying in space and time. While tiered and spatiotemporally variable in structure, ecological patterns and processes (e.g., species distributions, co-occurrence, and interference competition) are described at singular or multiple dimensions and scales in ecology. For instance, fundamental models describe inter-species' dynamics at the level of ecological populations without consideration for peripheral associations in space or time (e.g., Lotka and Volterra's predator-prey models; Volterra 1926, Lotka 1927, Volterra 1927, Wangersky 1978). In contrast, contemporary models describe intra- and inter-species' dynamics at the levels of populations or communities while accounting for space, time, or both (e.g., univariate/multivariate state-space models; Kéry and Schaub 2011, Royle and Dorazio 2008, Kéry and Royle 2016, 2021). Describing dynamics of wildlife at one level of hierarchical organization or spatiotemporal dimension limits inferences to cause, association, or mechanism in ecology. However, incorporating multiple hierarchical levels and spatiotemporal dimensions into modeling and management decisions is often limited by data acquisition, funding limitations, and lack of established theory.

In spite of such limitations, modern ecology is increasingly data rich (Luo et al. 2011, Soranno and Schimel 2014, Elliott et al. 2016) yet global biodiversity continues to decline at an accelerated rate (Newbold et al. 2016, Dinerstein et al. 2020, Mori 2020, Schmeller et al. 2020). In response, modern ecologists must leverage "Big Data" to address difficult conservation problems informed by inter-connected (hierarchical) conceptualizations of ecological systems. Several key knowledge gaps exist in hierarchical ecology today, including: (1) unique contributions of macro-scale perspectives toward enhancing ecological restoration efforts, (2)

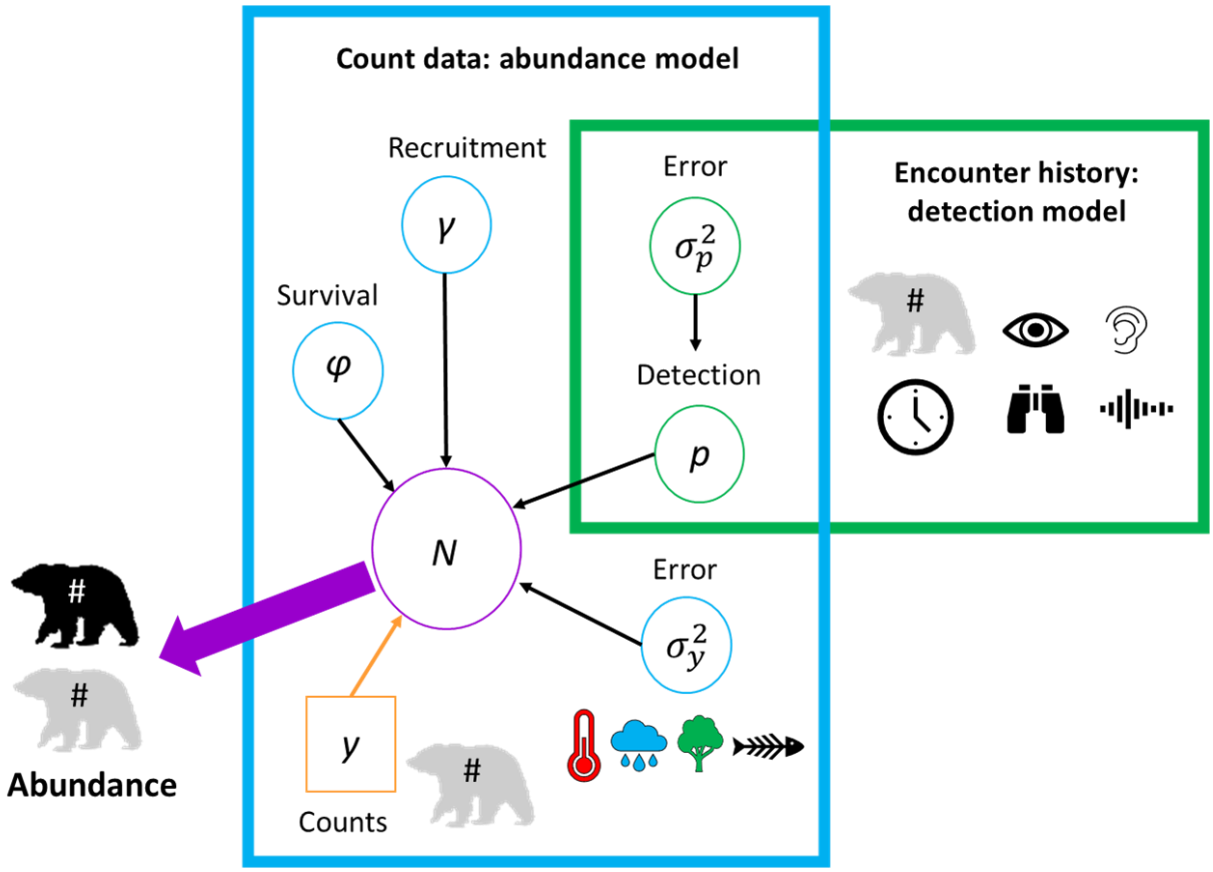
multi-species community change in environments degraded well beyond historical states (e.g., freshwater lake and grassland systems), and (3) single-species (range-wide) population change and its association with (non-traditional) allometric-scaling and (traditional) ecological covariates—all of which are informed by data collected on broad spatiotemporal scales. My dissertation addresses each of these knowledge gaps using literature review and synthesis of macro-scale perspectives for ecological restoration (Chapter 1) as well as two empirical studies of aquatic (Chapter 2) and terrestrial (Chapter 3) community-level systems and one empirical study of a terrestrial (Chapter 4) population-level system in North America (Figure 0.1). Improved conservation and enhanced understanding of key knowledge gaps informed by research describing ecological hierarchies also requires comprehensive investigations of latent states.

Figure 0.1. Conceptual diagram describing several foci of my dissertation. Ecological hierarchies are investigated based on studies of single-species populations (i.e., species demography) and metapopulations (i.e., species population dynamics across multiple locations connected via dispersal) or multi-species community (i.e., ecological assembly) and metacommunities (i.e., multi-species community dynamics across multiple locations connected via dispersal). Studies vary (x-axis) from local to regional (or broader) spatial scales, influenced by species dispersal and habitat heterogeneity and connectivity. Studies also vary (y-axis) from populations to communities in terms of biological organization level, influenced by interactions between biota. Dissertation chapter icons (i.e., images of each study system) are denoted in different (unrelated) colors along the y-axis, and icon positions indicate the level(s) of organization studied. While chapter icons reside around the center of the x-axis, study spatial scale(s) varied from fine to broad scales in each chapter. Three example species are denoted by unique shape and color. This diagram is modeled after conceptual foundations presented in Chase et al. (2020).



Between and within levels of hierarchical organization and spatiotemporal scales, ecological patterns and processes can be hidden or partially observed. Hidden to observers is the latency (or unobservability) of true ecological states, which are governed by deterministic and stochastic processes that shape the dynamics of species and their populations, communities, and environments in space and time (Kéry and Schaub 2011, Royle and Dorazio 2008, Kéry and Royle 2016, 2021). Example observable indicators of latent ecological states include species relative movements (e.g., tracked locations), relative abundance (e.g., counts) and relative occupancy (e.g., detections and non-detections), and typical latent states include species movement behavior (Patterson et al. 2008), population abundance (Royle 2004, Dail and Madsen 2011), and occupancy rates (MacKenzie et al. 2002, Rota et al. 2016). Latent ecological states are statistically estimated using probability distributions (e.g., binomial and Bernoulli processes, among others) in hierarchical state-space models (Figure 0.2), and estimates of latent states are further adjusted by effects of important covariates and nuisance parameters to help account for sampling and measurement error (e.g., how available and detectable species are to observers; MacKenzie et al. 2002, Kellner and Swihart 2014).

Figure 0.2. Example hierarchical state-space model of the multi-season abundance of a brown bear (*Ursus arctos*) population in North America, comprising a hypothetical exercise. Brown bears available for detection are either detected (black) or not detected (gray), where species-level observations (i.e., hierarchical level 1) comprise repeated counts, y, of unmarked individuals at multiple spatial locations (i.e., hierarchical level 2) over time. While variables and parameters exclude indices for space and time, this simplified diagram follows the form of a dynamic *N*-mixture model (Dail and Madsen 2011), where the ecological (abundance) model and its parameters are outlined in blue, and the observation (detection) model and its parameters are outlined in green. At level 1 of the data hierarchy, detection probability, p, and its error variance, σ_p^2, are estimated using predictors related to time- and method-of-detection variables hypothesized to influence location- and survey-level detection and non-detection records—predictors indicated by multiple icons (e.g., visual detection and identification using binoculars). At level 2 of the data hierarchy, derived population abundance, N, (i.e., adjusted by detection probability and inter-season bear survival, φ, and recruitment, γ, rates in space and time) and its error variance, σ_y^2, are estimated using predictors related to environmental resources and conditions hypothesized to influence location-level abundance—predictors indicated by multiple icons (e.g., prey fish quality or quantity). Hypothesized predictors per level of the data hierarchy are used to explain variation and account for spatiotemporal autocorrelation in bear counts, and such uncertainties are typically evaluated *post hoc* in hierarchical state-space models.



Importantly, human observers may make errors by falsely detecting or non-detecting species, termed false positive and negative rates, respectively—rates that bias resultant inference about latent states (Manel et al. 2001, Royle and Link 2006, Chambert et al. 2015, Guillera-Arroita et al. 2017). Additionally, estimation errors occur due to inherent relatedness between observed variables in space and time (e.g., due to ecological associations or survey-design artifacts), termed spatiotemporal autocorrelation (Cressie 1993, Cressie and Wikle 2011). Spatiotemporal autocorrelation is also important to account for in ecological models, particularly because it impacts precision around estimated parameters of interest. Taken together, latent states of ecological organization (i.e., things humans manage to conserve) are thus estimated from observable indicators of states based on probabilistic statistical models, important error rates, and inherent relatedness between observations.

Overall, my dissertation's primary knowledge gap involves accurately identifying appropriate hierarchical levels and spatiotemporal scales necessary to sufficiently characterize latent ecological states, including essential factors that influence them. Beyond example models, error rates, and relatedness between observations, explorations of latent states are further informed by seminal theories about species organization and distribution, including special recognition of resources and conditions essential to species survival, reproduction, and persistence. In this dissertation, I apply principles from island biogeography (MacArthur and Wilson 1963, 1967), metapopulation (Levins 1970, Hanski 1998a, b, 1999), and metacommunity theory (Leibold et al. 2004, Holyoak et al. 2005) to improve understanding of patterns for aquatic and terrestrial species population and community dynamics in space and time. Macroecology originated to help explain broad-scale patterns in the distribution, abundance, and body size among species inhabiting continents (Brown and Maurer 1987, 1989), and macroecology itself

was preceded by the equilibrium theory of island biogeography, which was the first ecological model to describe how biodiversity in dispersal-connected populations, communities, and systems changes with island area and isolation distance from mainland continents (MacArthur and Wilson 1963, 1967). While macroecological patterns manifest in research leveraging broad-scale data, such patterns can be difficult to fully explain with hypothesized process-relevant covariates (Brown 1995, Brown and Lomolino 1998, Maurer 2012, Gaston and Blackburn 2000). However, concepts such as the species-area relationship (Arrhenius 1921, Preston 1962, MacArthur and Wilson 1963, 1967, Rosenzweig 1995) and the unified neutral theory of biodiversity (Hubbell 2001, 2005, 2006) can be leveraged to help understand species diversity dynamics with changing ecosystem size, actors, resources, and conditions (e.g., studying isolated habitats as "islands" in human-dominated landscapes and aquascapes).

Conceptualizing ecological systems as islands or "stepping stones for biotic exchange" later led to development of metapopulation and metacommunity theories, which describe the maintenance and organization of ecological populations and communities occupying "species habitat islands" connected by dispersal and constrained by habitat size, structure, and configuration with respect to other habitable and inhospitable areas (Levins 1970, Hanski 1998a, b, 1999, Leibold et al. 2004, Holyoak et al. 2005). Macroecological concepts such as biogeography, metapopulations, and metacommunities regularly assume that (a) species are able to disperse to and from connected habitat patches (i.e., immigrate and emigrate), (b) distance, area, and isolation of habitat patches (and the permeability of non-habitat, called matrix) differentially impact species dispersal and persistence, (c) biotic/abiotic factors differentially influence species persistence (e.g., at varied scales or dimensions), and (d) common statistical properties may govern species assemblages and distributions from fine to broad scales. This thus

indicates that there are several important considerations for reliably characterizing ecological phenomena; namely, (1) to choose the hierarchical level(s) of ecological organization for inquiry, (2) to define the spatial, temporal, or spatiotemporal scale(s) of relevance to study species and systems, (3) to identify variable scales and dimensions in which target ecological phenomena manifest, and (4) to quantify biotic/abiotic variables at the spatiotemporal scale(s) that influence ecological phenomena of interest. These considerations are necessary such that *a priori* model hypotheses as well as research questions and objectives may be tested, answered, and achieved toward improvement of existing scientific knowledge.

In this dissertation, I quantify the hierarchical and spatiotemporal processes driving several wild animal populations and communities in North American landscapes and aquascapes. In Chapter 1, I review and synthesize literature from macroecology to illustrate how broad-scale concepts can enhance modern ecological restoration and species conservation globally. In Chapter 2, I present an empirical study of freshwater fish communities, in which I apply multi-species (hierarchical) dynamic factor analysis to estimate species abundance and associations with variables summarized at multiple locations and scales across the Canadian jurisdictional waters of Lake Huron. In Chapter 3, I present an empirical study of grassland bird communities, in which I apply multi-species (hierarchical) occupancy models to estimate species occupancy and associations with environmental variables summarized at multiple locations and scales across Conservation Reserve Enhancement Program lands in southeastern Michigan, USA. In Chapter 4, I present an empirical study of a common forest bird species, in which I apply single-species (hierarchical) dynamic *N*-mixture models to estimate abundance of the red-eyed vireo (*Vireo olivaceus*) using mass-abundance (allometric) scaling relationships as well as variables summarized at multiple locations and scales across the North American Breeding Bird Survey.

Finally, I conclude this dissertation with a summary and discussion of lessons learned as well as implications and recommendations for future research toward leveraging broad-scale data in hierarchical state-space models to enhance understanding of population and community ecology in the Anthropcene.

REFERENCES

REFERENCES

Arrhenius, O. 1921. Species and area. *Journal of Ecology* 9:95-99.

Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago, IL, USA.

Brown, J. H. and B. A. Maurer. 1987. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. *American Naturalist* 130:1-17.

Brown, J. H. and B. A. Maurer. 1989. Macroecology: the division of food and space among species on continents. *Science* 243:1145-1150.

Brown, J. H. and M. V. Lomolino. 1998. Biogeography. Sinauer Associates, Sunderland, MA, USA.

Chambert, T., D. A. Miller, and J. D. Nichols. 2015. Modeling false positive detections in species occurrence data under different study designs. *Ecology* 96:332-339.

Chase, J. M., A. Jeliazkov, E. Ladouceur, and D. S. Viana. 2020. Biodiversity conservation through the lens of metacommunity ecology. *Annals of the New York Academy of Sciences* 1469:86-104.

Cressie, N. A. C. 1993. Statistics for Spatial Data. John Wiley and Sons, Inc., New York, NY, USA.

Cressie, N. and C. Wikle. 2011. Statistics for Spatio-temporal Data. John Wiley and Sons, Inc., New York, NY, USA.

Dail, D. and L. Madsen. 2011. Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics* 67:577-587.

Dinerstein, E., A. R. Joshi, C. Vynne, A. T. L. Lee, F. Pharand-Deschênes, M. França, S. Fernando, et al. 2020. A “Global Safety Net” to reverse biodiversity loss and stabilize Earth’s climate. *Science Advances* 6:eabb2824.

Elliott, K. C., K. S. Cheruvelil, G. M. Montgomery, and P. A. Soranno. 2016. Conceptions of good science in our data-rich world. *BioScience* 66:880-889.

Gaston, K. J. and T. M. Blackburn. 2000. Pattern and Process in Macroecology. Oxford-Blackwell Science, Malden, MA, USA.

Guillera-Arroita, G., J. J. Lahoz-Monfort, A. R. van Rooyen, A. R. Weeks, and R. Tingley. 2017. Dealing with false-positive and false-negative errors about species occurrence at multiple levels. *Methods in Ecology and Evolution* 8:1081-1091.

Hanski, I. 1998a. Connecting the parameters of local extinction and metapopulation dynamics. *Oikos* 83:390-396.

Hanski, I. 1998b. Metapopulation dynamics. *Nature* 396:41-49.

Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos* 87:209-219.

Holyoak, M., M. A. Leibold, N. M. Mouquet, R. D. Holt, and M. F. Hoopes. 2005. Metacommuninites: a framework for large-scale community ecology. Pages 1-31 *in* Metacommunities: Spatial Dynamics and Ecological Communities, M. Holyoak, M. A. Leibold, and R. D. Holt (Eds.). University of Chicago Press, Chicago, IL, USA.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Monographs in Population Biology, Volume 32. Princeton University Press, Princeton, NJ, USA.

Hubbell, S. P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology* 19:166-172.

Hubbell, S. P. 2006. Neutral theory and the evolution of ecological equivalence. *Ecology* 87:1387-1398.

Kellner, K. F. and R. K. Swihart. 2014. Accounting for imperfect detection in ecology: a quantitative review. *PLoS One* 9:e111436.

Kéry, M. and J. A. Royle. 2016. Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance, and Species Richness in R and BUGS, Volume 1: Prelude and Static Models. Academic Press, Cambridge, MA, USA.

Kéry, M. and J. A. Royle. 2021. Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance, and Species Richness in R and BUGS, Volume 2: Dynamic and Advanced Models. Academic Press, Cambridge, MA, USA.

Kéry, M. and M. Schaub. 2011. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Cambridge, MA, USA.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601-613.

Levins, R. 1970. Extinction. *In* Some Mathematical Questions in Biology, M. Gerstenhaber (Ed.). American Mathematical Society, Providence, RI, USA.

Lotka, A. J. 1927. Fluctuations in the abundance of a species considered mathematically. *Nature* 119:12.

Luo, Y., K. Ogle, C. Tucker, S. Fei, C. Gao, S. LaDeau, J. S. Clark, et al. 2011. Ecological forecasting and data assimilation in a data-rich era. *Ecological Applications* 21:1429-1442.

MacArthur, R. H. and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373-387.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Monographs in Population Biology, Volume 1. Princeton University Press, Princeton, NJ, USA.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.

Manel, S., H. C. Williams, and S. J. Ormerod. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* 38:921-931.

Maurer, B. A. 2012. Continental scale patterns. Pages 152-155 *in* Encyclopedia of Theoretical Ecology, A. Hastings and L. J. Gross (Eds.). University of California Press, Berkeley, CA, USA.

Mori, A. S. 2020. Advancing nature-based approaches to address the biodiversity and climate emergency. *Ecology Letters* 23:1729-1732.

Newbold, T., L. N. Hudson, A. P. Arnell, S. Contu, A. De Palma, S. Ferrier, S. L. L. Hill, et al. 2016. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science* 353:288-291.

Patterson, T. A., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos. 2008. State-space models of individual animal movement. *Trends in Ecology and Evolution* 23:87-94.

Preston, F. W. 1962. The canonical distribution of commonness and rarity: Part I. *Ecology* 43:185-215.

Rosenzweig, M. L. 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge, MA, USA.

Rota, C. T., M. A.,Ferreira, R. W. Kays, T. D. Forrester, E. L. Kalies, W. J. McShea, A. W. Parsons, et al. 2016. A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution* 7:1164-1173.

Royle, J. A. 2004. *N*-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60:108-115.

Royle, J. A. and R. M. Dorazio. 2008. Hiearchical Modeling and Inference in Ecology. Academic Press, Cambridge, MA, USA.

Royle, J. A. and W. A. Link. 2006. Generalized site occupancy models allowing for false positive and false negative errors. *Ecology* 87:835-841.

Schmeller, D. S., F. Courchamp, and G. Killeen. 2020. Biodiversity loss, emerging pathogens and human health risks. *Biodiversity and Conservation* 29:3095-3102.

Soranno, P. A. and D. S. Schimel. 2014. Macrosystems ecology: big data, big ecology. *Frontiers in Ecology and the Environment* 12:3-3.

Volterra, V. 1926. Variations and fluctuations of the number of individuals in animal species living together. *Memoirs of the Royal National Academy of Lincei* 6:31-113.

Volterra, V. 1927. Fluctuations in the abundance of a species considered mathematically. *Nature* 119:12-13.

Wangersky, P. J. 1978. Lotka-Volterra population models. *Annual Review of Ecology and Systematics* 9:189-218.

CHAPTER 1: MACROECOLOGY AND THE THEORY OF ISLAND BIOGEOGRAPHY: ABUNDANT UTILITY FOR APPLICATIONS IN RESTORATION ECOLOGY

Dennhardt, A. J., M. E. K. Evans, A. Dechner, L. E. F. Hunt, and B. A. Maurer. 2016. Macroecology and the theory of island biogeography: abundant utility for applications in restoration ecology. Pages 455-483 *in* Foundations of Restoration Ecology, Second Edition, M. A. Palmer, J. B. Zedler, and D. A. Falk (Eds.).

Theory and Application

• Ecological systems are dynamic, which poses a number of challenges to restoration efforts because ecosystems can change at multiple spatiotemporal scales.

• With respect to practical application, an ecological restoration project must take into account issues regarding the size, macrogeographic composition, and connectedness of the system being restored.

• When restoring biota to locations in degraded landscapes, the ecosystem may depend on both the quality and quantity of colonists it receives from beyond its borders.

• Through explicit assessment of species' assemblages on broad scales, macroecology promotes insight into the structure of biodiversity and influences the success or failure of restoration efforts.

Restoration ecologists are tasked with the challenge of returning an ecological system to a configuration that approximates its natural state (Hobbs and Norton 1996, 2001). Restoring any altered ecosystem comprises a sizeable challenge in that it is critical to determine the appropriate target for restoration (Palmer et al. 2016), especially prior to disturbances such as novel anthropogenic impacts as well as the relevant scales thereof. Determining the target for restoration involves four main considerations: (1) the "natural" state of the system might include

pre-European human influences (e.g., widespread colonialism); (2) change is normal in ecological systems (i.e., systems exhibit a historical range of variation in disturbance regimes and species composition); (3) some system changes are completely irreversible (e.g., legacy effects), or nearly so (e.g., ecological tipping points); and (4) stochasticity plays a crucial role in shaping ecosystem state (Jackson and Hobbs 2009). Moreover, some historically important steady states may not be attainable because of legacy effects such as the emergence of novel configurations and the spread of invasive species (e.g., establishing new biotic interactions and ecosystems; Hobbs et al. 2014), prevalence of historical contingencies (e.g., immigration of despotic breeders to isolated populations; Hedrick et al. 2014), or altered boundary constraints (e.g., climatic thresholds such as critical thermal maxima; Lee and Rinne 1980). Nevertheless, historical knowledge of ecosystems may still play a critical role in the success of future restoration efforts in the face of modern-day ecological novelties (Higgs et al. 2014).

Ecosystems are dynamic and constantly in flux, which poses a number of difficulties to restoration efforts because ecosystems can change at a variety of spatiotemporal scales (Jackson and Hobbs 2009; Jackson 2012). Multiscale ecosystem dynamics (Suding et al. 2016) make it challenging to define the natural conditions that existed prior to novel disturbance of the system. Furthermore, various biotic processes within ecological systems may change at different rates in space and time. For instance, some population-level processes (e.g., immigration) operate at very different scales than processes associated with the geophysical template of the ecosystem (Heffernan et al. 2014). At the root of the aforementioned difficulties is the realization that multiple biotic components (e.g., species with respect to composition) and abiotic processes (e.g., fire, with respect to disturbance) of the original ecosystem may be significantly altered or even entirely absent at present, and thus unavailable to the restored system. Counter to this is the

notion that some abiotic and biotic processes may, in fact, be restored to the degraded system; however, to what degree can such processes be restored? It is likely that some impaired processes may never be fully restored. As a consequence of imperfect restoration, the resultant configuration and functional organization of "restored" systems is often attenuated and inadequate to sustain basic ecosystem functions and biodiversity over time (Hooper et al. 2012).

Another difficulty in defining natural system states is that many ecological communities (e.g., tallgrass prairie in central North America) likely occupied larger spatial extents than are presently available to the system designated for restoration. This implies that the current abiotic and biotic context within which the restored system must function may be very different from that of the historic context— which largely depended on ecosystem size and other relevant scales. Although there are many challenges to ecological restoration, the approaches to meet those challenges are also abundant. However, this only begs the question: are the scales and perspectives employed in restoration ecology adequate to meet the challenges of system restoration within complex, evolving contexts?

To answer this question, we begin by considering how ecosystem size affects ecological processes—considerations informed by advancements in ecological theory. Building upon reflections on system size and intrinsic processes, we then discuss the importance of scale in restoring ecological systems and ultimately propose a macroscale perspective for restoration efforts. We then outline four areas of rapid development in macroecology that offer important tools and insights to restoration ecologists: species distribution models, species-area relationships, metapopulation models, and neutral theory. Finally, we conclude this chapter with a discussion of its central themes—considerations of which may lead to improved ecological restoration efforts in the future.

System Size, Ecological Processes, and Theoretical Foundations

Biological systems of all kinds vary functionally with size (Brown and West 2000). It is fairly straightforward to understand the consequences of size variation when examining the properties of individual organisms or groups thereof. As biotic systems grow in size, physiological processes often change in a nonlinear fashion as a consequence of the fractal nature of organismal structure (West et al. 1999). These changes can have a number of profound implications for the structure of communities and ecosystems (Enquist et al. 1999a, b). For example, although much is known about organismal scaling, less is known about the way that populations, communities, and ecosystem functions change with system size (Enquist et al. 2003). The first model to address this problem was the equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967). In subsequent decades, the field of macroecology emerged as a paradigm for evaluating how spatial and temporal processes on macroscales affect the maintenance of species diversity and organization (Brown and Maurer 1987, 1989; Brown 1995; Gaston and Blackburn 2000).

Macroecology began as an attempt to explain patterns in geographical distribution, abundance, and body size among species inhabiting continents (Brown and Maurer 1987, 1989). However, it became evident that mechanistic explanations for such patterns required an expansion of perspective from focus on local ecological processes at smaller scales (e.g., individuals, populations, and ecosystems) to larger continental-scale processes (e.g., species' range distributions; Brown 1995; Maurer 2012; Gaston and Blackburn 2000). These insights were reinforced by advances in other fields, including studies of species diversity (Rosenzweig 1995), community ecology (Ricklefs and Schluter 1993), biogeochemistry (Schlesinger 1997), global ecology (Kareiva et al. 1993), and biogeography (Brown and Lomolino 1998; Hubbell

2001). Essentially, ecologists found that it was necessary to expand the spatiotemporal scales at which they viewed ecological systems in order to understand what processes were important in determining patterns in distribution, abundance, ecosystem function, and species diversity. Today, macroecology continues to enhance the present understanding of biodiversity conservation and management as well as ecological restoration, as we explore below.

By examining the properties of continental-scale species assemblages, macroecology provides the empirical basis for developing insights into the structure of biodiversity and how that organization influences the success or failure of ecological restoration efforts. Because of its focus on large-scale processes, macroecology explicitly assumes that the spatiotemporal scales of ecological systems extend far beyond political, geographical, and functional boundaries within which these systems are often managed. In this chapter, we examine the implications of a macroscale perspective for biodiversity conservation and management based on tools for ecological restoration.

Macroecology provides a benchmark for understanding the context within which ecological restoration efforts must operate as well as the limitations that are imposed by restricting the extent of restoration efforts because of mechanisms operating across scales. For example, macroecological systems (i.e., called macrosystems) consist of complexly interacting biological, geophysical, and sociocultural mechanisms that exhibit variation on spatiotemporal scales relevant to regions and continents such that system-wide restoration efforts now require much broader considerations than ever before (Heffernan et al. 2014; Soranno et al. 2014). Recent conceptual advances of direct relevance to ecological restoration include cross-scale interactions (i.e., how processes at one scale interact with processes at another scale; Soranno et al. 2014) and cross-scale emergence (i.e., how components at local scales interact and

accumulate across scales; Peters et al. 2007). Although the importance of scale across general ecological studies is duly noted historically, one of the major questions currently confronting macroecology is the functional extent(s) to which various macroscale patterns exert controls on species' distributions (see also Metzger and Brancalion 2016 on spatial context). This knowledge gap is a central consideration in restoration ecology, and cumulative results from recent work in macroecology may shed light on how macrogeographic characteristics shape species' distributions.

Focal Areas of Current Research in Macroecology

We now outline four areas of active research in macroecology that may offer valuable insights to ecological restoration efforts.

Species distribution models: macrogeographic controls and realized distributions

Macroecology integrates macrogeographic patterns and processes into explanations of local and continental dynamics that control species' distributions (Kerr et al. 2007; Mokany et al. 2012). For restoration ecology, there are numerous distribution-shaping processes that warrant greater consideration in the development and improvement of new and ongoing restoration efforts. First, understanding how conditions and resources (e.g., the multidimensional niche; Hutchinson 1957, 1965) shape species' distributions is crucial to the success of ecological restoration projects, for they represent boundary constraints for species—constraints mediated via macroevolutionary adaptations (Parnell and Streelman 2010). Examples of distributional constraints include species-specific climatic thresholds (e.g., critical temperatures; Lee and Rinne 1980), changing landscape pattern (e.g., patch-matrix composition and configuration; Koh and Ghazoul 2010; Kennedy et al. 2011), and density-mediated processes (e.g., availability and quality of breeding habitat as well as intra- and interspecific competition for space, mates, and resources). Here, we describe

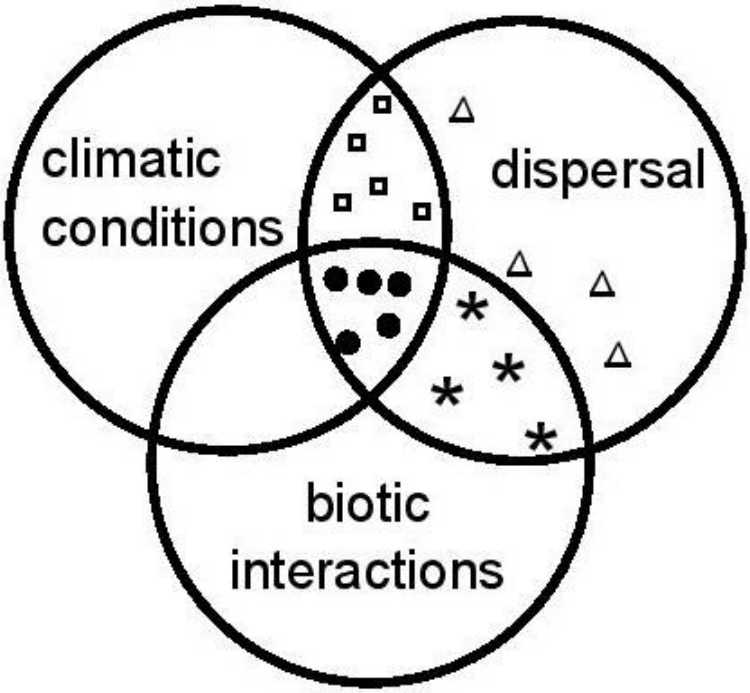
these distribution-shaping factors both in theory and in practice for modeling geographic distributions.

Hutchinson's concept of the niche as an "n-dimensional hypervolume" of conditions and resources rests at the foundation of niche-distribution theory (Naeem 2016), and the concept has shaped how ecologists have viewed species' distributions for decades (Hutchinson 1957, 1965; Blonder et al. 2014; Swanson et al. 2015). In terms of organismal distribution, the fundamental niche comprises the complete range of resources and environmental conditions a species can use and occupy. Recent decades have witnessed an explosion of efforts aimed at modeling species' distributions with what are termed bioclimatic envelope models, or species distribution models, wherein species' occurrence data are predicted solely as a function of climatic variables (Hampe 2004; Araújo and Peterson 2012; Falk and Millar 2016). While there is no reason, in theory, that other factors could not be included as covariates (e.g., density of competitors or mutualists, time since disturbance, land use classes, etc.), in practice, climate data are the most readily available sources of information for prediction. This contributes to the impression that bioclimatic envelope models estimate climatic boundary constraints for species' ranges on geographic scales. However, models fit to occurrence data are likely to confound climatic boundary constraints with other distribution-limiting factors (e.g., interspecific competition, dispersal limitation, etc.). In fact, to the degree that species distribution models are fit tightly to occurrence data, they model the realized niche and not the fundamental niche, where the former is the subset of geographic space a species is actually observed to occupy (i.e., in the presence of competitors, predators, mutualists, facilitators, etc.; Figure 1.1). This has raised concern that such approaches, (1) simply model the environmental conditions associated with the presence or abundance of a particular species (Kearney 2006; Morin and Lechowicz 2008); (2) fail to provide any mechanistic

understanding of what limits species' ranges (e.g., dispersal constraints; Colwell and Rangel 2009); and (3) may not produce reliable forecasts of how species' distributions might change under future climates.

Factors other than climate that limit species' presence at a given site demand additional attention in restoration efforts. This includes biotic interactions, from competition to mutualism to facilitation; from predation to parasitism to disease, and more; as well as the diversity of spatiotemporal scales at which such interactions operate—from fine to broad. Specifically, intra- and interspecific levels of competition may often be important for explaining species composition and configuration at both localized and geographic scales (e.g., sensu emergent or interactive ecological processes that operate across scales in a macrosystem; Heffernan et al. 2014). Species' realized geographic distributions are the result of all of the above processes acting at once, including abiotic conditions, biotic interactions, and landscape-scale ecological processes such as dispersal, succession, disturbance, irruptions of competitors, and outbreaks of disease (Figure 1.1; Soberón 2007).

Figure 1.1. Species' niches and geographical distributions are shaped by many factors, of which, three important categories are illustrated here: climatic conditions, biotic interactions, and dispersal. The *upper left* circle indicates the geographical area in which climatic conditions support an intrinsic population growth rate at or above population replacement level. The *bottom* circle designates the geographical area in which the species can persist in the presence of interfering species (e.g., competitors or predators) or beneficial species (e.g., mutualists or facilitators). The *top right* circle signifies the geographical area within the species' capacity to disperse (i.e., over a specified time frame). The open triangles represent sink populations wherein both the climatic and biotic components of the environment are (collectively) insufficient for the population to replace itself, on average. The asterisks and open squares denote sink populations in which the climatic and biotic components of the environment, respectively, are (separately) insufficient for the population to replace itself, on average. Finally, the filled circles specify source populations wherein the climatic and biotic components are sufficient for the population to replace itself on average. This diagram is modeled after the conceptual foundations laid by Soberón (2007).



Given these considerations, the frontier of distribution-modeling research aims to better represent these processes in models of species' distributions. One avenue for doing so is the integration of macrogeographic (occurrence) data into process-based or mechanistic models of species' distributions. Examples of process-based or mechanistic distribution models include those based on phenology (Chuine and Beaubien 2001; Morin et al. 2008), physiology (Kearney and Porter 2009), and demography (Vanderwel et al. 2013; Lynch et al. 2014; Merow et al.

2014). A second avenue is to model distributions in terms of landscape-scale processes using metapopulation models, stochastic patch-occupancy models, integrated population models, or other formulations that treat dispersal explicitly (Pagel and Schurr 2012; García-Valdés et al. 2013; Chandler and Clark 2014; Newman et al. 2014; Yackulic et al. 2015).

Another example of this landscape-scale approach is the use of a spatially explicit dynamic macroecological model. Mokany et al. (2012) projected the future geographic distributions of the native plants in Tasmania (2,051 species) under climate and land use scenarios using dynamic, climate-driven models of α- and β-diversity. Addition or loss of species in each 250-m grid cell was governed by a species' proximity to a focal cell in geographic and environmental space. Though the number of species modeled and spatial scope are impressive, the explanatory power (i.e., R^2) of the underlying diversity models was poor, and all species were assigned an identical dispersal capacity. The next step would be to account for nonclimatic drivers of species diversity (e.g., biotic interactions or disturbance)— that is, incorporate additional processes into these models along with their relevant data.

Hierarchical and inverse models are promising tools to integrate occurrence data into process-based range models, or add more processes into coarse landscape-scale models. These integrated models have the capacity to fuse data across natural hierarchies of both biological organization and spatiotemporal scales, reflecting the multitude of processes, from fine to broad scales, which shape species' distributions (Marion et al. 2012; Pagel and Schurr 2012; Schurr et al. 2012). Models that more explicitly treat the underlying processes that shape species' distributions should improve understanding of which ecological processes ensure local persistence of species in space and time—which, in turn, should help increase the success of restoration efforts.

Species-area relationships: ecosystem size and species diversity

Ecologists have long sought to understand how ecosystem size determines the number of species inhabiting it (Rosenzweig 1995; Metzger and Brancalion 2016). MacArthur and Wilson (1963, 1967) first proposed that the number of species in an ecosystem of a given size reflects a dynamic balance between immigration of new species into the system and local extinction of species already residing in the system. Although capable of predicting some aspects of a species-area relationship (SAR), the island biogeographic model proved too simplistic to completely explain how species richness varies with ecosystem size (Lomolino 2000a, b, c; Lomolino et al. 1995). Clearly, mechanisms underlying SARs on continents and island archipelagos must incorporate both dispersal and population viability, as MacArthur and Wilson (1967) envisioned. However, ecological processes that regulate population rates and determine population viability, as well as individual dispersal, depend on a large number of complexly interacting mechanisms. These components include, among other things, the ecological attributes of individual organisms, abundance and variety of resources, spatiotemporal patterns of those resources, and the context in which the ecosystem exists (McGill et al. 2007; Morlon et al. 2009).

A macroscale perspective on the processes that generate SARs provides a different viewpoint that, in some ways, simplifies the problem and may take the place of mechanistic-based explanations. The basic idea is that SARs are generated as a consequence of overlapping distributions of species in geographic space (Maurer 1999; McGill and Collins 2003). However, explaining why each species has a unique geographic distribution is difficult if the focus is solely on the particular mechanisms bounding each species in space and time. If the patterns in demography of species across their ranges are examined, the myriad components underlying SARs may be condensed into simpler models describing population-level mechanisms

responsible for SARs (Hubbell 2001; Maurer 1999; McGill and Collins 2003). Consider the following simple model for distributions of species in space (Maurer 1999; McGill and Collins 2003). Suppose species are distributed across space in a unimodal manner (Figure 1.2). Each species has a different-sized geographic range, some with larger ranges and others with smaller ones. At any given point in space, this results in a skewed distribution of abundance. The SAR resulting from this pattern is similar to empirical patterns seen in many collections of species at the level of metacommunities (Figure 1.3). This approach can thus be expanded to examine SARs at different geographic scales, leading to the prediction that SAR exponents will vary with the scale at which they are measured (Rosenzweig 1995).

Of particular relevance to ecological restoration is the observation that the smallest islands often depart from a SAR for an archipelago (MacArthur and Wilson 1967; Brown and Lomolino 1998; Rybicki and Hanski 2013). Many such islands are too small to maintain viable populations of any species, and must therefore be maintained by immigration alone. This observation has important implications for ecological restoration projects. Island biogeographic theory predicts that small or isolated areas may require closer proximity to a source of colonists, or greater connectivity to such source pools if the objective of restoration is to maintain the species diversity of a larger ecosystem. Many local populations persist as parts of larger metapopulations (Hanski 1998a, b, 1999); therefore, if the size of the area to be restored is too small, or too isolated from colonist source pools, then the likelihood of maintaining the original species richness and diversity of the restored ecosystem may be relatively small (Haddad et al. 2015; Jarzyna et al. 2015; but see also Sabatino et al. 2010).

Figure 1.2. Graphical representation of the distribution of species in geographic space hypothesized to be responsible for species-area relationships.

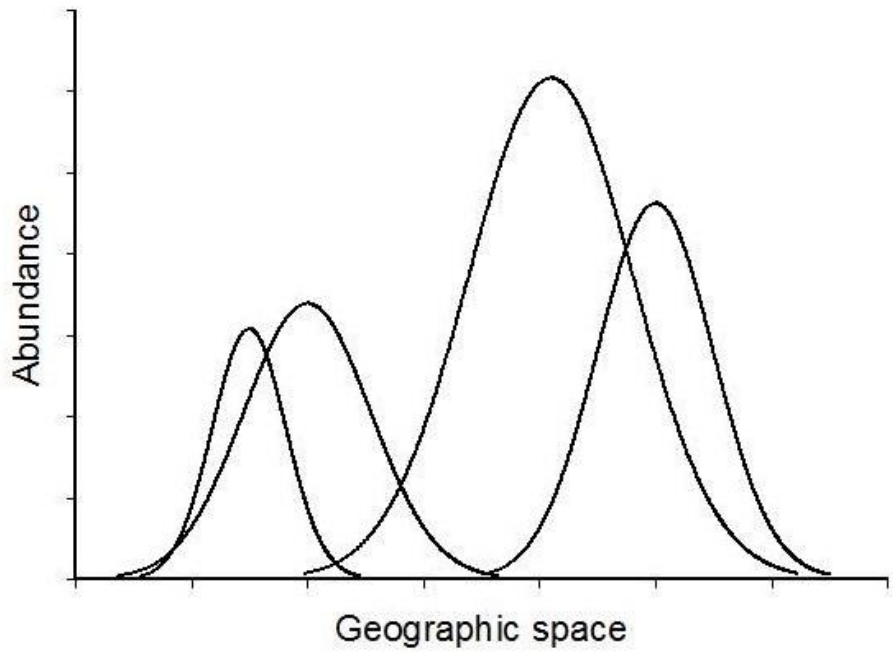
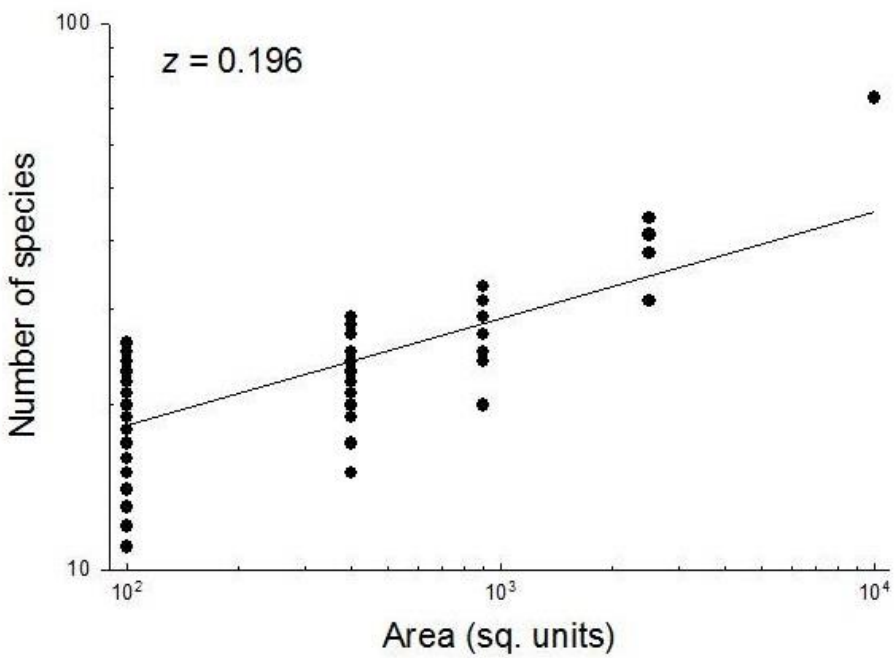


Figure 1.3. An example species-area relationship derived from a simulation of a two-dimensional version of the model represented in Figure 1.2.



Such consequences regarding species diversity have been debated for many years (Brown and Lomolino 1998; Whittaker 1998). What is less clear is whether there are additional properties of ecosystems that are affected by ecosystem size, patch composition, and configuration. Some unknown properties might involve ecosystem stability, functional redundancy (or equivalence) between species, and spatiotemporally autocorrelated system states. One system property that is likely to be important is the unique characteristics of the landscape matrix in which habitat islands are embedded and the degree to which the matrix is inhospitable to dispersers (Debinski 2006; Nowicki et al. 2014). In some situations, altered portions of the matrix may even facilitate connections between habitat islands. For example, Barnes et al. (2014) demonstrated that restored matrix habitat mediated responses of dung beetle (i.e., family Scarabaeidae and subfamily Scarabaeinae) communities to edge effects in Nigerian tropical rainforests. Beetle community responses were so striking, in fact, that formerly extirpated species reestablished themselves in the restored matrix habitat, which led to improved capture rates of individual beetles in the matrix as well as more abundant populations in areas adjacent to it (Barnes et al. 2014). In similar cases where the landscape is manipulated and restored in some functional manner, the once hostile matrix may act as a networked conduit for colonists, helping to sustain crucial ecological processes at the level of populations and communities.

Metapopulation models: the matrix and connectivity between habitat islands

Metapopulation dynamics comprise a fundamental ecological process that operates across scales and is relevant to the long-term success of any restoration project (Hanski 1998a, b, 1999; see also Maschinski and Quintana-Ascencio 2016; Metzger and Brancalion 2016). How metapopulations operate emphasizes the importance of external transport processes in maintaining a viable ecological system. A metapopulation is simply an aggregate of local

populations connected via dispersal. The metapopulation can only persist if there is sufficient exchange of individuals among local populations to offset extinctions with colonization of new local populations—a type of ecological restoration that is organism-driven (Zhang et al. 2012). Although local populations may experience negative growth rates (e.g., "sink" populations), a metapopulation may persist indefinitely as a consequence of the external transport of colonists between subpopulations (Maschinski and Quintana-Ascencio 2016). Metapopulation dynamics are essential to buffering population size against demographic and environmental stochasticity as well as maintaining gene flow across populations.

For ecological restoration, this means that the species diversity of a restored ecosystem may depend heavily on the quality and quantity of colonists the ecosystem receives from beyond its borders. In the face of degraded and fragmented landscapes, subpopulations are coerced into colonizing remaining areas of suitable habitat, which often have complex shapes, greater amounts of edge habitat, and reduced connectivity between disparate and isolated fragments. Such patch fragments have been termed habitat islands—ecological units readily conducive to island biogeographic theory and its applications (Fernández-Juricic and Jokimäki 2001; Kennedy et al. 2011; Szlavecz et al. 2011). Moreover, the concept of habitat islands allows for direct integration with ideas about ecosystem size and species diversity as well as restoration efforts that help recover connectivity between species-specific habitat patches in a frequently inhospitable matrix on landscape-scales.

Facilitation of colonist dispersal through the landscape matrix is a relatively new idea. For decades, the landscape matrix was assumed in practice to be wholly inhospitable to species moving between disparate patches of habitat, and to some extent, the matrix does affect several species in this manner (Debinski 2006; Nowicki et al. 2014). For example, Nowicki et al. (2014)

found that forest-dominated matrix was an inhospitable environment to focal grassland butterflies such that dispersal mortality was highest in forested matrix compared to other areas of open matrix, which suggested that forests impose strong selection against colonist dispersal in their study system. Though examples such as these exist, recent data suggest that for some systems the landscape matrix may, in fact, aid colonist dispersal to new population patches when the matrix is managed and improved for dispersers (Barnes et al. 2014; Kang et al. 2015). Such findings are clearly relevant to ecological restoration efforts in that managing landscape matrices to produce gradients of hospitability for various species may facilitate colonist dispersal by connecting isolated habitat islands (Figure 1.4; Blaum and Wichmann 2007; Szlavecz et al. 2011; Kang et al. 2015). These conceptual advancements may thus allow for improved mitigation of the effects of fragmentation by ensuring demographic and genetic exchange between separated subpopulations via landscape connectivity (Fernández-Juricic and Jokimäki 2001; Blaum and Wichmann 2007; Storfer et al. 2007; Hedrick et al. 2014; Wang et al. 2014) as well as in the context of connected stream networks (Dunham et al. 1997; Neville et al. 2006).

Macroecology contributes to this conceptual understanding by promoting management of population connectivity across the landscape matrix. Findings from fragmentation experiments worldwide indicate that landscapes deficient in connectivity between habitat islands lead to more broad and accelerated extinctions on localized scales over time and may exacerbate ecosystem changes (Hooper et al. 2012) on broad scales via biodiversity loss in the face of increased landscape fragmentation (Haddad et al. 2015; Jarzyna et al. 2015). Properties of metacommunities (e.g., the size, shape, composition, configuration, and connectivity between like communities) are also of great interest to restoration projects that intend to alter

characteristics of the matrix to improve landscape connectivity and dispersal conditions (Kang et al. 2015).

Consider the following example, which highlights the importance of avian metacommunity properties on a broad spatial scale. Maurer et al. (2013) developed methods for describing spatial properties of metacommunities based on avian species' sampled during 1996–2000 from the North American Breeding Bird Survey (Pardieck et al. 2014). Maurer et al. (2013) used information on species' abundances, local environmental variation, and avian phylogenetic relationships to estimate the extent of metacommunities for breeding bird assemblages across 1,393 survey routes (Figure 1.5). Metacommunity extent (i.e., distance, in km) was estimated as a function of ecological similarity between survey sites. By plotting the similarity among sites as a function of the distance between them, Maurer et al. (2013) were able to estimate a maximum distance beyond which the similarity decreased as more sites were added to the pool of metacommunity-eligible sites. Interpreting this maximum distance as a measure of metacommunity extent thus facilitates understanding of spatial patterns of metacommunity size.

Figure 1.4. Schematic of a hypothetical landscape where habitat islands (A–D; i.e., supporting disparate local populations) are separated by a gradient of matrix. This gradient represents changing matrix habitat that is either, (a) conducive, (b) semiconducive (e.g., an agricultural field), or (c) unconducive (e.g., a lake) to dispersal between patches for two hypothetical organisms, a mammal (i.e., high vagility; thick black arrows) and an insect (i.e., low vagility; thin black arrows). Dispersal events are assumed low risk (e.g., to mortality (solid lines), high risk (dashed lines), or impossible (e.g., for the insect between B and C; no lines) between habitat islands for each organism across the matrix. Obstacles to dispersal include an open agricultural hayfield (H), a fast-moving waterway (W), and a highly trafficked roadway (R); while one corridor is a green-way (G) bridge constructed for wildlife. In all cases, local population persistence across the landscape is mediated by immigration and colonization, influenced by the dispersal limitations of the organism and connectedness of patches as well as subsets of a connected and permeable matrix.

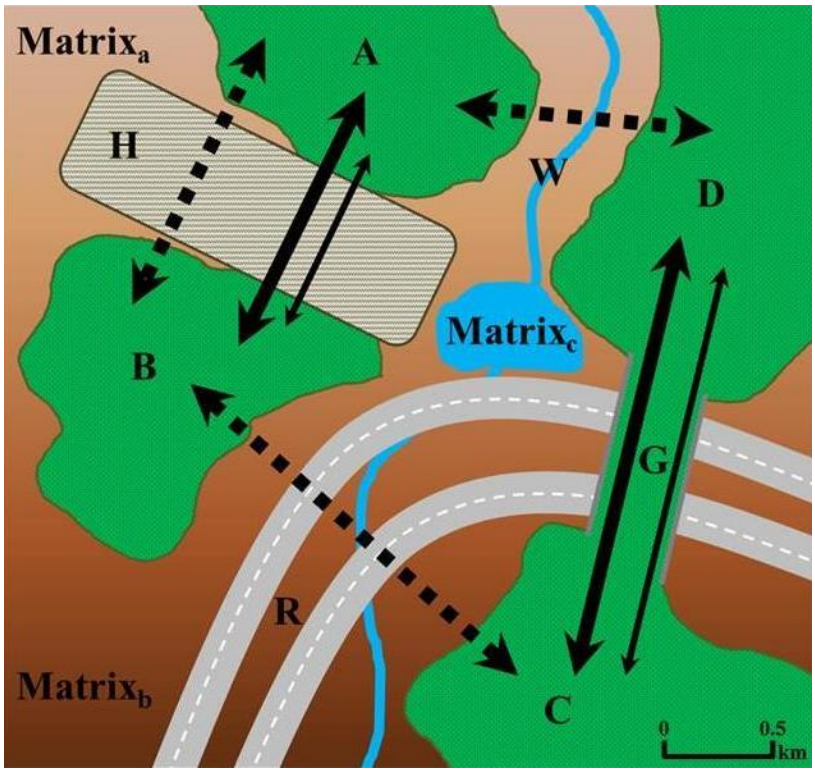
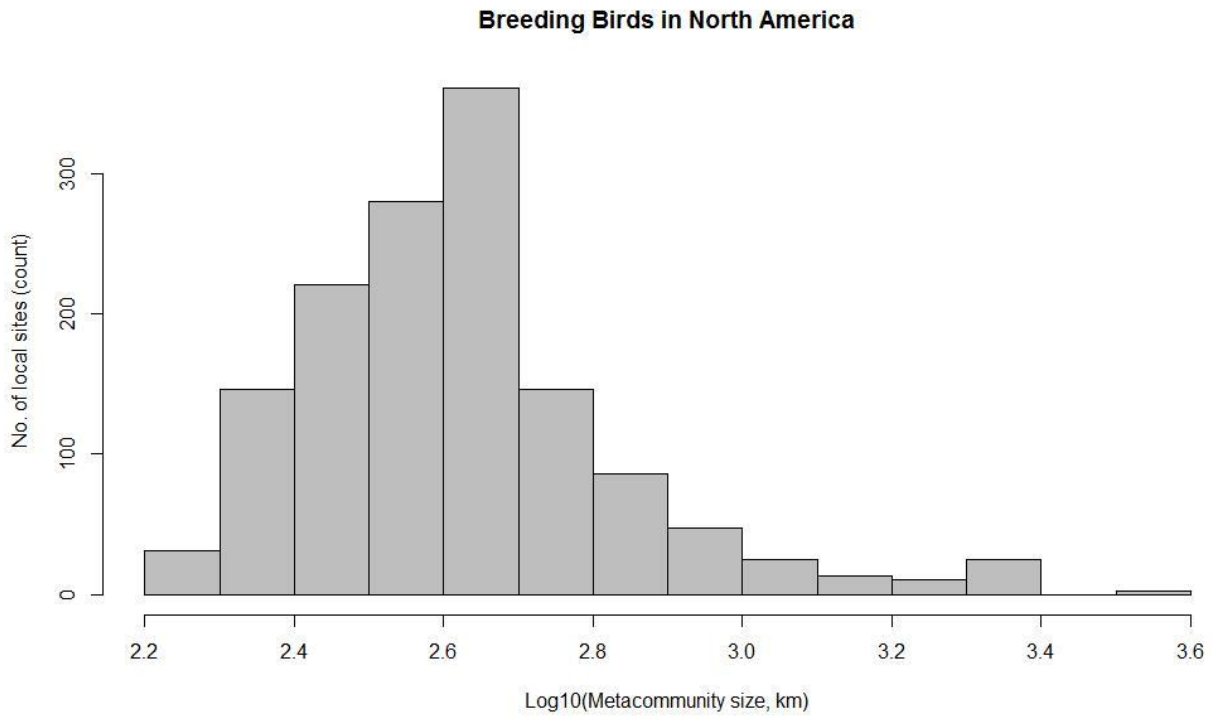


Figure 1.5. Distribution of metacommunity size (i.e., distance, units of log10 km) for 1,393 avian assemblages sampled by the North American Breeding Bird Survey (Maurer et al. 2013).

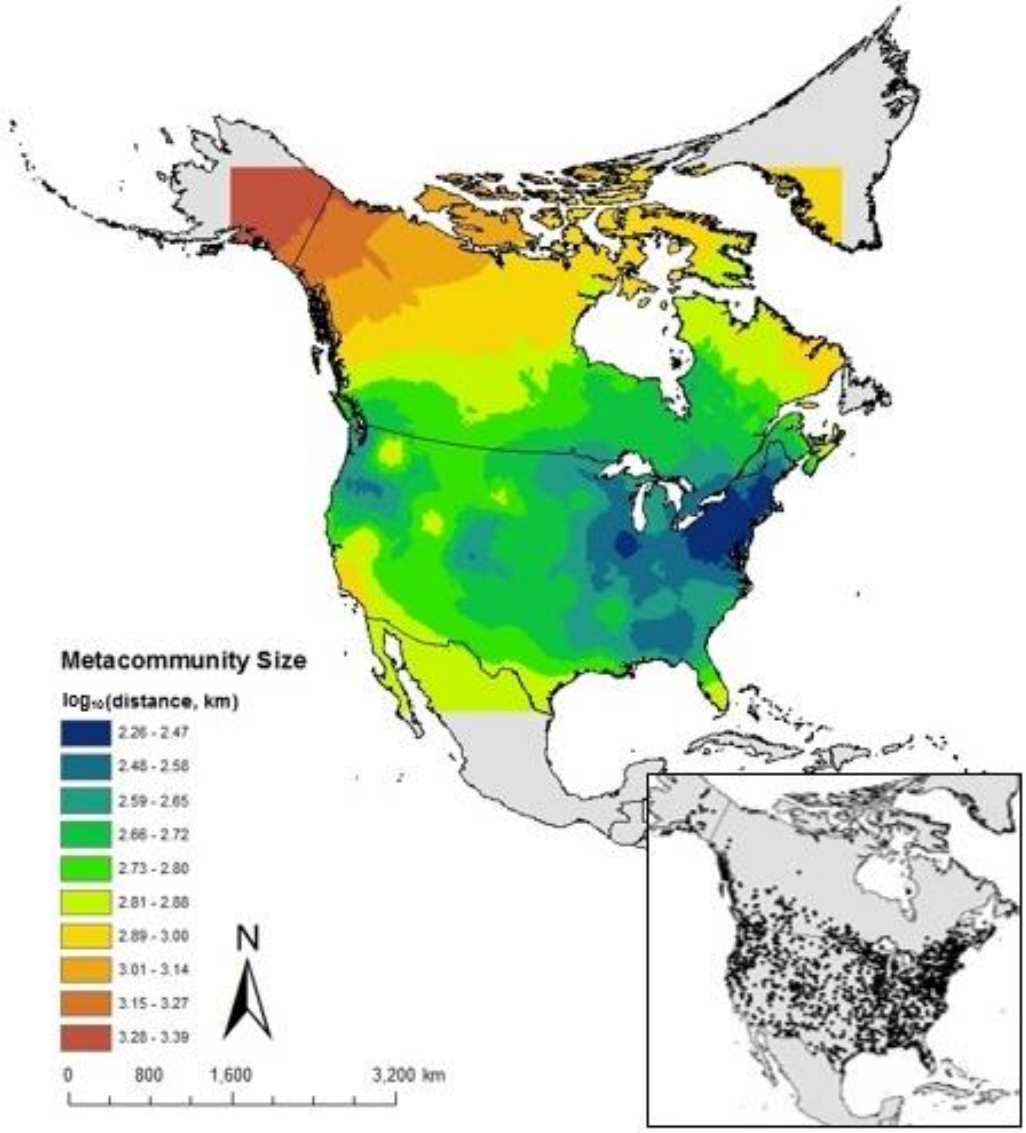


Applying this method to data on North American terrestrial birds during the breeding season, the size of metacommunities (in terms of geographic distance) reveals that breeding bird assemblages are diverse in the spatial extent from which local communities draw colonists from other communities. Interestingly, patterns of metacommunity size reflect the underlying structure of important ecoregions in North America. For instance, metacommunity sizes tend to be much smaller in the eastern temperate forests than in the northwestern forested mountains and southwestern deserts (Figure 1.6). In contrast, metacommunity size tends to be larger in the Great Plains and northern boreal forests.

These patterns imply that the region from which a restoration project might draw colonists will likely be smaller in the eastern temperate forests than in the Great Plains, for example. Metacommunity extents illustrate the importance of macroecological context in

restoring ecological systems. Analyses such as these demonstrate that no ecological community is entirely isolated, and sites vary in the degree to which they are able to draw upon colonists. This suggests that spatial connectivity among habitat patches must play an important role in local community persistence over time. Furthermore, connectivity between ecologically similar communities likely relies upon the unique ecoregion to which a community belongs as well as influences from human populations and other disturbances.

Figure 1.6. Geographic variation in metacommunity size (i.e., distance) for avian assemblages across 1,393 Breeding Bird Survey routes in North America—produced via an ordinary kriged interpolation. Metacommunity distances are measured as a function of site similarity based on species relative abundance, local environmental variation, and phylogenetic relationships between species (Maurer et al. 2013). The inset displays the spatial distribution of routes (*n* = 1,393) sampled during 1996–2000. The geographic patterns in metacommunity size suggest the immediate significance of spatial context in system restoration efforts—settings which likely depend on ecoregion type, connectivity between ecological communities, and relative anthropogenic influences, among other potential factors.



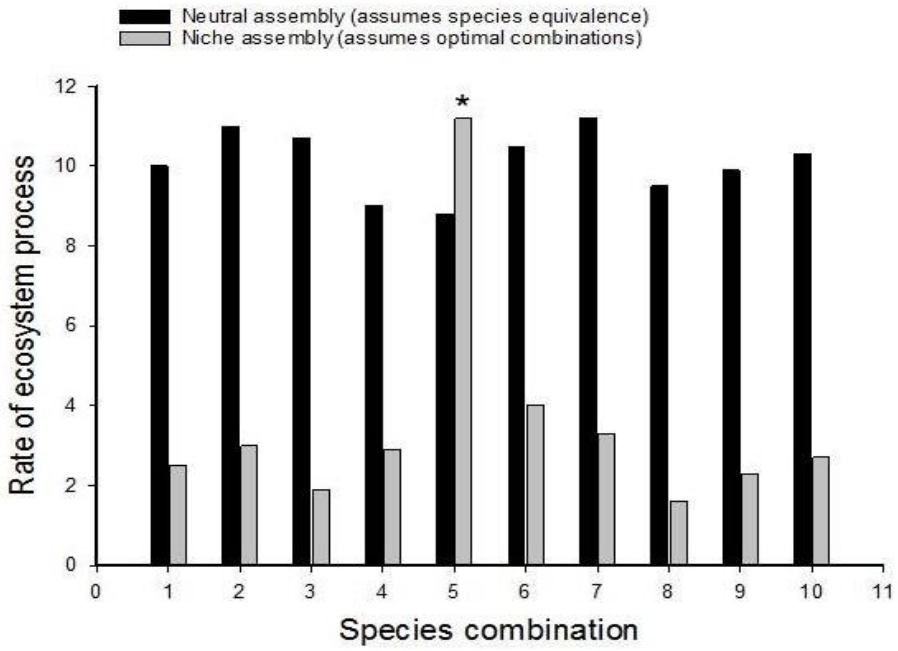
Neutral theory: species equivalence and the maintenance of biodiversity

In attempting to understand the underlying causes for patterns such as SARs, the neutral theory of biodiversity (Hubbell 2001) posits a specific population mechanism responsible for macroscale diversity patterns is based on the assumption of functional equivalence among species. From the perspective of restoration ecology, neutral theory implies that a complete, functional ecosystem can be constituted from an arbitrary set of species from the pool of available organisms that could occupy a given site. Because one species is substitutable for another in this model, the relative abundances and identities of species in a community should have little impact on the final structure and function of the ecosystem (Figure 1.7). Contrast this with an ecosystem where species differences were important and where an "optimal" set of species best adapted to local conditions existed. In such a context, maximal ecosystem functioning would only exist for a few (or even just one) set of species best adapted for the local conditions. As such, restoration would require identification of the best set of species necessary to meet functional goals of the restoration endeavor.

To what degree are the assumptions of the neutral theory met in nature? The initial response to this question by many ecologists would be that differences among species are ecologically important. However, demonstrating that differences among species have a cumulative impact on the structure and function of ecosystems has not been straightforward (Loreau et al. 2001). Furthermore, successful ecological restoration may often depend on bringing together the right combination of species to generate and maintain a functional ecosystem. If this is generally true, then restoration projects can be viewed as experiments that can provide tests for the assumption of functional equivalence among species. If functional equivalence is true, then there may be a relatively large number of species combinations that

might produce a persistent, functional ecosystem. If functional equivalence is false, then there would only be a few appropriate combinations of species that will produce an ecosystem that can persist and function appropriately over time (Figure 1.7). There are a number of ways that these hypotheses might be tested. In fact, a survey of restoration activities that were evaluated based on whether or not they led to an appropriately functioning ecosystem might provide a test of functional equivalence if it was found that species composition was an important factor in determining the success of the restoration attempt.

Figure 1.7. Graphical representation of the differences between the neutral assembly and niche assembly hypotheses. The vertical axis is the rate of some ecosystem process of interest to restoration efforts. Suppose that there are ten different combinations of species that could occupy the local ecosystem. In this hypothetical system, the neutral theory would predict that all ten species combinations would generate roughly the same rate of the process because each species was composed of the same kind of ecologically equivalent individuals. Under the niche assembly hypothesis, there is a combination of species (x = 5, asterisked) that maximizes the rate of the ecosystem process. This combination contains the species that are best adapted to the local conditions in the ecosystem. As illustrated, it is apparent that restoration efforts for a particular system would necessitate different goals, given these two hypotheses of community assembly.



Adaptive management of restored ecosystems might also provide opportunities to design experiments to test the degree to which degraded habitats and ecosystems are restored (Millar et al. 2007; Theiling et al. 2015). Because of the importance of understanding how species composition of an ecosystem affects its structure and function, it is imperative that restoration projects be monitored carefully and thoroughly after they are completed (Heer et al. 2013; Theiling et al. 2015). Such monitoring will serve the dual purpose of establishing criteria to judge the degree to which restoration objectives are met via decision support tools (e.g., Optimal Restoration of Altered Habitats; Lethbridge et al. 2010) and provide data to test models of community assembly that make assumptions about the functional equivalence of species (Temperton et al. 2016). In this way, ecological restoration can become not only a practical field that deals with the what of restoring ecosystems, but it can also provide a fertile field to test scientific theories that provide answers to why and how degraded ecosystems should be restored in order to maintain their integrity in space and time. Macroscale concepts thus provide restoration ecology with a conceptual framework for long-term management on landscape scales with the goal of maintaining biodiversity and the functional integrity of restored ecosystems (Hooper et al. 2012).

Thematic Considerations for Applied Developments in Restoration Ecology

A comprehensive discussion of how large and connected specific restored ecosystems must be in order to preserve target species and ecosystem functions is beyond the scope of this chapter. For the present purpose, we can say confidently, as a basic principle, that any restoration project needs to take into account practical issues regarding the size, macrogeographic composition, and connectedness of the ecosystem being restored (Aronson and Le Floc'h 1996; White and Walker 1997). Since ecosystem functions often require input from processes not physically contained

within the boundary of the ecosystem, a fundamental principle of ecosystem restoration should be to ensure that the restored ecosystem resides within a comprehensive landscape context (Weinstein et al. 2014). Such a setting must be conducive to providing adequate flux of individual organisms, energy, and resources between populations inhabiting patch islands in order to maintain ecosystem viability over long-term temporal scales. To understand the importance of the aforementioned concepts to restoration ecology, we briefly consider management challenges that the planet faces today.

Although global societies foster a well-connected landscape for human populations, the same cannot be said for numerous floral and faunal populations. While landscape fragmentation is an important issue today, increasing trends in land use change that are detrimental to wildlife are likely to continue (Sala et al. 2000). Moreover, landscape changes in composition and configuration will likely produce harmful synergistic effects with future climate scenarios as species begin to track their climatic constraints. The emergence of species' range shifts poses a great challenge to biodiversity management and conservation (Morin and Lechowicz 2008; Chambert et al. 2015). However, analytical tools exist now that can help managers address multiscaled environmental drivers of range shifts. For example, once again, species distribution models may provide valuable capacity for anticipating conservation concerns such as forecasting species' range shifts (Pagel and Schurr 2012; Schurr et al. 2012).

One of the emerging challenges to restoration ecology is managing ecological systems in the face of nonstationary climate regimes (Falk and Millar 2016). Such climatic shifts suggest that the targets for restoration are moving targets, including the composition and functionality of ecological communities (García-Valdés et al. 2013).

Case Study Box 1-1: Hypothetical Restoration of Wild Populations Facing Demographic Consequences Mediated by Landscape Structure on Broad Spatiotemporal Scales

Marys River watershed, Great Basin Desert, US

The Marys River (41°33´ N, 115°18´ W) is a 500 km^2 watershed located in the Lahontan Basin of the Great Basin Desert, US, and the area supports federally threatened populations of the Lahontan cutthroat trout (Oncorhynchus clarkia henshawi). These trout are endemic to the region and often restricted to small isolated streams. This makes investigation of demographic consequences from landscape structure on their populations a model case for restoration considerations on broad scales. In this stream network system, Neville et al. (2006), hereafter researchers, assessed the genetic characteristics of trout populations with respect to attributes of the local landscape, research that we now summarize and discuss with respect to macroecological considerations for ecological restoration.

Expectations informed by island biogeographic and metapopulation theory

Given the longstanding recognition that landscape patterns have important influences on ecological processes that shape and constrain populations, researchers sought to investigate the influence of dispersal barriers on genetic population structure in this stream network.

Results of the population-level assessment

Trout populations facing low spatial connectivity exhibited sedentism and also occupied habitats of poor quality, which contributed to lower genetic diversity than subpopulations inhabiting connected, higher quality habitats. Concomitant increases in genetic differentiation were also associated with isolated populations in response to decreased gene flow across one-way dispersal barriers in contrast to more connected populations, which were able to move to and from the river main stem or were able to traverse more passable barriers throughout the stream network.

Researchers found no evidence that genetic differences arose solely based on the type of dispersal barrier present (e.g., man-made dams or natural waterfall features); however, the response of trout to such barriers depended markedly on the habitat that isolated populations occupied. For example, one subpopulation inhabited broad, high quality habitats above a waterfall yet was also subject to asymmetrical gene flow across that same barrier. Despite deficiencies in gene flow, over time, these areas still supported larger and more stable populations than did areas with fine, poor quality habitats in the face of similar constraints with respect to gene flow. Finally, researchers found that spatial structure, rather than temporal structure, was more important for shaping population genetic diversity in the system.

Research implications

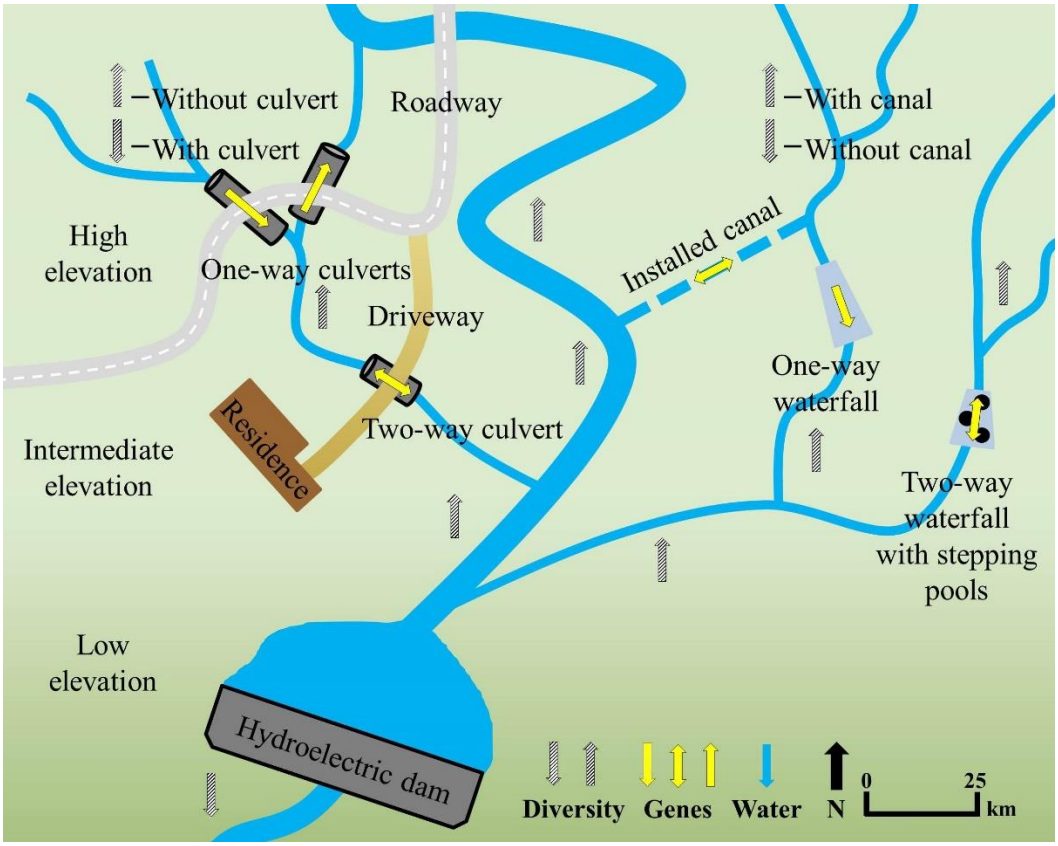
Spatial aspects such as habitat connectivity and quality, as well as concomitant genetic effects on dispersal behavior or individual fitness, may be important factors for limiting population productivity, recruitment, and persistence over time. Researchers concluded that population persistence concurrently depends on the life history strategy (i.e., sedentary versus migratory behavior), the connectedness of habitat patches (i.e., whether symmetric or asymmetric gene flow across barriers), and general habitat complexity (i.e., in both quantity and quality) in order to sustain the greater metapopulation of cutthroat trout.

Considerations for ecological restoration and management objectives

If we imagine that this region was of interest to restoration ecologists, then what solutions might we offer to managers of this region with respect to conservation of Lahontan cutthroat trout? Our discussion suggests that we should consider several criteria for restoration: (1) the size of the system (e.g., a 500 km^2 freshwater catchment); (2) the macrogeographic constraints on the system (e.g., multiple subpopulations of migratory trout capable of moving > 50 km annually

and also constrained by the distribution of quality habitats); (3) the connectedness of the system (e.g., the variable flux of genes, energy, and resources throughout the stream network); and (4) the broader context of the system's landscape (e.g., the proximate influences of genes, energy, and resources beyond the stream network). Management solutions relevant to each of these considerations might include regular long-term assessments of individual trout (e.g., via genetic methods), macroscale enhancement of key habitat resources and movement corridors (e.g., via in-stream manipulations of habitat or via facilitation across dispersal barriers, whether by permanent removal or retrofitting thereof), and recurrent monitoring surveys beyond the stream network in order to improve conditions for the species' metapopulation to persist across the system (Figure 1.8).

Figure 1.8. Schematic of a hypothetical riverscape where water predominantly flows southward and fish populations are either connected or isolated across tributary waters that contain both natural (i.e., waterfalls) and man-made barriers (i.e., dams and culverts) to individual dispersal. If this area were unmanaged for fish, then we might imagine that movement barriers would remain in place and meet their intended purposes. However, these barriers might also produce various unintended consequences (e.g., changes in gene flow [white arrows] and genetic diversity [gray arrows]). For example, inhibited dispersal could lead to decreased genetic diversity in isolated fish populations, and thus produce increased probabilities of local extinction. Despite these conditions and their associated demographic consequences (e.g., hindered productivity, recruitment, and persistence), restoration efforts could provide solutions through management intervention (e.g., barrier removal, retrofitting, or facilitation measures, such as installing movement corridors) intended to promote spatial (genetic) connectivity throughout the watershed and ensure greater probability of metapopulation persistence for the target species over time.



References: MacArthur and Wilson 1967; Slatkin 1985; Dunham et al. 1997; Davies et al. 1999; Manel et al. 2003; Neville et al. 2006.

Distribution models or bioclimatic envelope models have been used extensively to project future species' distributions (Thuiller et al. 2005; Jetz et al. 2007; Falk and Millar 2016),

and these projections may offer key guidance to restoration ecologists in terms of anticipating appropriate targets of species composition and associated ecosystem function at a given location. For example, adaptive strategies aimed at managing forests in the face of climate change include mixed species plantings, neonative translocations (e.g., assisted migration), and enhancing genetic diversity in managed populations (Millar et al. 2007; Storfer et al. 2007), which can be informed by forecasts of the distributions of species, subspecies, varieties, or haplotypes.

Management actions such as assisted migration and the use of future climate-adapted genotypes have thus far been discussed more in theory than attempted in practice (McLachlan et al. 2007; Vitt et al. 2010; Maschinski and Haskins 2012). Nonetheless, it seems likely that restoration ecology is poised to use macroecological distribution models in such ways. Reconstructions of species' past distributions, as well as past ecological communities, indicate consistently that organismal distributions can change dramatically over time and often lead to the realization that some local communities in the past have no analogues in the present (Jackson and Hobbs 2009). Furthermore, individualistic trajectories of species' past distributions (sensu Gleason 1926) suggest that species-level prediction, as opposed to community-level forecasting, is most appropriate for coordinated conservation and management. Pairing species distribution models and other conservation tools with innovative ideas, such as efficient theories (Marquet et al. 2014), may also provide unique insights into ecological patterns and processes on macroscales— insights useful to applied management and restoration efforts.

Moreover, species distribution models and similar tools may provide guidance for establishing new, and managing existing, set-aside areas for conservation (e.g., national reserves, parks, and local easements). What is certain from our review of current literature is that connectivity between habitat islands is an essential component for dispersing organisms, genetic

flow, and persistent metapopulations (Cushman et al. 2011). Additionally, macroscale management of wild populations across landscapes is also important for the maintenance of such crucial ecosystem properties (i.e., populations that are connected, genetically diverse, and stable; McKinney et al. 2010; Hobbs et al. 2014). In addition, set-aside areas and reserves should incorporate management procedures that enhance landscape connectivity between habitat islands, especially those areas confronted with increased isolation as well as shifting rates of local population growth and genetic diversity (Rybicki and Hanski 2013; Wang et al. 2014). Such management practices will enable ecological restoration to advance beyond efforts at localized scales (e.g., individuals, populations, and ecosystems) to conservation of the properties of single ecosystems and their connections to other systems at broader scales, such as those of continents, biomes, and the biosphere—coarse scales that structure and interact with ecological patterns and processes at finer scales (Cattarino et al. 2014).

Closing Remarks

Ecological systems are dynamic and constantly in flux, and systems in need of restoration are certainly no exception to such fundamental characteristics. Restoration of degraded ecosystems thus requires special consideration of features such as the target system's former natural state, its alternative steady states, inherent legacy effects and ecological tipping points, and the role of stochasticity in shaping the target system's state. These requirements underscore the numerous difficulties facing ecological restoration efforts. Such complications include issues with, (1) identifying ecosystem size and restoration scales; (2) analyzing macrogeographic controls and selecting tools to forecast or hindcast species' distributions based on those controls; and (3) applying mechanistic or process-based (e.g., metapopulation) tools versus species-area or neutral system relationships to inform restoration objectives. Despite these challenges, macroecological

perspectives may provide guidance to restoration efforts moving forward, especially with respect to accounting for historic and current ecosystem factors, both abiotic and biotic, in space and time.

The macroscale perspective we have described strongly suggests that ecosystem restoration cannot be successfully carried out without thoughtful consideration of the spatiotemporal context within which the restored system will exist. Ecosystems are composed of numerous collections of species, each of which are shaped by unique macrogeographic controls (e.g., abiotic and biotic factors) on their distributions and abundance in space and time. Consequently, ecological restoration should not lose sight of these species-specific controls that partly assemble ecological systems. An ecosystem is not only defined by the species composition, edaphic conditions, and interaction networks that exist within its boundaries, but also by the ebbs and flows across its boundaries that connect its internal processes with broader external systems and their processes, for example, nutrient, energy, and hydrological (Baer 2016; Marín-Spiotta and Ostertag 2016; Moreno-Mateos and Palmer 2016). Accordingly, restoration efforts must acknowledge the emergent novel dynamics of habitat islands for populations that exist in modified landscapes. This also necessitates focused recognition and management of landscape-scale factors, such as habitat matrices for increased hospitability, to connect and facilitate flows of colonists between distinct habitat islands and ecological communities—factors well-grounded in island biogeographic and metapopulation theory.

Through explicit incorporation of established theory to assess the properties of species assemblages and distributions on broad spatiotemporal scales, macroecology provides an empirical basis that can generate insight into the structure of biodiversity and how that organization influences the success or failure of ecological restoration efforts. Because of its

focus on regional- and continental-scale processes, macroecology readily identifies the importance of landscape connectivity between, as well as the relative isolation of, ecological communities, because ecosystems extend far beyond political, geographical, and functional boundaries—even though such systems are frequently managed at these scales. Therefore, a restoration project that fails to consider external transport processes (e.g., species dispersal across project boundaries) over managed landscapes may be unable to meet crucial project objectives, because the restored system may be governed (e.g., limited or enhanced) by flows across its borders such as from neighboring landscapes (Maschinski and Quintana-Ascencio 2016; Metzger and Brancalion 2016). One important way to maintain the integrity of a restored ecosystem is to replace external transport processes with intensive management activities that serve or enhance the same function, but such approaches represent a more or less permanent commitment that may not be logistically or fiscally viable.

Furthermore, data on the relationship between species composition and the success of restoration activities can be used to test the functional equivalence of species, an assumption that underlies neutral models of macroecological patterns. In particular, carefully planned restoration projects can be used as active experiments in adaptive management to test this (and other) important assumption(s) about the assembly, functionality, and persistence of disparate ecological communities and systems, especially on landscape-level scales. Restoration ecology must become increasingly able to anticipate and address species' range shifts, novel system configurations, and accelerated extinction rates in response to complex synergies amidst changing land use practices, expanding human populations, and future climate dynamics (Falk and Millar 2016). In the face of these substantial interacting processes, macroecology thus provides a foundational framework to enhance endeavors in restoration ecology on vast

spatiotemporal scales as well as aid the future of biodiversity conservation and management in a nonstationary and ever-challenged world.

REFERENCES

REFERENCES

Araújo, M. B. and A. T. Peterson. 2012. Uses and misuses of bioclimatic envelope modeling. *Ecology* 93:1527-1539.

Aronson, J. and E. Le Floc'h. 1996. Vital landscape attributes: missing tools for restoration ecology. *Restoration Ecology* 4:377-387.

Baer, S. G. 2016. Nutrient dynamics as determinants and outcomes of restoration. Pages 333-364 *in* Foundations of Restoration Ecology, Second Edition, Palmer, M. A., J. B. Zedler, and D. A. Falk (Eds.). Island Press, Washington, DC, USA.

Barnes, A. D., R. M. Emberson, H. M. Chapman, F.-T. Krell, and R. K. Didham. 2014. Matrix habitat restoration alters dung beetle species responses across tropical forest edges. *Biological Conservation* 170:28-37.

Blaum, N. and M. C. Wichmann. 2007. Short-term transformation of matrix into hospitable habitat facilitates gene flow and mitigates fragmentation. *Journal of Animal Ecology* 76:1116-1127.

Blonder, B., C. Lamanna, C. Violle, and B. J. Enquist. 2014. The n-dimensional hypervolume. *Global Ecology and Biogeography* 23:595-609.

Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago, IL, USA.

Brown, J. H. and B. A. Maurer. 1987. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. *American Naturalist* 130:1-17.

Brown, J. H. and B. A. Maurer. 1989. Macroecology: the division of food and space among species on continents. *Science* 243:1145-1150.

Brown, J. H. and G. B. West. 2000. Scaling in Biology. Oxford University Press, New York, NY, USA.

Brown, J. H. and M. V. Lomolino. 1998. Biogeography. Sinauer Associates, Sunderland, MA, USA.

Cattarino, L., C. A. McAlpine, and J. R. Rhodes. 2014. Land-use drivers of forest fragmentation vary with spatial scale. *Global Ecology and Biogeography* 23:1215-1224.

Chambert, T., W. L. Kendall, J. E. Hines, J. D. Nichols, P. Pedrini, J. H. Waddle, G. Tavecchia, et al. 2015. Testing hypotheses on distribution shifts and changes in phenology of imperfectly detectable species. *Methods in Ecology and Evolution* 6:638-647.

Chandler, R. B. and J. D. Clark. 2014. Spatially explicit integrated population models. *Methods in Ecology and Evolution* 5:1351-1360.

Chuine, I. and E. G. Beaubien. 2001. Phenology is a major determinant of tree species range. *Ecology Letters* 4:500-510.

Colwell, R. K. and T. F. Rangel. 2009. Hutchinson's duality: the once and future niche. *Proceedings of the National Academy of Sciences of the United States of America* 106:19651-19658.

Cushman, S. A., T. N. Wasserman, and K. McGarigal. 2011. Modeling landscape fire and wildlife habitat. Pages 223-245 *in* The Landscape Ecology of Fire, D. McKenzie, C. Miller, and D. A. Falk (Eds.). Springer-Verlag, Dordrecht, Netherlands.

Debinski, D. M. 2006. Forest fragmentation and matrix effects: the matrix does matter. *Journal of Biogeography* 33:1791-1792.

Dennhardt, A. J., M. E. K. Evans, A. Dechner, L. E. F. Hunt, and B. A. Maurer. 2016. Macroecology and the theory of island biogeography: abundant utility for applications in restoration ecology. Pages 455-483 *in* Foundations of Restoration Ecology, Second Edition, M. A. Palmer, J. B. Zedler, and D. A. Falk (Eds.). Copyright © 2016 Island Press. Reproduced by permission of Island Press, Washington, DC, USA.

Dunham, J. B., G. L. Vinyard, and B. E. Rieman. 1997. Habitat fragmentation and extinction risk of Lahontan cutthroat trout. *North American Journal of Fisheries Management* 17:1126-1133.

Enquist, B. J., E. P. Economo, T. E. Huxman, A. P. Allen, D. D. Ignace, and J. F. Gillooly. 2003. Scaling metabolism from organisms to ecosystems. *Nature* 423:639-642.

Enquist, B. J., G. B. West, E. L. Charnov, and J. H. Brown. 1999b. Allometric scaling of production and life-history variation in vascular plants. *Nature* 401:907-911.

Enquist, B. J., J. H. Brown, and G. B. West. 1999a. Plant energetics and population density. *Nature* 398:573.

Falk, D. A. and C. I. Millar. 2016. The influence of climate variability and change on the science and practice of restoration ecology. Pages 484-513 *in* Foundations of Restoration Ecology, Second Edition. Palmer, M. A., J. B. Zedler, and D. A. Falk (Eds.). Island Press, Washington, DC, USA.

Fernández-Juricic, E. and J. Jokimäki. 2001. A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. *Biodiversity and Conservation* 10:2023-2043.

García-Valdés, R., M. A. Zavala, M. B. Araújo, and D. W. Purves. 2013. Chasing a moving target: projecting climate change-induced shifts in non-equilibrial tree species distributions. *Journal of Ecology* 101:441-453.

Gaston, K. J. and T. M. Blackburn. 2000. Pattern and Process in Macroecology. Oxford-Blackwell Science, Malden, MA, USA.

Gleason, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53:7-26.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, et al. 2015. Habitat fragmentation and its lasting impacts on earth's ecosystems. *Science Advances* 1:e1500052.

Hampe, A. 2004. Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography* 13:469-476.

Hanski, I. 1998a. Connecting the parameters of local extinction and metapopulation dynamics. *Oikos* 83:390-396.

Hanski, I. 1998b. Metapopulation dynamics. *Nature* 396:41-49.

Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos* 87:209-219.

Hedrick, P. W., R. O. Peterson, L. M. Vucetich, J. R. Adams, and J. A. Vucetich. 2014. Genetic rescue in Isle Royale wolves: genetic analysis and the collapse of the population. *Conservation Genetics* 15:1111-1121.

Heer, P., J. Pellet, A. Sierro, and R. Arlettaz. 2013. Evidence-based assessment of butterfly habitat restoration to enhance management practices. *Biodiversity Conservation* 22:239-252.

Heffernan, J. B., P. A. Soranno, M. J. Angilleta, Jr., L. B. Buckley, D. S. Gruner, T. H. Keitt, J. R. Kellner, et al. 2014. Macrosystems ecology: understanding ecological patterns and processes at continental scales. *Frontiers in Ecology and the Environment* 12:5-14.

Higgs E., D. A. Falk, A. Guerrini, M. Hall, J. Harris, R. J. Hobbs, S. T. Jackson, et al. 2014. The changing role of history in restoration ecology. *Frontiers in Ecology and the Environment* 12:499-506.

Hobbs, R. J. and D. A. Norton. 1996. Towards a conceptual framework for restoration ecology. *Restoration Ecology* 4:93-110.

Hobbs, R. J. and D. A. Norton. 2001. Restoration ecology: repairing the earth's ecosystems in the new millennium. *Restoration Ecology* 9:239-246.

Hobbs, R. J., E. Higgs, C. M. Hall, P. Bridgewater, F. S. Chapin III, E. C. Ellis, J. J. Ewel, et al. 2014. Managing the whole landscape: historical, hybrid, and novel ecosystems. *Frontiers in Ecology and the Environment* 12:557-564.

Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, et al. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486:105-108.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Monographs in Population Biology, Volume 32. Princeton University Press, Princeton, NJ, USA.

Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415-427.

Hutchinson, G. E. 1965. The ecological theater and the evolutionary play. Yale University Press, New Haven, CT, USA.

Jackson, S. T. 2012. Conservation and resource management in a changing world: extending historical range of variation beyond the baseline. Pages 92-109 *in* Historical Environmental Variation in Conservation and Natural Resource Management, J. A. Wiens, G. D. Hayward, H. D. Safford, and C. M. Giffen (Eds.). John Wiley and Sons, Inc., London, UK.

Jackson, S. T. and R. J. Hobbs. 2009. Ecological restoration in the light of ecological history. *Science* 325:567-568.

Jarzyna, M. A., W. F. Porter, B. A. Maurer, B. Zuckerberg, and A. O. Finley. 2015. Landscape fragmentation affects responses of avian communities to climate change. *Global Change Biology* 21:2942-2953.

Jetz, W., D. S. Wilcove, and A. P. Dobson. 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology* 5:1211-1219.

Kang, W., E. S. Minor, C.-R. Park, and D. Lee. 2015. Effects of habitat structure, human disturbance, and habitat connectivity on urban forest bird communities. *Urban Ecosystems* 18:857-870.

Kareiva, P. M., J. G. Kingsolver, and R. B. Huey. 1993. Biotic Interactions and Global Change. Sinauer Associates, Sunderland, MA, USA.

Kearney, M. 2006. Habitat, environment, and niche: what are we modeling? *Oikos* 115:186-191.

Kearney, M. and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12:334-350.

Kennedy, C. M., E. H. Campbell Grant, M. C. Neel, W. F. Fagan, and P. P. Marra. 2011. Landscape matrix mediates occupancy dynamics of neotropical avian insectivores. *Ecological Applications* 21:1837-1850.

Kerr, J. T., H. M. Kharouba, and D. J. Currie. 2007. The macroecological contribution to global change solutions. *Science* 316:1581-1584.

Koh, L. P. and J. Ghazoul. 2010. A matrix-calibrated species-area model for predicting biodiversity losses due to land-use change. *Conservation Biology* 24:994-1001.

Lee, R. M. and J. N. Rinne. 1980. Critical thermal maxima of five trout species in the southwestern United States. *Transaction of the American Fisheries Society* 109:632-635.

Lethbridge, M. R., M. I. Westphal, H. P. Possingham, M. L. Harper, N. J. Souter, and N. Anderson. 2010. Optimal restoration of altered habitats. *Environmental Modelling and Software* 25:737-746.

Lomolino, M. V. 2000a. A call for a new paradigm of island biogeography. *Global Ecology and Biogeography* 9:1-6.

Lomolino, M. V. 2000b. Ecology's most general, yet protean pattern: the species-area relationship. *Journal of Biogeography* 27:17-26.

Lomolino, M. V. 2000c. A species-based theory of insular zoogeography. *Global Ecology and Biogeography* 9:39-58.

Lomolino, M. V., J. H. Brown, and R. Davis. 1995. Analyzing insular distribution patterns: statistical approaches and biological inferences. *Annales Zoologici Fennici* 32:435-437.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges." *Science* 294:804-808.

Lynch, H. J., M. Rhainds, J. M. Calabrese, S. Cantrell, C. Cosner, and W. F. Fagan. 2014. How climate extremes—not means—define a species' geographic range boundary via a demographic tipping point. *Ecological Monographs* 84:131-149.

MacArthur, R. H. and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373-387.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Monographs in Population Biology, Volume 1. Princeton University Press, Princeton, NJ, USA.

Manel, S., M. K. Schwartz , G. Luikart, and P. Taberlet. 2003. Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology and Evolution* 18:189-197.

Marín-Spiotta, E. and R. Ostertag. 2016. Recovery of ecosystem processes: carbon and energy flows in restored wetlands, grasslands, and forests. Pages 365-394 *in* Foundations of Restoration Ecology, Second Edition, Palmer, M. A., J. B. Zedler, and D. A. Falk (Eds.). Island Press, Washington, DC, USA.

Marion, G., G. J. McInerny, J. Pagel, S. Catterall, A. R. Cook, F. Hartig, and R. B. O'Hara. 2012. Parameter and uncertainty estimation for process-oriented population and distribution models: data, statistics, and the niche. *Journal of Biogeography* 39:2225-2239.

Marquet, P. A., A. P. Allen, J. H. Brown, J. A. Dunne, B. J. Enquist, J. F. Gillooly, P. A. Gowaty, et al. 2014. On theory in ecology. *BioScience* 64:701-710.

Maschinski, J. and K. E. Haskins (Eds.). 2012. Plant Reintroductions in a Changing Climate: Promises and Perils. Island Press, Washington, DC, USA.

Maschinski, J. and P. F. Quintana-Ascencio. 2016. Implications of population and metapopulation theory for restoration science and practice. Pages 182-215 *in* Foundations of Restoration Ecology, Second Edition, Palmer, M. A., J. B. Zedler, and D. A. Falk (Eds.). Island Press, Washington, DC, USA.

Maurer, B. A. 1999. Untangling Ecological Complexity: The Macroscopic Perspective. University of Chicago Press, Chicago, USA.

Maurer, B. A. 2012. Continental scale patterns. Pages 152-155 *in* Encyclopedia of Theoretical Ecology, A. Hastings and L. J. Gross (Eds.). University of California Press, Berkeley, CA, USA.

Maurer, B. A., S. W. Kembel, A. J. Rominger, and B. J. McGill. 2013. Estimating meta-community extent using data on species abundances, environmental variation, and phylogenetic relationships across geographic scales. *Ecological Informatics* 13:114-122.

McGill, B. and C. Collins. 2003. A unified theory for macroecology based on spatial patterns of abundance. *Evolutionary Ecology Research* 5:469-492.

McGill, B. J., R. S. Etienne, J. S. Gray, D. Alonso, M. J. Anderson, H. Kassa Benecha, M. Dornelas, et al. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters* 10:995-1015.

McKinney, M., L. Scarlett, and D. Kemmis. 2010. Large Landscape Conservation: A Strategic Framework for Policy and Action. Lincoln Institute of Land Policy, Cambridge, MA, USA.

McLachlan, J. S., J. J. Hellmann, and M. W. Schwartz. 2007. A framework for debate of assisted migration in an era of climate change. *Conservation Biology* 21:297-302.

Merow, C., A. M. Latimer, A. M. Wilson, S. M. McMahon, A. G. Rebelo, and J. A. Silander, Jr. 2014. On using integral projection models to generate demographically-driven predictions of species' distributions: development and validation using sparse data. *Ecography* 37:1167-1183.

Metzger, J. P. and P. H. S. Brancalion. 2016. Landscape ecology and restoration processes. Pages 90-120 *in* Foundations of Restoration Ecology, Second Edition, Palmer, M. A., J. B. Zedler, and D. A. Falk (Eds.). Island Press, Washington, DC, USA.

Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications* 17:2145-2151.

Mokany, K., T. D. Harwood, K. J. Williams, and S. Ferrier. 2012. Dynamic macroecology and the future for biodiversity. *Global Change Biology* 18:3149-3159.

Moreno-Mateos, D. and M. A. Palmer. 2016. Watershed processes as drivers for aquatic ecosystem restoration. Pages 395-423 *in* Foundations of Restoration Ecology, Second Edition, Palmer, M. A., J. B. Zedler, and D. A. Falk (Eds.). Island Press, Washington, DC, USA.

Morin, X. and M. J. Lechowicz. 2008. Contemporary perspectives on the niche that can improve models of species range shifts under climate change. *Biology Letters* 4:573-576.

Morin, X., D. Viner, and I. Chuine. 2008. Tree species range shifts at a continental scale: new predictive insights from a process-based model. *Journal of Ecology* 96:784-794.

Morlon, H., E. P. White, R. S. Etienne, J. L. Green, A. Ostling, D. Alonso, B. J. Enquist, et al. 2009. Taking species abundance distributions beyond individuals. *Ecology Letters* 12:488-501.

Naeem, S. 2016. Biodiversity as a goal and driver of restoration. Pages 57-89 *in* Foundations of Restoration Ecology, Second Edition, Palmer, M. A., J. B. Zedler, and D. A. Falk (Eds.). Island Press, Washington, DC, USA.

Neville, H. M., J. B. Dunham, and M. M. Peacock. 2006. Landscape attributes and life history variability shape genetic structure of trout populations in a stream network. *Landscape Ecology* 21:901-916.

Newman, K. B., S. T. Buckland, B. J. T. Morgan, R. King, D. L. Borchers, D. J. Cole, P. Besbeas, et al. 2014. Integrated population modelling. Pages 169-195 *in* Modelling Population Dynamics, Methods in Statistical Ecology Series. Springer-Verlag, New York, NY, USA.

Nowicki, P., V. Vrabec, B. Binzenhöfer, J. Feil, B. Zakšek, T. Hovestadt, and J. Settele. 2014. Butterfly dispersal in inhospitable matrix: rare, risky, but long-distance. *Landscape Ecology* 29:401-412.

Pagel, J. and F. M. Schurr. 2012. Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Global Ecology and Biogeography* 21:293-304.

Palmer, M. A., J. B. Zedler, and D. A. Falk. 2016. Ecological theory and restoration ecology. Pages 3-26 *in* Foundations of Restoration Ecology, Second Edition, Palmer, M. A., J. B. Zedler, and D. A. Falk (Eds.). Island Press, Washington, DC, USA.

Pardieck, K. L., D. J. Ziolkowski, Jr., and M.-A. R.Hudson. 2014. North American Breeding Bird Survey Dataset 1966–2013, version 2013.0. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD, USA. <http://www.pwrc.usgs.gov/BBS/>. Accessed Apr 2015.

Parnell, N. F. and J. T. Streelman. 2010. The macroecology of rapid evolutionary radiation. *Proceedings of the Royal Society B: Biological Sciences* 278:2486-2494.

Peters, D. P. C., B. T. Bestelmeyer, and M. G. Turner. 2007. Cross-scale interactions and changing pattern-process relationships: consequences for system dynamics. *Ecosystems* 10:790-796.

Ricklefs, R. E. and D. Schluter. 1993. Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press, Chicago, IL, USA.

Rosenzweig, M. L. 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge, MA, USA.

Rybicki, J. and I. Hanski. 2013. Species-area relationships and extinctions caused by habitat loss and fragmentation. *Ecology Letters* 16:27-38.

Sabatino, M., N. Maceira, and M. A. Aizen. 2010. Direct effects of habitat area on interaction diversity in pollination webs. *Ecological Applications* 20:1491-1497.

Sala, O. E., F. S. Chapin, III, J.J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, et al. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770-1774.

Schlesinger, W. H. 1997. Biogeochemistry: An Analysis of Global Change. Academic Press, San Diego, CA, USA.

Schurr, F. M., J. Pagel, J. Sarmento Cabral, J. Groeneveld, O. Bykova, R. B. O'Hara, F. Hartig, et al. 2012. How to understand species' niches and range dynamics: a demographic research agenda for biogeography. *Journal of Biogeography* 39:2146-2162.

Slatkin, M. 1985. Gene flow in natural populations. *Annual Review of Ecology, Evolution, and Systematics* 16:393-430.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10:1115-1123.

Soranno, P. A., K. S. Cheruvelil, E. G. Bissell, M. T. Bremigan, J. A. Downing, C. E. Fergus, C. T. Filstrup, et al. 2014. Cross-scale interactions: quantifying multi-scaled cause-effect relationships in macrosystems. *Frontiers in Ecology and the Environment* 12:65-73.

Storfer, A., M. A. Murphy, J. S. Evans, C. S. Goldberg, S. Robinson, S. F. Spear, R. Dezzani, et al. 2007. Putting the 'landscape' in landscape genetics. *Heredity* 98:128-142.

Suding, K., E. Spotswood, D. Chapple, E. Beller, and K. Gross. 2016. Ecological dynamics and ecological restoration. Pages 27-56 *in* Foundations of Restoration Ecology, Second Edition, Palmer, M. A., J. B. Zedler, and D. A. Falk (Eds.). Island Press, Washington, DC, USA.

Swanson, H. K., M. Lysy, M. Power, A. D. Stasko, J. D. Johnson, and J. D. Reist. 2015. A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. *Ecology* 96:318-324.

Szlavecz, K., P. Warren, and S. Pickett. 2011. Biodiversity on the urban landscape. Pages 75-101 *in* Human Population: Its Influences on Biological Diversity, R. P. Cincotta and L. J. Gorenflo (Eds.). Ecological Studies Series, Volume 214. Springer-Verlag, Berlin, Germany.

Temperton, V. M., A. Baasch, P. von Gillhaussen, and A. Kirmer. 2016. Assembly theory for restoring ecosystem structure and functioning: timing is everything? Pages 245-270 *in* Foundations of Restoration Ecology, Second Edition, Palmer, M. A., J. B. Zedler, and D. A. Falk (Eds.). Island Press, Washington, DC, USA.

Theiling, C. H., J. A. Janvrin, and J. Hendrickson. 2015. Upper Mississippi River restoration: implementation, monitoring, and learning since 1986. *Restoration Ecology* 23:157-166.

Thuiller, W., S. Lavorel, M. B. Araújo, M. T. Sykes, and I. C. Prentice. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America* 102:8245-8250.

Vanderwel, M. C., V. S. Lyutsarev, and D. W. Purves. 2013. Climate-related variation in mortality and recruitment determine regional forest-type distributions. *Global Ecology and Biogeography* 22:1192-1203.

Vitt, P., K. Havens, A. T. Kramer, D. Sollenberger, and E. Yates. 2010. Assisted migration of plants: changes in latitudes, changes in attitudes. *Biological Conservation* 143:18-27.

Wang, S., W. Zhu, X. Gao, X. Li, S. Yan, X. Liu, J. Yang, et al. 2014. Population size and time since island isolation determine genetic diversity loss in insular frog populations. *Molecular Ecology* 23:637-648.

Weinstein, M. P., S. Y. Litvin, and J. M. Krebs. 2014. Restoration ecology: ecological fidelity, restoration metrics, and a systems perspective. *Ecological Engineering* 65:71-87.

West, G. B., J. H. Brown, and B. J. Enquist. 1999. The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science* 284:1677-1679.

White, P. S. and J. L. Walker. 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. *Restoration Ecology* 5:338-349.

Whittaker, R. J. 1998. Island Biogeography: Ecology, Evolution, and Conservation. Oxford University Press, Oxford, UK.

Yackulic, C. B., J. D. Nichols, J. Reid, and R. Der. 2015. To predict the niche, model colonization and extinction. *Ecology* 96:16-23.

Zhang, F., Y. Tao, and C. Hui. 2012. Organism-induced habitat restoration leads to bi-stability in metapopulations. *Mathematical Biosciences* 240:260-266.

CHAPTER 2: DYNAMIC STATE-SPACE MODELS SUGGEST WIDESPREAD DECLINES OF NEARSHORE AND OFFSHORE FISH POPULATIONS RELATE TO PARASITIC LAMPREY AND CLIMATE INFLUENCES IN LAKE HURON

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Abstract

Understanding changes in nearshore and offshore environments of lentic systems is essential for the conservation of freshwater fisheries. Nearshore and offshore environments are diverse, complex, and heterogeneous, with numerous fish species reliant on conditions in both environments because of ontogenetic shifts in habitat use and feeding. Like many lentic systems globally, nearshore and offshore environments of North America's Laurentian Great Lakes have been subjected to a suite of disturbances, including invasive species, climate change, pollution, and habitat degradation. Identifying how disturbances have broadly affected aquatic communities can be challenging because disturbances often occur concurrently, and sampling is typically selective for just one or a few species. We acquired annual count data for multiple fish species from a gillnet assessment program conducted in Ontario waters of Lake Huron (4 zones: two nearshore and two offshore) and fit a set of multivariate state-space models to investigate how zonal fish communities changed from 1998 to 2011. Candidate models allowed for up to three latent trends (i.e., indices of local community change) and considered effects of different anthropogenic and environmental factors on fish communities. We also estimated both local- and regional-scale measures of species diversity (e.g., richness, evenness, turnover) between and among sampled zones. While multi-scale species diversity was stable within and between zones

over the course of study, each of the four zonal fish communities incurred abundance declines for many species—declines influenced by changes in sea lamprey (*Petromyzon marinus*) abundance, lake nutrient cycling, or surface water temperatures over time. Based on our findings, we recommend that conservation efforts focus on ecosystem-level governance of fisheries, including collaborative data networks, inter-jurisdictional fisheries management, and expanded sea lamprey control efforts as well as structural-climatic conditions that help maintain stationary water temperatures and promote nutrient cycling in Lake Huron and other freshwater environments over time in an era of rapidly intensifying anthropogenic change.

Introduction

Understanding changes in nearshore and offshore environments of lentic systems is essential for the conservation of freshwater fisheries. Nearshore and offshore environments are diverse, complex, and heterogeneous, and convey numerous benefits to both human and aquatic organisms. For humans, these environments deliver multiple ecological services, including water supply, hydroelectric power, production of freshwater biota, aesthetics, navigation, and recreation (Barbier et al. 2011). For aquatic organisms, habitats critical for growth, survival, and reproduction occur in these environments (Postel et al. 1997, Giller et al. 2004, Schallenberg et al. 2013, Boulton et al. 2016). In many fish species, reliance on nearshore and offshore environments shifts with ontogeny, with nearshore areas being important nursery habitats for juvenile life stages and offshore areas being where adult life stages primarily reside. Owing to their diverse ecological services, human communities regularly use both nearshore and offshore environments, which influences the myriad threats that lentic systems face globally (Dudgeon et al. 2006, Darwall et al. 2009, Seelbach et al. 2013, Arthington et al. 2016).

Threats to the integrity of nearshore and offshore aquatic communities include climate change, pollution, eutrophication, invasive species, overfishing, habitat degradation, and hydrological regime change (Arthington et al. 2016). These threats pose significant risks to the social, economic, and ecological integrity of nearshore and offshore environments, particularly via disruption of important ecosystem processes and associated services or critical habitats (Giller et al. 2004). Together, such anthropogenic and environmental threats can also diminish the stability of nearshore and offshore environments. The broad-scale patterns of ecosystem and fish community change has been previously described (Bhagat and Ruetz 2011, Larson et al. 2013, Ivan et al. 2014, Fetzer et al. 2017); however, most studies have focused attention on either nearshore or offshore areas (Owens et al. 2003, Connerton et al. 2014, Janetski and Ruetz 2015, Fetzer et al. 2017); rarely have both environments been evaluated concurrently (Gamble et al. 2011a,b).

In North America's Laurentian Great Lakes, nearshore and offshore environments are primarily distinguished based on water depth, with nearshore environments being < 30 m deep and offshore environments being > 30 m deep (Edsall and Charlton 1997). Secondarily, these environments are distinguished based on differences in their supported habitat types. Nearshore environments include nearshore wetlands, river estuaries, and coastal embayments, which are shaped by heterogeneous biotic and abiotic drivers. Offshore environments are open- and deep-water areas, which are shaped by more homogeneous biotic and abiotic drivers at least relative to nearshore environments (Uzarski et al. 2005, Wang et al. 2015). In the Great Lakes, many nearshore and offshore environments have experienced strong ecological disruptions over the past century, including changes in aquatic thermal conditions, lake productivity, and composition of biotic communities (Wehrly et al. 2012). Recent trends in lentic systems suggest that thermal

stratification in the summer months is prolonging (McCormick and Fahnenstiel 1999), and surface water temperatures on average are increasing (Dobiesz and Lester 2009). Changes in trophic status for fish indicate that eutrophication may be occurring, and reduced nutrient loadings and introductions of non-native species (e.g., *Dreissena* spp.) may have shifted primary production from offshore to nearshore areas (Hecky et al. 2004, Vanderploeg et al. 2010). Consequently, it is important to understand the effects these and other ecological changes are having on freshwater fish communities.

Recent research on freshwater ecological change has demonstrated responses of fish communities to assorted drivers (e.g., anthropogenic, environmental) of long-term system dynamics (Dobiesz et al. 2005, Fetzer et al. 2017), particularly in either space or time, nearshore or offshore regions, or various combinations of these; rarely, have all four been evaluated together. Existing nearshore and offshore research has focused on describing spatial dynamics (Uzarski et al. 2005, Trebitz et al. 2009), temporal dynamics (Ludsin et al. 2001, Ivan et al. 2014), or the community dynamics of very nearshore areas (Bhagat and Ruetz 2011, Larson et al. 2013, Janetski and Ruetz 2015). Freshwater fish communities and their spatiotemporal dynamics are controlled by physical, chemical, and biotic factors operating across multiple spatial scales (Wang et al. 2015), thus, highlighting the need for multi-site, broad-scale investigations of fish community change over time (Fetzer et al. 2017).

The purpose of this study was to evaluate how fish communities in Ontario jurisdictional waters of Lake Huron changed from 1998 to 2011 and to investigate what anthropogenic and environmental factors may have spurred these changes. Specifically, our approach was to analyze multi-species abundance time series using multivariate state-space models to elucidate spatiotemporal dynamics of Lake Huron fish communities. Our research objectives included (1)

assessing the degree of similarity in fish communities, (2) determining whether fish communities responded similarly to perturbations during the evaluated time period, (3) correlating individual species to observed fish community changes, and (4) identifying what environmental factors possibly influence fish community changes. We hypothesized that fish community structure would be heterogeneous between nearshore and offshore locations and that changes in fish community trajectories between locations would be best explained by multiple factors summarized at different spatial scales (Mathews and Marsh-Mathews 2016, Fetzer et al. 2017). Finally, we expected that community changes would be driven by species abundance trends and be predicted well by anthropogenic and environmental changes in the lake (Dobiesz and Lester 2009, Fetzer et al. 2017), particularly inferred via the use of state-space time series models (Zuur et al. 2003a,b, Zuur and Pierce 2004). Collectively, our work demonstrates the utility of evaluating multi-species abundance data on broad spatiotemporal scales in the Great Lakes ecosystem, especially when fish community data can be simultaneously tested for identifying dynamics of nearshore and offshore lentic systems.

Methods

Study area

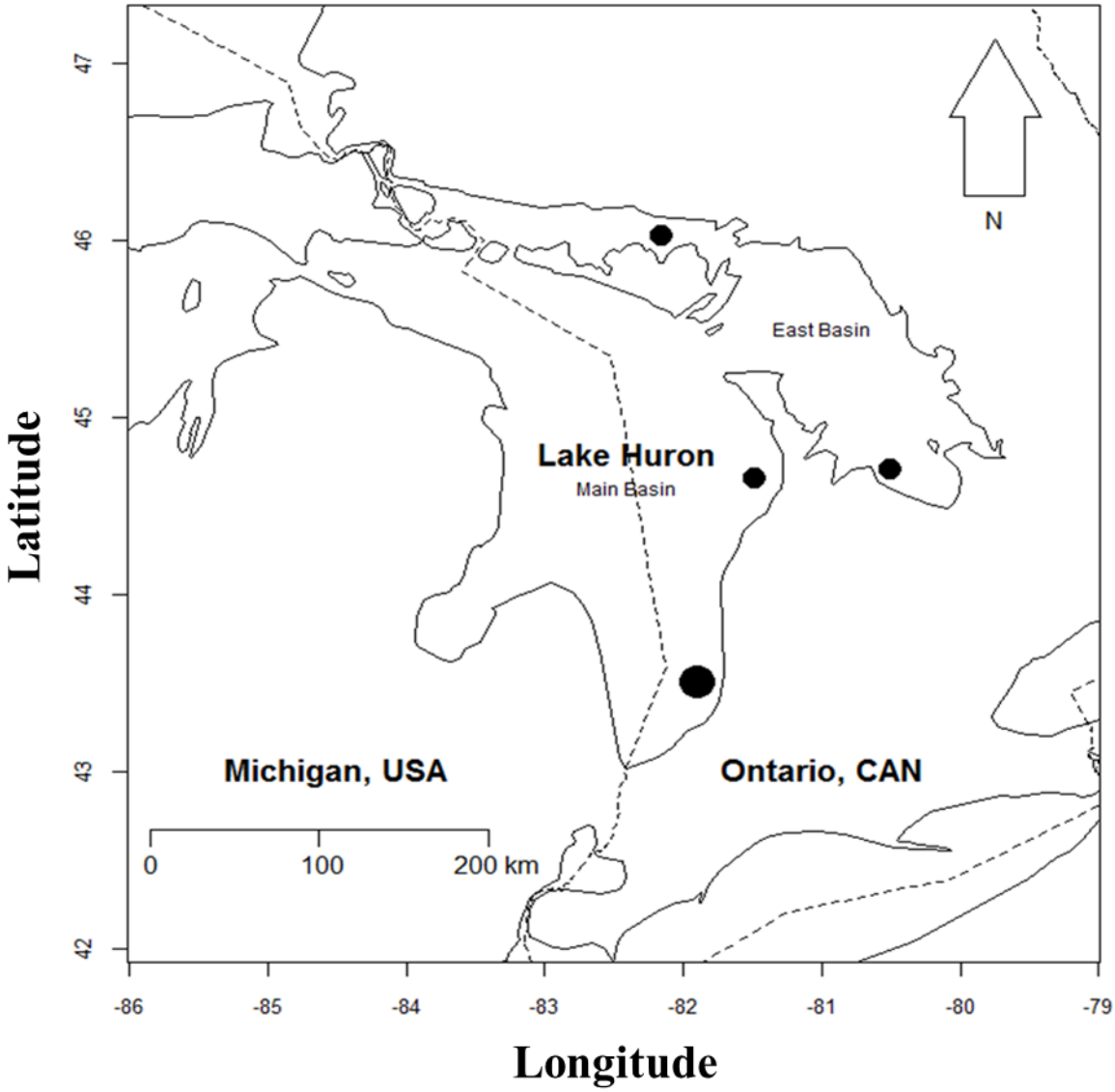
We investigated freshwater fish community dynamics in both nearshore and offshore environments of Ontario jurisdictional waters of Lake Huron (Figure 2.1). Lake Huron is the second largest of the Laurentian Great Lakes, with a surface area of approximately 59,570 km^2 (DesJardine et al. 1995). Geologically, Lake Huron is rimmed to the north and east by the Precambrian Shield formation, which gave rise to the Bruce Peninsula and Manitoulin Islands. These formations separate Lake Huron into two basins, the main and east basin. The smaller east basin consists of the North Channel (3,950 km^2) and Georgian Bay (15,108 km^2), with the larger

main basin comprising 67% of the lakes surface area (DesJardine et al. 1995). Lake Huron is a deep and oligotrophic lake, with an overall mean depth of 59 m and 67% of the lake having depths greater than 30 m (DesJardine et al. 1995).

Lake Huron thermally stratifies each year, typically in late June, with a thermocline at approximately 15-30 m. Historically, summer surface water temperature ranged from 15 to 20˚C, although temperatures have been increasing due to global climate change (Dobiesz and Lester 2009). With respect to nutrient cycling in the lake, upwellings of cold, hypoliminial water are most frequent on exposed basin shorelines (DesJardine et al. 1995).

The native fish community of Lake Huron was historically dominated by lake trout (*Salvelinus namaycush*), walleye (*Sander vitreus*), burbot (*Lota lota*), *Coregonus* spp., and *Cottidae* spp. During the first half of the 20th Century, fish communities in Lake Huron were affected by a multitude of factors, including commercial fishing, introductions of invasive species, including sea lamprey (*Petromyzon marinus*), alewife (*Alosa pseuodoharengus*), rainbow smelt (*Osmerus mordax*), and *Dreissena* spp., habitat degradation, and pollution. In the late 1960s, stocking of Pacific salmonid (*Oncorhynchus* spp.) was initiated to reduce densities of invasive plantktivore species. In the early 2000s, alewife and rainbow smelt populations decreased significantly in abundance, which in turn led to major reduction in Pacific salmonid abundances. This in turn has led to a resurgence in abundance of native species, including lake trout, walleye, and bloater (*Coregonus hoyi*).

Figure 2.1. Nearshore and offshore fish sampling zones (i.e., black circles) in Ontario jurisdictional waters of Lake Huron. Areas of the eastern basin of Lake Huron, listed from north to south, include the eastern North Channel and southern Georgian Bay (i.e., two nearshore locations). Areas of the main basin of Lake Huron, listed from north to south, include central Lake Huron and southern Lake Huron (i.e., two offshore locations). Southern Lake Huron sampling locations were defined by a within-threshold distance of 11 km to one another; whereas, central Lake Huron and the east basin sampling locations were defined within 8 km, which is represented by the relative size of the black circles.



Data collection and preparation

We obtained data on counts of multiple fish species from 1998 to 2011 caught at four zones in Lake Huron: eastern North Channel (nearshore), southern Georgian Bay (nearshore), central

Lake Huron (offshore), and southern Lake Huron (offshore). Species-level count data were collected through a fish community survey involving gillnet sampling conducted by the Ontario Ministry of Natural Resources and Forestry (OMNRF). For each sampling event, gill nets were set for multiple days. The number of gillnet sets (sample) per year varied within and between the four zones. Consequently, we calculated the mean number of fish caught per species across all samples each year as the raw dependent variable. For each gillnet set, eight nets with different mesh sizes were used to sample available fish species. Species-level counts were adjusted by annual sampling effort (i.e., catch per unit of effort) and gillnet configurations (i.e., net mesh size and associated species selectivity), and these adjusted counts are what we modeled.

Mean number of fish caught per species in a sampling year was calculated by summing species-specific catches across all mesh sizes and dividing by the number of gillnet sets (i.e., gillnet set per zone, per year)—an aggregate catch per unit of effort per species. Gillnet configuration remained largely consistent throughout the time series, especially within each sampling zone. In several years, however, two different gillnet configurations were used to evaluate catch differences between the configurations, an objective unrelated to the current study. In our analyses, we did not account for potential differences in catch between gillnet configurations, and although there were some differences in catches, those differences were not sufficiently large to influence community-response patterns. Species we evaluated, but were not necessarily captured at all locations within the four zones, included: alewife, bloater, burbot, Chinook salmon, lake chub (*Couesius plumbeus*), lake whitefish, longnose sucker (*Catostomus catostomus*), rainbow smelt, round whitefish (*Prosopium cylindraceum*), splake (*Salvelinus namaycush fontinalis*), white sucker (*Catostomus commersonii*), and yellow perch.

For relating how fish community and individual species responded to changes in the Lake Huron ecosystem, we acquired time-series data on (a) annual surface water temperatures, (b) estimated number of upwelling days, and (c) water depth, (d) lakewide commercial fish harvest, (e) lakewide zooplankton density, and (f) lakewide estimated abundance of sea lamprey (J. Barber, U.S. Fish and Wildlife Service, *unpublished data*; Table 2.1). For our analysis, we considered zonal and lakewide summaries of predictor variables; however, final predictors were summarized at either the zonal or lakewide scale, owing both to their available resolution and estimated correlation with multi-species (adjusted) abundances (e.g., lakewide, rather than zonal, commercial harvest correlated more highly with zonal fish abundance). Our final predictor variables also correlated Pearson's $|r| < 0.60$ (i.e., pairwise), which help us avoid issues associated with predictor collinearity during model fitting (see *Statistical analysis*). We characterized surface water temperatures as the annual mean number of cumulative degree days > 10°C, which we considered to be a minimum threshold for adequate growth and reproduction of fish species (and primary productivity) at each zone (Magnuson et al. 1979, Cambridge et al. 1987). We also considered the annual mean in the number of days that upwelling—the occurrence of cooler water rising to the lake's surface as warm water is pushed from offshore during high wind events—has occurred at each zone as an index of nutrient cycling in the local area. We characterized mean water depth per zone and assumed it to be constant throughout the study period.

Table 2.1. List of dependent and independent variables for analysis of fish community dynamics in Lake Huron from 1998 to 2011, including each variable's definition, spatial scale(s), and source. With respect to temporal scale, all variables were summarized annually from 1998 to 2011. With respect to spatial scale, variables were either summarized at the zonal, lakewide, or both scales. Zones included central and southern Lake Huron, eastern North Channel, and southern Georgian Bay. All variables were *Z*-score standardized to ensure convergence of the models evaluated. For the commercial harvest predictor, we jointly classified burbot, lake whitefish, and yellow perch as the top predators of other fish species within our sample across the lake, summarized to their collective total catch. For the zooplankton predictor, we used the areal density of calanoid and cylcopoid copepods, daphnid, non-daphnid, and predatory cladocerans, summarized to their joint total estimated.

Variable	Definition	Spatial Scale(s)	Source
Dependent			
Multi-species abundance	Index of abundance for each fish species sampled with gill nets at each location in each nearshore and offshore zone (count)	Zonal	Current study[a]
Independent			
Sea lamprey abundance	Estimated annual number of sea lamprey (*Petromyzon marinus*) in the lake (count)	Lakewide	USFWS[b]
Lake depth	Depth of the lake (m)	Zonal	GLAHF[c]
Lake upwelling	Estimated annual number of upwelling days derived from satellite imagery (count)	Zonal	GLAHF[c]
Commercial harvest	Total annual catch of top fish predators detected in our sample (kg)	Zonal, Lakewide	OMNRF[a]
Zooplankton density	Total annual density of zooplankton species in the lake (count/m^2)	Zonal, Lakewide	GLNPO[d]
Surface water temperature	Annual cumulative degree days derived from satellite imagery (total count of days > 10˚C)	Zonal, Lakewide	GLAHF[c]

[a]OMNRF = Ontario Ministry of Natural Resources and Forestry, Peterborough, ON, CAN and Quantitative Fisheries Center, Michigan State University, East Lansing, MI, USA.
[b]USFWS = U.S. Fish and Wildlife Service, Washington, DC, USA (J. Barber *unpublished data*).
[c]GLAHF = Great Lakes Aquatic Habitat Framework, University of Michigan, Ann Arbor, MI, USA (Wang et al. 2015).
[d]GLNPO = Great Lakes National Program Office, Chicago, IL, USA.

To summarize zonal measures, we used the Aggregate Points tool in ArcGIS v 10.1 (ESRI Inc., Redlands, CA) to form polygons around gillnet sampling locations within an 8 km radius per zone, except at the southern Lake Huron zone for which we used a radius of 11 km for sampling locations. We used an 11-km distance for southern Lake Huron due to its greater number of sampling locations—which comprised two nearby sampling areas (e.g., near Bayfield and Grand Bend, Ontario, CAN)—compared to the other three zones. Threshold distances defined which sampling locations would form the shape of the boundary (i.e., total sampling area) per zone; we chose 8 and 11 km as distances to retain locations spatially similar to one another per zone (Wang et al. 2015). With respect to lakewide variables, for commercial fish harvest, we calculated the annual mean lakewide total yield (kg) of top fish predators detected in our sample—burbot, lake whitefish, and yellow perch. We chose to test lakewide yield because it was more strongly correlated (Pearson's $|r| > 0.60$) with observed zone-level fish communities than were zone-level yields (Pearson's $|r| < 0.40$). We also characterized the annual mean density of zooplankton using lakewide abundances of calanoid and cylcopoid copepods, daphnid, non-daphnid, and predatory cladocerans.

Prior to statistical analysis, we *Z*-score standardized each of the dependent and independent variables (Table 2.1) to facilitate model fitting (Zuur et al. 2003a,b, Zuur and Pierce 2004, Holmes et al. 2012). Standardizing both the dependent and independent variables thus requires that coefficients estimated from the models numerically represent the expected standard deviate (or standard unit) changes in the dependent variables in response to a hypothetical one standard unit increase in each independent variable (Zuur et al. 2003a,b, Zuur and Pierce 2004, Holmes et al. 2012). Regarding the dependent variables (i.e., multi-species fish [adjusted] abundance) per zone, all fish species were sampled each year, except during 2010 at the eastern

North Channel. To account for this missing year, we imputed abundance estimates for each fish species by calculating the mean species (i.e., effort- and selectivity-adjusted) count between years 2009 and 2011, assuming stationarity of the time series. We did not have additional variables available to predict missingness in the eastern North Channel data, which is why we elected to not use model-based imputation approaches.

Statistical analysis

We expected that nearshore and offshore fish communities would differ in the anthropogenic and environmental factors they associated strongest with in Lake Huron (Connerton et al. 2014, Janetski and Ruetz 2015, Gamble et al. 2011a,b, Fetzer et al. 2017). To evaluate this, we examined spatiotemporal trends in species (adjusted) abundance at individual zones (i.e., one candidate model set per zone) using dynamic factor analysis (DFA; Zuur et al. 2003a,b, Zuur and Pierce 2004, Holmes et al. 2012). While other models extend classical factor analysis to consider changing species distributions in space (Thorson et al. 2015, Ovaskainen et al. 2016, Thorson et al. 2016, Tikhonov et al. 2020), DFA evaluates changing species distributions over time (Zuur et al. 2003a,b, Zuur and Pierce 2004, Holmes et al. 2012). DFA belongs to a class of ecological (latent) factor models (Walker and Jackson 2011, Hui et al. 2015), and it estimates x_t, the $m \ll n$ common (latent) trends (i.e., indices of local community change) influencing n species time series. This is a multivariate state-space model, with the state model consisting of the $k < n$ latent trends and an observation model for the vector of observed (adjusted) counts of different species at a given time (y_t), connected to the state variable at that same time (x_t). DFA is an autoregressive model that also allows for linear relation of common latent trends to predictors based on m (i.e., $m \ll n$) hidden random walks. This structure allows for estimation of factor loadings (e.g., correlation coefficients) between species abundances and latent trends (e.g.,

species that correlate positively or negatively with the estimated trends; Zuur et al. 2003a,b, Zuur and Pierce 2004, Holmes et al. 2012). The DFA model is structured as:

$$x_t = Bx_{t-1} + w_t \,, \qquad w_t \sim MVN(0,\ I) \,, \tag{2.1}$$

$$y_t = Zx_t + Dd_t + v_t \,, \qquad v_t \sim MVN(0,\ R) \,, \tag{2.2}$$

$$x_0 \sim MVN(0,\ 5 * I) \,, \tag{2.3}$$

where in Eq. 1, the latent trend x at time t is estimated as a function of the latent trend at time $t-1$ multiplied by the identity matrix B plus the process-level errors w_t, which are multivariate normally distributed with a mean of zero and a variance-covariance matrix I (i.e., the identity matrix). In Eq. 2, the observed multi-species (adjusted) count observations y_t are modeled as a function of randomly varying latent trends x_t multiplied by the factor loadings' matrix Z plus a vector of predictors d_t multiplied by a predictor effects' matrix D plus the observation-level errors v_t, which are also multivariate normally distributed with a mean of zero and a variance-covariance matrix R for the observation errors. In other words, multi-species abundance is estimated by the latent variables plus a deterministic environmental effect, with observed values differing from this due to error. To fit the model, we defined an initial (community, multi-species abundance) state x_0, which was assumed to be multivariate normally distributed with a mean of zero and a variance $5 * I$ (Holmes et al. 2012, Holmes et al. 2018). Because we modeled abundance of individual species over time (i.e., counts adjusted both by sampling effort [e.g., annual catch per unit effort] and gillnet configurations [e.g., net mesh size and associated species selectivity]), we did not need to estimate the catchability (or relative vulnerability to catch) of each species. We also evaluated four variance-covariance matrix structures for Equation 2 as part of the model fitting process (Figure 2.2).

Figure 2.2. Examples of variance-covariance matrices ordered from most to least parsimonious (i.e., least to most complex), assuming a multivariate time series with three hypothetical species. (A) Diagonal and equal variance-covariance, wherein species covariances are equal to zero, and estimated species variances are σ^2. (B) Diagonal and unequal variance-covariance, wherein species covariances are equal to zero, and estimated species variances are σ_i^2 for species i. (C) Equal variance-covariance, wherein estimated species covariances are β, and estimated species variances are σ^2. (D) Unconstrained variance-covariance, wherein estimated species covariances are $\sigma_{i,j}$ for species i and j, and estimated species variances are σ_i^2 for species i.

A

$$\begin{bmatrix} \sigma^2 & 0 & 0 \\ 0 & \sigma^2 & 0 \\ 0 & 0 & \sigma^2 \end{bmatrix}$$

B

$$\begin{bmatrix} \sigma_1^2 & 0 & 0 \\ 0 & \sigma_2^2 & 0 \\ 0 & 0 & \sigma_3^2 \end{bmatrix}$$

C

$$\begin{bmatrix} \sigma^2 & \beta & \beta \\ \beta & \sigma^2 & \beta \\ \beta & \beta & \sigma^2 \end{bmatrix}$$

D

$$\begin{bmatrix} \sigma_1^2 & \sigma_{1,2} & \sigma_{1,3} \\ \sigma_{1,2} & \sigma_2^2 & \sigma_{2,3} \\ \sigma_{1,3} & \sigma_{2,3} & \sigma_3^2 \end{bmatrix}$$

We estimated candidate sets of DFA models to each sampling zone in Lake Huron to evaluate fish community dynamics in the zones independently. However, prior to model fitting, we found that many of our candidate predictor variables were highly collinear (e.g., likely due to variable associations across spatial scales). To avoid estimation issues associated with predictor collinearity, we limited our initial list of predictors to include only those final variables that were correlated Pearson's $|r| < 0.60$ with each other individually on a pairwise basis (Table 2.1). Specifically, we chose to estimate candidate DFA models using only the set of available predictors that were (a) most correlated with multi-species abundance over time, and (b) less correlated with other predictors in the same model. For example, to choose whether to estimate the either effect of zonal- or lakewide-scale commercial harvest (i.e., total annual catch of top

piscivores in kg, a measure which was highly correlated at both spatial scales) on multi-species abundance, we chose to use the scale of harvest that exhibited the highest (mean) correlation to multi-species abundance over time as well as did not too highly correlate with other available predictors (e.g., lakewide sea lamprey numbers).

We fit all possible model combinations of the remaining independent variables because we did not have sufficient information to *a priori* hypothesize unique mechanisms behind the structuring of each zone's fish community individually. Instead, we used a data-driven approach to identify the most parsimonious and best explanatory models of the fish community time series, given the information available. Estimated models also included up to three common latent trends (Zuur et al. 2003a,b, Zuur and Pierce 2004, Holmes et al. 2012). We fit one candidate model set per zone, evaluating the effects of predictors at their annual means. We estimated 768 candidate models (e.g., 64 parameter combinations*4 variance-covariance structures*3 latent trends) to the time-series abundances per zone. We did not include intercept-only models among our set of candidate models because the main aim of this study was to evaluate the effects of chosen predictors on fish community dynamics (Burnham and Anderson 2002). Additionally, we fit all possible candidate models per zone to log-log convergence, as recommended for preliminary model selection (Holmes et al. 2012, Holmes et al. 2018).

We estimated each of our 768 candidate DFA models using maximum-likelihood estimation based on an expectation-maximization algorithm with Kalman-filtering and smoothing for hidden-state estimation (Holmes 2010). As model settings, we initially used the default optimization criteria of 200 minimum iterations, 10,000 maximum iterations, a log-log absolute tolerance level of 0.001 (i.e., called the "abstol" argument), and a slope for the log parameter versus the log iteration tolerance of 0.1 (i.e., called the "conv.test.slope.tol" argument)

to encourage model convergence on stable parameter estimates (Holmes et al. 2012, Holmes et al. 2018). For models that failed to converge under the initial conditions, we relaxed the optimization criteria by 0.1 increments for both the "abstol" and "conv.test.slope.tol" arguments until convergence was achieved. Neither of these arguments exceeded 2.0, and we made such changes to the optimization settings based on recommendations listed in the MARSS user manual, especially for troubleshooting model convergence errors. We fit all our DFA models using the "MARSS.dfa" function in the "MARSS" package version 3.10.10 in R version 4.0.2 (Holmes et al. 2012, Holmes et al. 2018, R Core Development Team 2020).

Best-performing models were selected for each zone based on Akaike's (second-order) Information Criterion (AICc). We considered models with ΔAICc values < 2.0 of the top-ranked model as competitive (Burnham and Anderson 2002); however, we did not use model-averaging because such techniques have not yet been designed for DFA applications (Zuur et al. 2003a,b, Zuur and Pierce 2004, Holmes et al. 2012). Reported results from top-ranked models included: (1) the estimated common latent trends in multi-species fish abundance over time, (2) parameter estimates of coefficient effects on each species, (3) the factor loadings on each species, and (4) patterns of observed versus predicted values including estimates of the relative mean-squared error (relative MSE; i.e., $1 - MSE/var(x_i)$, where x_i represents the observed abundance for fish species i across the time series) of the models—a measure of absolute model fit whereby values closer to 1.0 represent better-fitting models to the data.

In addition to our expectation of different nearshore and offshore community responses to various factors of interest, we also predicted that within- and between-zone community diversity would differ between nearshore and offshore areas (e.g., nearshore communities may respond strongest to impacts from climate warming, leading to local dominance by warm-water species;

Connerton et al. 2014, Janetski and Ruetz 2015, Gamble et al. 2011a,b, Fetzer et al. 2017). To compare community diversity between and among zones, we estimated species richness and evenness (e.g., Shannon-Wiener and inverse-Simpson indices) for each zone using R's "vegan" package version 2.5-6 (Oksanen et al. 2019). We additionally calculated α-, β-, and γ-diversity scores using R's "betapart" package version 1.5.1 (Baselga et al. 2018). To do this, we used raw (unstandardized, adjusted) counts of fish species per zone, and estimated Bray-Curtis distances from the community data per zone. From there, we estimated both Shannon-Wiener and inverse-Simpson diversities per zone. We used permutational multivariate analysis of variation (PERMANOVA) to test for significant differences in fish communities based on Bray-Curtis distances between the four zones. The total number of permutations that was conducted was 999. The PERMANOVA was conducted using the "adonis2" function in the "vegan" package (Oksanen et al. 2019). We tested for homogeneity of dispersion of the fish communities using the "betadisper" function in the *vegan* (Oksanen et al. 2019). After evaluating whether zonal communities were similar in fish community dispersion (Figure A2.1), we computed multiple-site dissimilarities (i.e., β-diversity indices) based on Bray-Curtis distances using the "beta.multi.abund" function in the "betapart" package (Baselga et al. 2018). This calculation allowed us to quantify the balance variation, abundance-gradient variation, and overall dissimilarity components of fish communities between zones (i.e., multiplicative β-diversity = γ / α), which gives insights to the effective number of distinct compositional units within the region (Baselga and Orme 2012, Baselga 2017). All analyses were conducted in R version 4.0.2 (R Core Development Team 2020).

Results

Broad- and local-scale drivers of nearshore and offshore fish communities

Nearshore Environment, Eastern North Channel. A total of nine fish species were collected from the eastern North Channel zone during the study period; individual species (i.e., catch-per-unit-effort and net-selectivity adjusted) abundances ranged from 0.00 to 6,826.03 annually (Table A2.1). Across the entire study period, the mean abundance of collected species was 824.58 (± 2,079.20) fish. The species with the lowest abundances were either burbot, lake chub, longnose sucker, or round whitefish; the species with the highest abundance was yellow perch in all sampling years. Chinook salmon was not observed in the eastern North Channel. Fish community dynamics in the eastern North Channel were best explained by a model with one latent trend (i.e., an index of local community change) and one predictor. A one-trend model with the number of sea lamprey as a predictor, assuming a diagonal and equal variance-covariance matrix for model errors, comprised the top-ranked model; however, this model also competed with a second lamprey model (i.e., < 2.0 ΔAICc) that assumed an equal variance-covariance matrix for the errors (Table 2.2). For simplicity, we only present and interpret the results for the top-ranked model in this zone.

Table 2.2. Subset of candidate dynamic factor analysis models estimated with one latent trend and fit to multi-species fish abundance in the eastern North Channel zone during 1998-2011. Models summarized here only include those that best explained the sampled fish community in the zone, based on Akaike's (second-order) Information Criterion, AICc. "Model" indicates the predictor set evaluated, where "1" represents the model Intercept and "Lamprey" represents the sea lamprey predictor. "VarCov" indicates the form of variance-covariance matrix evaluated, where "DE," "DU," "EVC," and "UN" represent diagonal and equal, diagonal and unequal, equal variance-covariance, and unconstrained matrix forms, respectively. "k" indicates the number of parameters for each model.

Model	**VarCov**	**ΔAICc**	**AICc Weight**	***k***
~1 + Lamprey	DE	0.000	0.684	19
~1 + Lamprey	EVC	1.546	0.316	20
~1 + Lamprey	DU	14.894	0.000	27
~1 + Lamprey	UN	110.520	0.000	63

Table 2.3. Parameter estimates from the top-ranked dynamic factor analysis model estimated with one latent trend and the number of sea lamprey as a predictor and fit to multi-species fish abundance in the eastern North Channel zone during 1998-2011. Standardized (*Z*-scored) estimates and 95% Confidence Intervals are listed per species, and significant effects (i.e., $\alpha <$ 0.05) are noted in bold. The model is summarized in Table 2.2.

Species	**Estimate**	**95% CI**
Alewife	0.009	(-0.468, 0.486)
Burbot	-0.086	(-0.547, 0.376)
Lake chub	-0.137	(-0.609, 0.336)
Lake whitefish	-0.020	(-0.467, 0.426)
Longnose sucker	-0.209	(-0.678, 0.260)
Rainbow smelt	0.343	(-0.103, 0.788)
Round whitefish	-0.174	(-0.631, 0.284)
White sucker	0.233	(-0.244, 0.711)
Yellow perch	0.667	**(0.217, 1.116)**

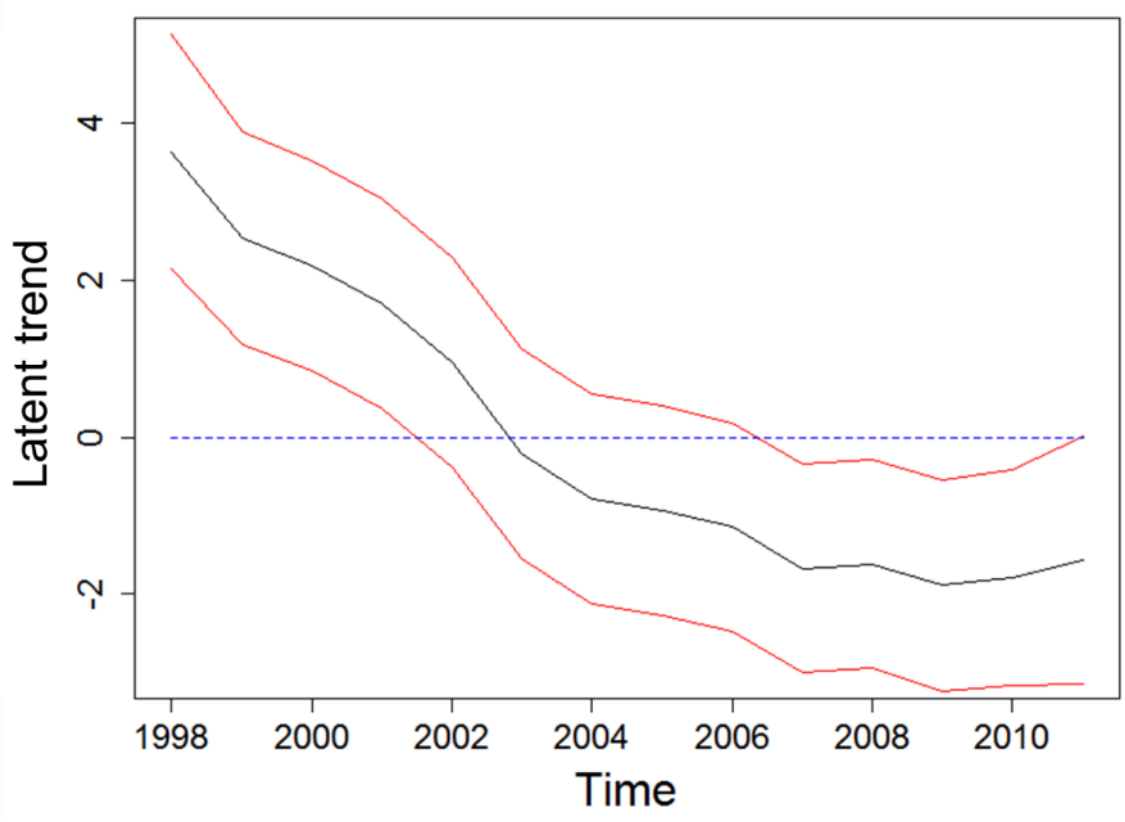
The estimated mean trajectory of the fish community (i.e., latent trend) declined steadily throughout the study period, based on the top-ranked model (Figure 2.3). Of the nine species sampled, only yellow perch responded significantly (and positively) to the effect of sea lamprey numbers lakewide (Table 2.3). Factor loadings from the top-ranked model indicated that 67% of species correlated positively with the declining latent trend (Table 2.4). Alewife, lake chub, and

white sucker loaded most positively on the latent trend, suggesting their abundance declined over time. Burbot, rainbow smelt, and round whitefish loaded negatively on the latent trend, suggesting their abundance increased over time; however, rainbow smelt factor loading was also small. Based on predictions of the top-ranked model of this set, across species, grand mean (± SD) relative MSE was 0.35 (± 0.22; range: 0.06-0.70; Figure A2.2).

Table 2.4. Factor loadings from the top-ranked dynamic factor analysis model estimated with one latent trend and the number of sea lamprey as a predictor and fit to multi-species fish abundance in the eastern North Channel zone during 1998-2011. "Factor Loading" indicates the correlation coefficient per species linearly associated with the direction of its latent trend (see Figure 2.3). The model is summarized in Table 2.2.

Species	Factor Loading
Alewife	0.363
Burbot	-0.245
Lake chub	0.322
Lake whitefish	0.086
Longnose sucker	0.299
Rainbow smelt	-0.052
Round whitefish	-0.211
White sucker	0.353
Yellow perch	0.104

Figure 2.3. Estimated latent trend (± 95% confidence limits) of a top-ranked dynamic factor analysis model fit to multi-species fish abundance in the eastern North Channel zone during 1998-2011. In addition to the effect of the latent trend, the model included the effect of the number of sea lamprey on fish species abundance. The model is summarized in Table 2.2



Nearshore Environment, Southern Georgian Bay. A total of ten fish species were collected from the southern Georgian Bay zone during the study period; individual species (i.e., catch-per-unit-effort and net-selectivity adjusted) abundances ranged from 0.00 to 1,477.27 annually (Table A2.2). Across the entire study period, the mean abundance of collected species was 200.09 (± 401.91) fish. The species with the lowest abundances annually were either lake chub or yellow perch; the most abundance species each year was alewife. Fish community dynamics in southern Georgian Bay were best explained by a model with one latent trend (i.e., an index of local community change) and one predictor. This set did not involve any competing models (i.e., < 2.0 ΔAICc of the top-ranked model), and the top-ranked model including the number of upwelling days as a predictor evidenced the most support from the data (Table 2.5). This model assumed a diagonal and equal variance-covariance matrix for the errors.

Table 2.5. Subset of candidate dynamic factor analysis models estimated with one latent trend and fit to multi-species fish abundance in the southern Georgian Bay zone during 1998-2011. Models summarized here only include those that best explained the sampled fish community in the zone, based on Akaike's (second-order) Information Criterion, AICc. "Model" indicates the predictor set evaluated, where "1" represents the model Intercept and "Upwelling" represents the upwelling predictor. Refer to Table 2.1 for other variable descriptions.

Model	**VarCov**	**ΔAICc**	**AICc Weight**	***k***
~1 + Upwelling	DE	0.000	0.679	21
~1 + Upwelling	EVC	2.649	0.181	22
~1 + Upwelling	DU	3.165	0.140	30
~1 + Upwelling	UN	147.813	0.000	75

Table 2.6. Parameter estimates from the top-ranked dynamic factor analysis model estimated with one latent trend and the number of upwelling days as a predictor and fit to multi-species fish abundance in the southern Georgian Bay zone during 1998-2011. Standardized (*Z*-scored) estimates and 95% Confidence Intervals are listed per species, and significant effects (i.e., $\alpha <$ 0.05) are noted in bold. The model is summarized in Table 2.5.

Species	**Estimate**	**95% CI**
Alewife	-0.021	(-0.469, 0.427)
Burbot	-0.048	(-0.489, 0.392)
Chinook salmon	-0.013	(-0.488, 0.461)
Lake chub	-0.232	(-0.675, 0.211)
Lake whitefish	-0.054	(-0.526, 0.417)
Longnose sucker	0.189	(-0.298, 0.677)
Rainbow smelt	-0.067	(-0.520, 0.386)
Round whitefish	0.867	**(0.426, 1.309)**
White sucker	0.004	(-0.465, 0.474)
Yellow perch	-0.155	(-0.597, 0.286)

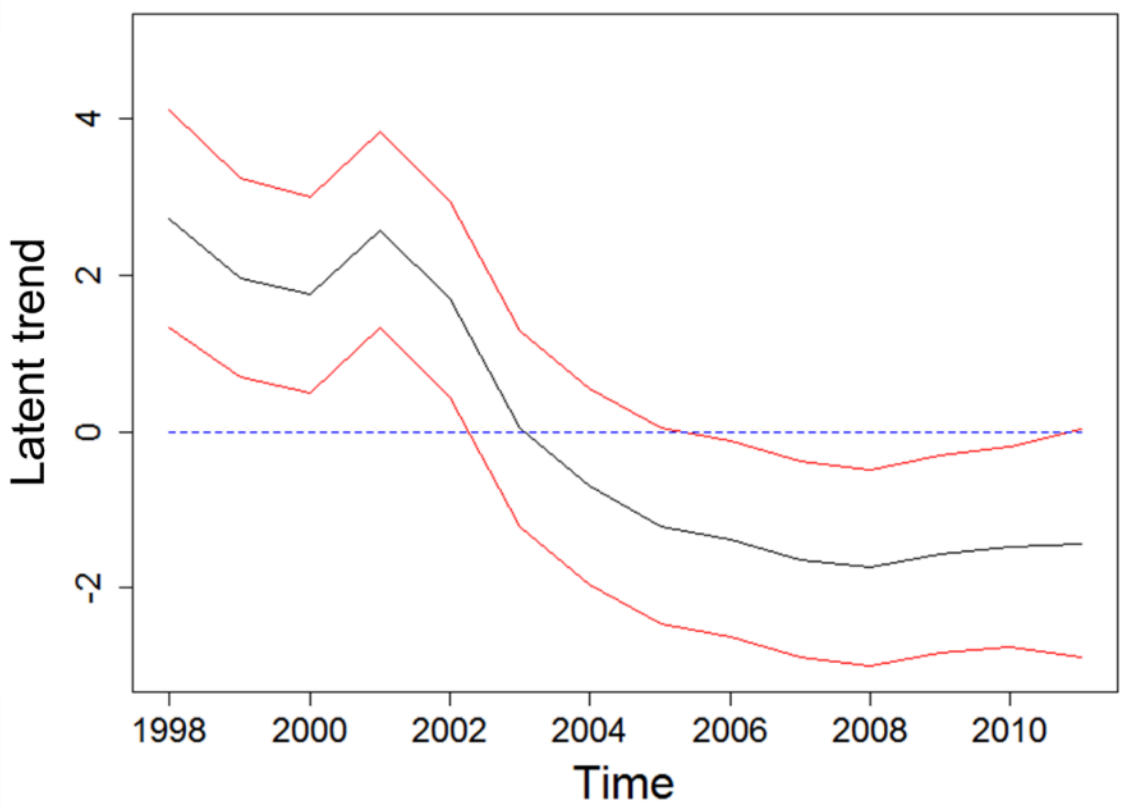
The estimated mean trajectory of the fish community (i.e., latent trend) declined steadily throughout the study period, based on the top-ranked model, including sharp declines detected during 2001-2006 (Figure 2.4). Of the ten species sampled, only round whitefish responded significantly (and positively) to the effect of the number of upwelling days (Table 2.6). Factor loadings from the top-ranked model revealed that 70% of species correlated positively with the declining latent trend (Table 2.7). Chinook salmon, lake whitefish, and longnose sucker loaded

most positively on the latent trend, suggesting their abundance declined over time. Lake chub, round whitefish, and yellow perch loaded negatively on the latent trend, suggesting their abundance increased over time; however, all three factor loadings were quite small. For burbot, the factor loading on the latent trend was very close to zero, suggesting that abundance for the species was stable over time. Based on predictions of the top-ranked model of the mean set, grand mean (± SD) relative MSE was 0.33 (± 0.28; range: 0.07-0.80) across species (Figure A2.3).

Table 2.7. Factor loadings from the top-ranked dynamic factor analysis model estimated with one latent trend and the number of upwelling days as a predictor and fit to multi-species fish abundance in the southern Georgian Bay zone during 1998-2011. "Factor Loading" indicates the correlation coefficient per species linearly associated with the direction of its latent trend (see Figure 2.4). The model is summarized in Table 2.5.

Species	**Factor Loading**
Alewife	0.174
Burbot	0.001
Chinook salmon	0.387
Lake chub	-0.084
Lake whitefish	0.368
Longnose sucker	0.465
Rainbow smelt	0.215
Round whitefish	-0.025
White sucker	0.361
Yellow perch	-0.048

Figure 2.4. Estimated latent trend (± 95% confidence limits) of a top-ranked dynamic factor analysis model fit to multi-species fish abundance in the southern Georgian Bay zone during 1998-2011. In addition to the effect of the latent trend, the model included the effect of the number of upwelling days. The model is summarized in Table 2.5.



Offshore Environment, Central Lake Huron. A total of ten fish species were collected from the central Lake Huron zone; individual species (i.e., catch-per-unit-effort and net-selectivity adjusted) abundances ranged from 0.00 to 153.28 annually (Table A2.3). Across the entire study period, the mean (± SD) abundance of collected species was 17.37 (± 32.58) fish. The species with the lowest abundance during each sampling even was either lake chub or white sucker. The species with the highest abundance was alewife. Fish community dynamics in central Lake Huron were best explained by a model with two latent trends (i.e., indices of local community change) and three predictors: number of upwelling days, cumulative degree days > 10° C, and number of sea lamprey. The top-ranked model assumed a diagonal and equal variance-covariance matrix for model errors; however, this model also competed with two other models (i.e., < 2.0 ΔAICc) that assumed either a diagonal and unequal or equal variance-covariance matrix for the errors (Table 2.8). For simplicity, we only present and interpret the results for the top-ranked model in this zone.

Table 2.8. Subset of candidate dynamic factor analysis models estimated with two latent trends and fit to multi-species fish abundance in the central Lake Huron zone during 1998-2011. Models summarized here only include those that best explained the sampled fish community in the zone, based on Akaike's (second-order) Information Criterion, AICc. "Model" indicates the predictor set evaluated, where "1" represents the model Intercept, "Upwelling" represents the upwelling predictor, "CDD" represents the cumulative degree days > 10˚C predictor, and "Lamprey" represents the sea lamprey predictor. Refer to Table 2.1 for other variable descriptions.

Model	**VarCov**	**ΔAICc**	**AICc Weight**	***k***
~1 + Upwelling + CDD + Lamprey	DE	0.000	0.360	50
~1 + Upwelling + CDD + Lamprey	DU	0.044	0.352	59
~1 + Upwelling + CDD + Lamprey	EVC	0.446	0.288	51
~1 + Upwelling + CDD + Lamprey	UN	347.073	0.000	104

Table 2.9. Parameter estimates from the top-ranked dynamic factor analysis model estimated with two latent trends and fit to multi-species fish abundance in the central Lake Huron zone during 1998-2011. "Predictor" indicates the coefficient effects summarized across both latent trends, where "Upwelling" represents the upwelling predictor, "CDD" represents the cumulative degree days > 10˚C predictor, and "Lamprey" represents the sea lamprey predictor. Standardized (*Z*-scored) estimates and 95% Confidence Intervals are listed per species, and significant effects (i.e., $\alpha < 0.05$) are noted in bold. The model is summarized in Table 2.8.

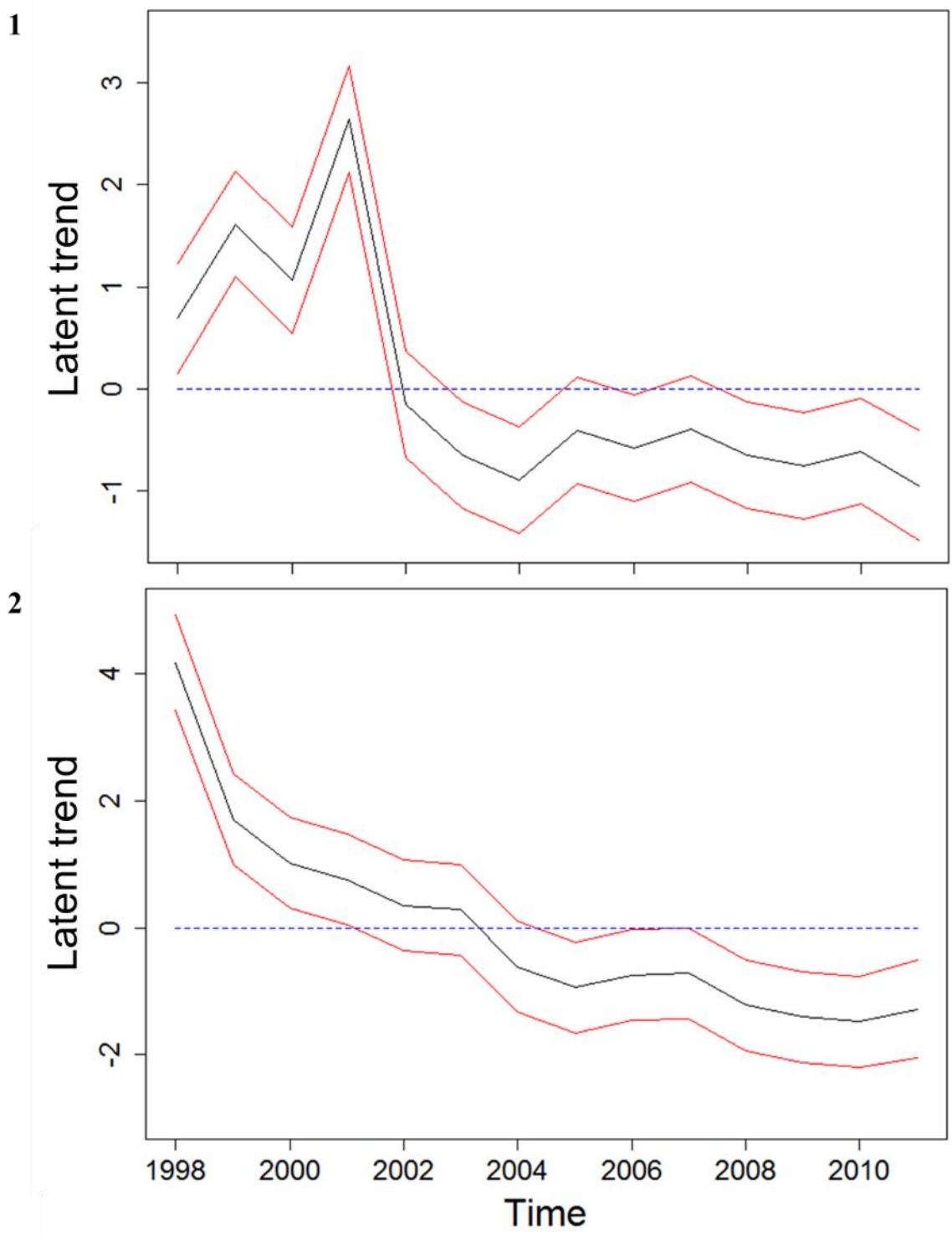
Predictor	Species	Estimate	95% CI
Upwelling	Alewife	0.023	(-0.488, 0.534)
	Burbot	-0.082	(-0.475, 0.312)
	Chinook salmon	-0.189	(-0.692, 0.314)
	Lake chub	-0.014	(-0.443, 0.415)
	Lake whitefish	-0.231	(-0.717, 0.254)
	Longnose sucker	-0.457	**(-0.771, -0.143)**
	Rainbow smelt	-0.064	(-0.444, 0.316)
	Round whitefish	-0.106	(-0.584, 0.371)
	White sucker	-0.145	(-0.644, 0.355)
	Yellow perch	-0.064	(-0.390, 0.262)
CDD	Alewife	-0.221	(-0.688, 0.245)
	Burbot	0.218	(-0.145, 0.581)
	Chinook salmon	-0.244	(-0.704, 0.215)
	Lake chub	0.132	(-0.261, 0.525)
	Lake whitefish	-0.058	(-0.501, 0.386)
	Longnose sucker	0.355	**(0.061, 0.648)**
	Rainbow smelt	0.299	(-0.050, 0.649)
	Round whitefish	0.034	(-0.403, 0.470)
	White sucker	-0.411	(-0.867, 0.045)
	Yellow perch	0.261	(-0.040, 0.562)
Lamprey	Alewife	-0.250	(-0.723, 0.222)
	Burbot	-0.034	(-0.403, 0.335)
	Chinook salmon	-0.513	**(-0.979, -0.048)**
	Lake chub	-0.315	(-0.714, 0.084)
	Lake whitefish	-0.170	(-0.620, 0.279)
	Longnose sucker	0.341	**(0.041, 0.642)**
	Rainbow smelt	-0.018	(-0.374, 0.338)
	Round whitefish	-0.040	(-0.482, 0.402)
	White sucker	-0.272	(-0.734, 0.191)
	Yellow perch	0.727	**(0.418, 1.036)**

Both estimated mean trajectories of the fish community (i.e., latent trends) declined throughout the study period, based on the top-ranked model—including sharp declines detected during 2001-2004 on the first latent trend, alongside steady declines during 1998-2004 on the second trend (Figure 2.5). Of the ten species sampled, and across latent trends, (a) only longnose sucker responded significantly (and negatively) to the effect of the number of upwelling days, (b) only longnose sucker responded significantly (and positively) to the effect of the cumulative degree days > 10˚C, and (c) both longnose sucker and yellow perch responded significantly (and positively) to the effect of sea lamprey numbers lakewide, while Chinook salmon responded significantly (and negatively) to the same factor (Table 2.9). Factor loadings from the top-ranked model revealed that 50% of species correlated positively with each of the two declining latent trends (Table 2.10). Alewife, burbot, Chinook salmon, lake whitefish, and white sucker loaded positively on the first latent trend, suggesting their declining abundance during 2002-2011, despite previous increases during 1998-2001. The other five species loaded negatively on the first latent trend, suggesting increases in their abundance over time. Burbot, lake chub, rainbow smelt, and round whitefish loaded positively on the second latent trend, suggesting declines in their abundance over time. Alewife loaded positively and neutrally on the first and second latent trends, respectively, suggesting declines in its abundance in the zone over time. Based on predictions of the second-ranked model of this set, across species, grand mean (± SD) relative MSE was 0.35 (± 0.32; range: 0.07-0.85) and 0.33 (± 0.36; range: 0.01-0.92), for the first and second latent trends, respectively (Figure A2.4).

Table 2.10. Factor loadings from a dynamic factor analysis model estimated with two latent trends and the cumulative degree days > 10˚C, number of upwelling days, and number of sea lamprey as predictors and fit to multi-species fish abundance in the central Lake Huron zone during 1998-2011. "Trend" indicates the trend to which the loadings belong. "Factor Loading" indicates the correlation coefficient per species linearly associated with the direction of its latent trend (see Figure 2.5). The model is summarized in Table 2.8.

Trend	Species	Factor Loading
1	Alewife	0.900
	Burbot	0.012
	Chinook salmon	0.877
	Lake chub	-0.178
	Lake whitefish	0.829
	Longnose sucker	-0.004
	Rainbow smelt	-0.184
	Round whitefish	-0.410
	White sucker	0.854
	Yellow perch	-0.161
2	Alewife	0.000
	Burbot	0.546
	Chinook salmon	-0.075
	Lake chub	0.632
	Lake whitefish	-0.070
	Longnose sucker	-0.235
	Rainbow smelt	0.470
	Round whitefish	0.687
	White sucker	-0.178
	Yellow perch	-0.230

Figure 2.5. Estimated latent trends (± 95% confidence limits) of a top-ranked dynamic factor analysis model fit to multi-species fish abundance in the central Lake Huron zone during 1998-2011. In addition to the effects of the first and second latent trends, the model included the effects of the cumulative degree days > 10˚C, number of upwelling days, and number of sea lamprey. The model is summarized in Table 2.8.



Offshore Environment, Southern Lake Huron. A total of nine fish species were collected from the southern Lake Huron zone during the study period; individual species (i.e., catch-per-unit-effort and net-selectivity adjusted) abundances ranged from 0.00 to 1,951.15 annually (Table A2.4). Across the entire study period, the mean abundance of collected species was 276.32 (± 583.05) fish. Per year, the fewest fish observed were either burbot, longnose sucker, or round whitefish, and the most fish observed per year were always yellow perch. Contrasted with the eastern North Channel, Chinook salmon was observed, but lake chub was not observed in southern Lake Huron. Fish community dynamics in southern Lake Huron were best explained by a model with one latent trend (i.e., an index of local community change) and one predictor. This set did not involve any competing models (i.e., < 2.0 ΔAICc of the top-ranked model), and the top-ranked model including the number of sea lamprey as a predictor evidenced the most support from the data (Table 2.11). This model assumed a diagonal and equal variance-covariance matrix for the errors.

Table 2.11. Subset of candidate dynamic factor analysis models estimated with one latent trend and fit to multi-species fish abundance in the southern Lake Huron zone during 1998-2011. Models summarized here only include those that best explained the sampled fish community in the zone, based on Akaike's (second-order) Information Criterion, AICc. "Model" indicates the predictor set evaluated, where "1" represents the model Intercept and "Lamprey" represents the sea lamprey predictor. Refer to Table 2.1 for other variable descriptions.

Model	**VarCov**	**ΔAICc**	**AICc Weight**	***k***
~1 + Lamprey	DE	0.000	0.703	19
~1 + Lamprey	EVC	2.559	0.195	20
~1 + Lamprey	DU	3.859	0.102	27
~1 + Lamprey	UN	66.291	0.000	63

Table 2.12. Parameter estimates from the top-ranked dynamic factor analysis model estimated with one latent trend and the number of sea lamprey as a predictor and fit to multi-species fish abundance in the southern Lake Huron zone during 1998-2011. Standardized (*Z*-scored) estimates and 95% Confidence Intervals are listed per species, and significant effects (i.e., $\alpha <$ 0.05) are noted in bold. The model is summarized in Table 2.11.

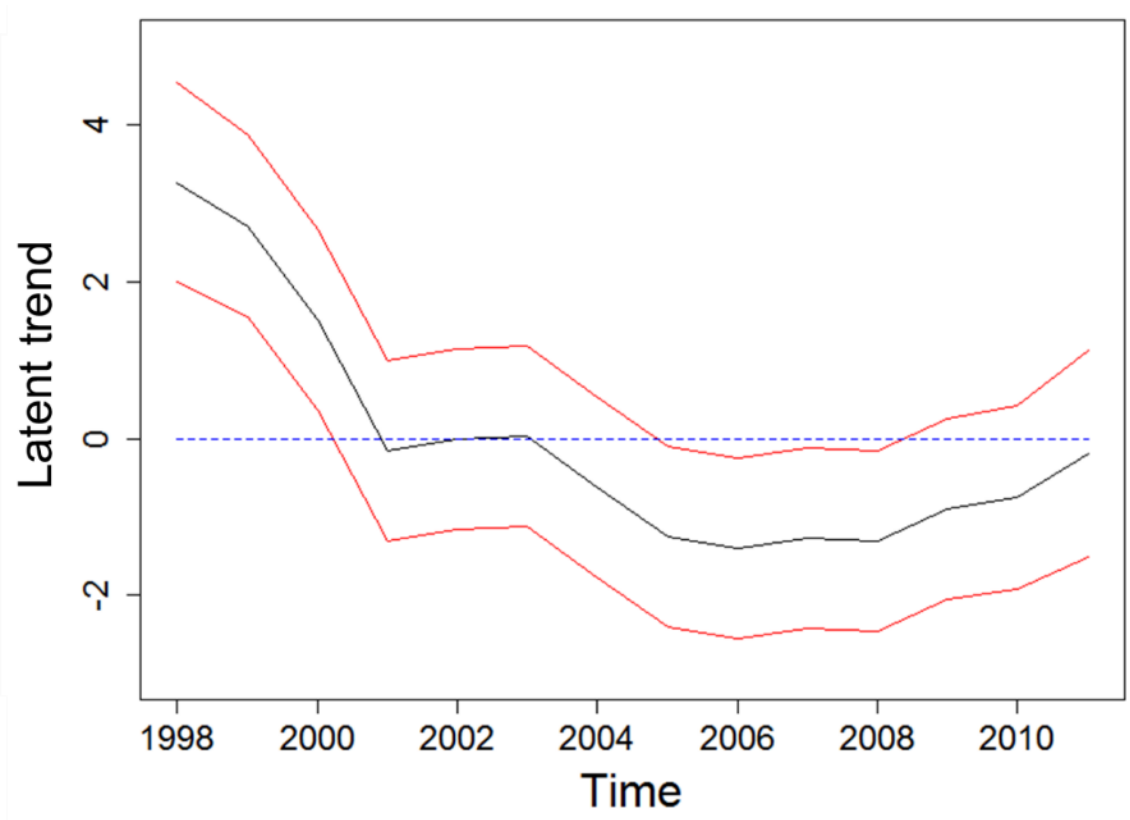
Species	Estimate	95% CI
Alewife	-0.227	(-0.716, 0.263)
Burbot	0.147	(-0.366, 0.660)
Chinook salmon	0.351	(-0.116, 0.818)
Lake whitefish	0.462	**(0.004, 0.921)**
Longnose sucker	-0.408	(-0.872, 0.055)
Rainbow smelt	-0.023	(-0.513, 0.468)
Round whitefish	0.337	(-0.135, 0.808)
White sucker	-0.180	(-0.642, 0.282)
Yellow perch	0.496	**(0.040, 0.953)**

Estimated mean trajectories of the fish community (i.e., latent trend) declined throughout the study period, including sharp declines detected during 1998-2001, based on the top-ranked model (Figure 2.6). Of the nine species sampled, both lake whitefish and yellow perch responded significantly (and positively) to the effect of sea lamprey numbers lakewide (Table 2.12). Factor loadings from the top-ranked model revealed that 67% of species correlated positively with the declining latent trend (Table 2.13). Alewife, burbot, and rainbow smelt loaded most positively on the latent trend, suggesting their abundance declined over time. Lake whitefish, longnose sucker, and white sucker loaded negatively on the latent trend, suggesting their abundance increased over time. Based on predictions of the top-ranked model of the mean set, grand mean (± SD) relative MSE was 0.36 (± 0.25; range: 0.10-0.91) across species (Figure A2.5).

Table 2.13. Factor loadings from the top-ranked dynamic factor analysis model estimated with one latent trend and the number of sea lamprey as a predictor and fit to multi-species fish abundance in the southern Lake Huron zone during 1998-2011. "Factor Loading" indicates the correlation coefficient per species linearly associated with the direction of its latent trend (see Figure 2.6). The model is summarized in Table 2.11.

Species	Factor Loading
Alewife	0.419
Burbot	0.529
Chinook Salmon	0.236
Lake Whitefish	-0.174
Longnose Sucker	-0.242
Rainbow Smelt	0.392
Round Whitefish	0.288
White Sucker	-0.173
Yellow Perch	0.093

Figure 2.6. Estimated latent trend (± 95% confidence limits) of a top-ranked dynamic factor analysis model fit to multi-species fish abundance in the southern Lake Huron zone during 1998-2011. In addition to the effect of the latent trend, the model included the effect of the number of sea lamprey. The model is summarized in Table 2.11.



Diversity patterns in nearshore and offshore fish communities

Two tests of community dispersion corroborated that zonal fish communities were homogeneous in their variance: mean distances to median included 0.59, 0.53, 0.41, and 0.59 for eastern North Channel, southern Georgian Bay, and central and southern Lake Huron, respectively (i.e., Communities ~ Zones with $F_{3,28}$ =1.57 and 1.08 as well as p = 0.22 and 0.35 for "betadisper" conventional- and "adonis2" permutational-ANOVAs, respectively; Figure A2.1). Homogeneity of community variances thus promoted comparisons of within- and between-unit diversities. At the local scale (α-level) of species diversity, mean (± SD) species richness was estimated as 7.86 (± 0.86), 8.79 (± 0.70), 9.50 (± 0.65), and 7.50 (± 1.02) for eastern North Channel, southern Georgian Bay, and central and southern Lake Huron, respectively. Listing zones in the same order, Shannon-Wiener mean (± SD) species evenness was estimated as 2.06 (± 0.03), 2.14 (± 0.04), 2.12 (± 0.07), and 2.04 (± 0.05), and inverse-Simpson species mean (± SD) evenness was estimated as 7.74 (± 0.32), 8.26 (± 0.51), 8.03 (± 0.77), and 7.61 (± 0.42). At the regional scale (γ-level) of species diversity, a maximum of ten species were observed across the four zones. Between zones, site-to-site (β-level) species diversity was estimated near unity, 0.01 for the balanced variation, 0.96 for the abundance-gradient, and 0.97 for the overall dissimilarity components of diversity at this spatial scale.

Discussion

We found that multi-scale species diversity was similar across two nearshore and two offshore zones of Lake Huron's east and main basins, respectively, which was contrary to our hypothesis of community heterogeneity between nearshore and offshore locations. For example, we expected that offshore zones would be more speciose than nearshore zones, particularly due to impacts from accelerated warming in nearshore areas due to changes in regional climate. We

also found that diversity was not best explained by multiple factors acting in concert to shape fish community composition, contrasting our hypothesis that community dynamics would be best explained by multiple synergistic factors between nearshore and offshore areas. However, while zonal fish communities were similar in their composition, the fish community dynamics between zones slightly differed and were best explained by either one or two latent trends as well as species-specific deterministic effects of multiple independent variables (i.e., lakewide sea lamprey abundance, zonal upwelling days, zonal surface water temperatures, or all of the above)—patterns that we now describe and interpret in greater detail below.

Nearshore and offshore communities decline with broad- and local-scale drivers

Fish community dynamics in central Lake Huron (offshore) were best explained by annual lakewide changes in the abundance of sea lamprey and surface water temperatures as well as zonal changes in the number of upwelling days over time. Dynamics in the eastern North Channel (nearshore) and southern Lake Huron (offshore) were best explained by annual lakewide changes in the abundance of sea lamprey over time. Dynamics in the southern Georgian Bay (nearshore) zone were best explained by annual zonal changes in the number of upwelling days over time. Despite dissimilarity in species- and community-level responses to different factors, including minor differences between nearshore and offshore zones, many of the observed fish populations between communities declined over the course of the study period. Finally, in each of the four zones, many observed species associated positively with declining (latent) community trends, suggesting declines in their individual populations—contrasting species that loaded negatively on declining trends, indicating increases in their abundance over time.

Fish communities in the eastern North Channel (nearshore), southern Georgian Bay (nearshore), and central and southern Lake Huron (offshore) responded differently for a subset of jointly observed species. For example, alewife, lake whitefish, longnose sucker, and white sucker each declined in abundance at the nearshore locations over the study period; whereas, round whitefish increased in abundance. Additionally, alewife, burbot, Chinook salmon, rainbow smelt, and round whitefish each declined in abundance at the offshore locations over the study period; whereas, longnose sucker increased in abundance. Another subset of species also responded differently between the aforementioned nearshore and offshore zones. In nearshore areas, burbot, lake chub, rainbow smelt, and yellow perch either increased, decreased, or stabilized in abundance per zone over time, and only Chinook salmon was observed at southern Georgian Bay. In offshore areas, lake whitefish, white sucker, and yellow perch either increased, decreased, or stabilized in abundance per zone over time, and only lake chub was observed at central Lake Huron. Only alewife consistently decreased in abundance across the four zones over time, as indicated by its positive factor loadings on estimated latent trends.

Despite previous research identifying differences between nearshore communities attributed to fine-scale temperature and productivity regimes in coastal areas throughout U.S. jurisdictional waters of Lake Huron (Fetzer et al. 2017), we did not detect similar nearshore dynamics in the Ontario jurisdictional waters. In the absence of local productivity data, however, surface water temperatures were identified as influential in the central Lake Huron zone. Other studies found that fish communities typically differed across space and within, yet not between, years in Lake Michigan (i.e., nearshore; Bhagat and Ruetz 2011, Janetski and Ruetz 2015) and Lake Superior (i.e., offshore; Gamble et al. 2011b), and assemblage differences were attributed to inter-site variation in factors such as specific conductivity, dissolved oxygen, pH, vegetation

cover, turbidity, or water depth. While many such fine-scale covariates were unavailable to our study, we did not find that water depth influenced the composition or trajectory of nearshore and offshore fish communities. Additionally, our study describes similar fish community dynamics between sites and years. In Lake Superior, one study reported that while nearshore and offshore food webs varied in terms of their species richness, food webs between such areas exhibited incredibly similar trophic structures (Gamble et al. 2011a). In contrast, our study highlights community similarities partly attributable to a similar catch composition as well as an informative suite of multi-scale anthropogenic and environmental factors, including compositional and trajectory similarities between nearshore and offshore communities, despite lacking additional covariates to test (e.g., macroinvertebrate abundance, turbidity, water chemistry, vegetation characteristics, and more).

Comparable species responses between nearshore and offshore communities suggest several possible explanations (e.g., meta-community dynamics; Leibold et al. 2004) while differential species responses between related locations suggest others (e.g., differences in habitat quality and quantity as well as other fine-scale covariates; Fetzer et al. 2017). For instance, at both nearshore and offshore zones, population declines in alewife, burbot, Chinook salmon, lake whitefish, longnose sucker, rainbow smelt, round whitefish, and white sucker suggest that, besides sea lamprey (i.e., at the eastern North Channel and central and southern Lake Huron) or upwelling (i.e., at southern Georgian Bay) impacts indicated by our models, concomitant declines in the quality and quantity of benthic/limnic habitat and prey may also be involved in such species' declines (e.g., Chinook salmon declines coincided with declines in pelagic prey prior to 2004; Bence and Mohr 2008). Habitat quality may be most impacted by both long-term changes in surface water temperatures (e.g., implicated by the dynamics in

central Lake Huron), vegetation, or lake turbidity—among other differences between spawning and foraging habitats, which may influence changes in population recruitment dynamics. Additionally, prey availability for piscivores/benthivores between zones may be most impacted by long-term shifts in *Diporeia* species abundance, a benthic amphipod that historically was an important food resource for many fish species in the lake (Bence and Mohr 2008, Riley 2013). Declines in the abundance of other macroinvertebrates and alewife also likely contributes to decreased piscivore/benthivore growth, survival, and reproduction over time (Bence and Mohr 2008, Riley 2013). That said, however, we were not able to test such speculations in the current study because we lacked multi-scale habitat and prey data. For those species populations differentially responding between nearshore areas, other possibilities may be involved, including dissimilar surface water temperatures, habitat and prey availability, predatory pressures, or other mechanisms (e.g., compensatory and density-dependent relationships; Ivan et al. 2011).

Nearshore and offshore diversity suggests similar community-structuring dynamics

Parallel findings in fish community responses between nearshore and offshore areas have multiple possible explanations. The first explanation may relate to insufficient detection of incidentally omitted fish species, even though we accounted for this potential bias by using gill nets with an array of mesh sizes to capture fish from a variety of length categories, and we also made quantitative adjustments to abundances of observed fish (e.g., catch weighted by unit of effort). In turn, we have good reason to trust that imperfect species detection likely did not bias our final community results. A second explanation for why fish communities in nearshore and offshore areas may have responded differently is due to the scale of perturbations that have occurred recently in Lake Huron that were suspected to have broad impacts on fish communities. For example, alewife population abundance was severely reduced in Lake Huron in the early

2000s due to what is likely a combination of bottom-up and top-down effects (Dobiesz 2003, Dobiesz et al. 2005, Bence and Mohr 2008, Kao et al. 2016). Our study results captured this tremendous decline in alewife abundance across all zones. In the early 2000s, declines in alewife abundance had major repercussions on piscivores that preyed on alewife (Bence and Mohr 2008, Riley 2013, Kao et al. 2016). Our DFA models take such population patterns into account as part of their latent trend estimation. In other words, community trends may be unobserved, but the dynamics of important prey species (e.g., alewife) may shape trajectories of other species (e.g., salmonines). For instance, DFA estimates average patterns of local community change across species, patterns that likely reflect not only species-level population change, but also interspecies competition for food and other resources—especially responses of predators to prey population changes and vice versa. In fact, ecological correlations between species are implicitly accounted for in the different variance-covariance structures (Zuur et al. 2003a,b, Zuur and Pierce 2004, Holmes et al. 2012, Holmes et al. 2018). Taken together, it is therefore likely that simultaneous evaluation of interdependent fish species explains similar community declines observed for certain species between the four zones.

A third explanation for our common findings may involve two paradigms of meta-community theory (i.e., species-sorting and mass-effects dynamics; Leibold et al. 2004, Soininen 2014). The species-sorting perspective assumes that both dispersal and patch quality affect local community structure, but it also emphasizes spatial niché separation above and beyond the effects of dispersal alone. In other words, species-sorting assumes that species dispersal is sufficiently low enough to allow communities to match available nichés in a location, but not so low that species cannot track changes in conditions (Leibold et al. 2004, Holyoak et al. 2005). Therefore, local community dynamics are primarily driven by conditions in the local

environment, and species dispersal ability is of great importance (Padial et al. 2014, Heino et al. 2015). In the current study, we detected patterns suggestive of species-sorting dynamics across the zones that we sampled. For example, we observed population declines of lake whitefish at three of the four zones sampled; only the lake whitefish subpopulation at southern Lake Huron increased over time. Based on the work of Rennie et al. (2012), we know that lake whitefish disperse < 20 km from tagging/spawning locations in Lake Huron, and because each of the four zones we sampled were spaced > 100 km apart (Figure 2.1), it is possible that lake whitefish population dynamics suggest that the species may be tracking local conditions (e.g., changes in patch quality due to prey availability) and sorting along resource gradients between nearby nearshore and offshore areas. In freshwater environments, in general, dispersal ability is inversely related to species body size (Shurin et al. 2009, De Bie et al. 2012, Farjalla et al. 2012), and thus large-bodied organisms (e.g., fish and macrophytes) likely have relatively lower dispersal ability than small-bodied organisms (e.g., plankton and benthic invertebrates). Differences in fish dispersal ability may also explain why we observed larger-bodied species such as longnose sucker decline in abundance at only half of the zones we sampled (i.e., at the eastern North Channel and southern Georgian Bay); whereas, longnose sucker increased at the other two zones over time—suggesting that greater dispersal ability may allow this species to readily track local conditions and move between disparate nearshore and offshore locations in the lake.

Differences in species dispersal ability also allow for comparisons and contrasts to meta-community paradigms (i.e., other than species sorting) between distant sites inhabited by similar fish species (Padial et al. 2014). Unlike species-sorting dynamics, the mass-effects perspective assumes that heterogeneity in patch quality interacts with species' nichés to structure local

communities over space, yet this perspective further assumes dispersal from the broader meta-community has a strong and persistent influence on local community dynamics (Leibold et al. 2004). Under mass-effects dynamics, immigration rates of local communities may be high enough to allow local persistence of a population that, in the long term, may decline. (Mouquet and Loreau 2003). Given that species diversity did not change between the zones we sampled, and despite population declines for many species, we suspect that species dispersal rates in the lake remained relatively stable from 1998 to 2011, which suggests that either species-sorting or mass-effects dynamics may structure fish communities in Lake Huron. In the current study, we also did not detect evidence for fish communities to be structured based on other meta-community paradigms (e.g., patch or neutral dynamics with respect to habitat quantity and quality or species functional interchangeability, respectively). We also did not measure individual fish movements between the sampling zones (e.g., immigration and emigration rates) nor did we measure species competitive performance (e.g., dominance and subordinance trends), both characteristics that would strongly support the mass-effects paradigm. Therefore, our results suggest species-sorting is one plausible explanation for similar zonal trends detected in fish community change over time.

The species-sorting perspective is further implicated by responses of zonal fish communities to similar lake factors that we evaluated, particularly whether those factors were summarized on local- or broad-scales. Fish community patterns at the eastern North Channel, as well as southern Lake Huron, were best explained by only one factor, annual changes in lakewide sea lamprey numbers. Community patterns at the southern Georgian Bay were best explained only by changes in the annual number of upwelling days, and at the local scale. Community patterns at central Lake Huron were best explained by three factors: lamprey

numbers, surface water temperatures, and upwelling events. Latent community trends across zones, which correlated with declines in many fish species, likely also exacerbated changes to aquatic gradients in food, habitat, movement, survival, and reproduction in our study area over the period examined. Consequently, we further suspect a heightened role of species-sorting dynamics that both assembles and maintains fish communities in Lake Huron. Such community-structuring dynamics may also be likely because species-sorting best explains fish meta-community structure in other freshwater environments (Erős et al. 2012, Heino 2013, Davis et al. 2014, Padial et al. 2014); however, mass-effects dynamics are implicated to a lesser degree (Urban 2004, Stoffels et al. 2014, Heino et al. 2015).

Analysis limitations and research-management implications

Essential to discussion of common findings with respect to evaluating fish community dynamics between zones, our project has a few data limitations, which will be particularly important to future research of Lake Huron, especially during a period of stark ecological change (Wehrly et al. 2012, Fetzer et al. 2017). While our candidate DFA models evaluated the importance of potential effects of sea lamprey, commercial harvest, zooplankton, water depth, upwelling days, and surface water temperatures on fish communities over time, our candidate models did not consider impacts of other important environmental factors in the lake. Since the late-1990s, we know that the invasion of Dreissenid (i.e., zebra and quagga) mussels has negatively impacted lakewide water clarity (e.g., as measured by secchi disk depths), primary production (e.g., chlorophyll *a* concentrations), and macroinvertebrate production (e.g., *Diporeia* amphipod abundance). Subsequently, major shifts in lake water quality and its food web have had considerable effects on fish species dependent on phytoplankton and *Diporeia* as important food sources (Bence and Mohr 2008, Riley 2013); however, our models did not account for such

changes in lakewide productivity dynamics over time. This was because complete time-series data on such variables were not publicly available at the same spatiotemporal scale of our analyses, particularly during 1998-2011. Lacking data availability and completeness also highlights the importance of improved data sharing between research and management organizations in the Great Lakes (e.g., like the Great Lakes Aquatic Habitat Framework, among other programs; Wang et al. 2015). Based on our knowledge of historic reports on the state of Lake Huron and other published literature, we know that the aforementioned environmental variables would be important to evaluate in future state-space models of fish community dynamics, and we neither had sufficient spatiotemporal measures of nor adequate proxies for such recent environmental changes in Lake Huron. Therefore, we caution that not only should our results be judged considering such limitations, but future research should also consider the inclusion of interannual indices (or proxies) for invasive mussels, turbidity, primary production, and macroinvertebrate production, particularly on broad spatial scales. Additionally, future research should prioritize inclusion of fish communities from more areas of Lake Huron than simply its Ontario waters.

In conclusion, we found that while nearshore and offshore locations may be assumed to be different in terms of habitat conditions (e.g., due to water depth, temperature, and vegetation), and many Lake Huron fish communities responded similarly to environmental changes, based on only one to three environmental factors: annual (lakewide) sea lamprey numbers, (lakewide) surface water temperatures, or (zonal) number of upwelling days. We also found that annual (lakewide) zooplankton numbers, (zonal) water depth, and (zonal) harvest of top predators were not important for describing changes between zonal fish communities over time. While other environmental variables unavailable to this study might explain additional variability in the fish

communities we observed, our results highlight several important commonalities in fish assemblages between distant locations—patterns suggesting that related management be deployed to improve fish community status and sustainability on broad scales. Importantly, new collaborative networks and databases are still necessary for archiving, sharing, and distributing data on diverse macroecological processes in the Great Lakes ecosystem. These networks and their databases would further assist researchers with special attention given to the spatiotemporal coverage, extent, and resolution of archived variables. Relatedly, conservation efforts should likely focus their resources on continued support for ecosystem-level governance and collaborative data networks, increased sea lamprey control efforts, and structural and climatic conditions that help maintain stationary water temperatures and promote nutrient cycling in Lake Huron and other freshwater environments over time in an era of intensifying anthropogenic change.

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manuscript, respectively. We also thank the late B. Maurer for his leadership, legacy, and guidance on this project, and this manuscript is dedicated to his memory.

APPENDIX

APPENDIX

Table A2.1. Observed annual mean (± SD) number of total fish caught at the eastern North Channel zone, during 1998-2011. We also provide grand mean (± SD) summaries of the model predictors for this zone. Recall that sea lamprey abundance, commercial harvest of top predators, and zooplankton density were estimated at the lakewide scale, and thus were treated as similar between zones.

Year	**Value**[†]
1998	827.75 (± 2,181.24)
1999	837.02 (± 2,235.71)
2000	847.29 (± 2,247.47)
2001	834.74 (± 2,223.84)
2002	819.51 (± 2,180.35)
2003	813.40 (± 2,170.71)
2004	814.59 (± 2,171.83)
2005	825.35 (± 2,197.00)
2006	828.42 (± 2,192.33)
2007	821.09 (± 2,190.96)
2008	832.59 (± 2,224.00)
2009	814.44 (± 2,179.32)
2010	814.14 (± 2,178.03)
2011	813.84 (± 2,176.73)
Predictors	
Lake depth (m)	20.17 (± 13.07)
Sea lamprey (count)	162,799.30 (± 40,434.98)
Lake upwelling (count)	1.83 (± 1.33)
Harvest of top predators (kg)	782,001.70 (± 1,241,306)
Zooplankton density (count/m^2)	92,844.98 (± 46,854.28)
Cumulative degree days > 10˚C (count)	2,754.85 (± 27.55)

[†]For each year, "Value" summarizes the raw (observed) mean (± SD) number of total fish caught; whereas, for the model predictors, it summarizes the raw (observed) mean (± SD) of each variable.

Table A2.2. Observed annual mean (± SD) number of total fish caught at the southern Georgian Bay zone, during 1998-2011. Refer to Table 2.1 for other variable descriptions.

Year	**Value**[†]
1998	202.69 (± 415.27)
1999	198.70 (± 416.44)
2000	203.24 (± 423.87)
2001	209.32 (± 431.11)
2002	224.10 (± 483.90)
2003	198.07 (± 417.32)
2004	197.80 (± 418.11)
2005	195.36 (± 414.54)
2006	195.16 (± 413.66)
2007	195.46 (± 413.85)
2008	194.70 (± 414.00)
2009	195.36 (± 414.18)
2010	195.66 (± 413.80)
2011	195.58 (± 413.36)
Predictors	
Lake depth (m)	42.90 (± 17.59)
Sea lamprey (count)	162,799.30 (± 40,434.98)
Lake upwelling (count)	0.16 (± 0.12)
Harvest of top predators (kg)	782,001.70 (± 1,241,306)
Zooplankton density (count/m^2)	92,844.98 (± 46,854.28)
Cumulative degree days > 10˚C (count)	2,612.97 (± 33.19)

[†]For each year, "Value" summarizes the raw (observed) mean (± SD) number of total fish caught; whereas, for the model predictors, it summarizes the raw (observed) mean (± SD) of each variable.

Table A2.3. Observed annual mean (± SD) number of total fish caught at the central Lake Huron zone, during 1998-2011. Refer to Table 2.1 for other variable descriptions.

Year	Value[†]
1998	20.48 (± 35.30)
1999	19.69 (± 37.84)
2000	18.88 (± 34.24)
2001	22.09 (± 46.54)
2002	17.57 (± 34.37)
2003	16.44 (± 32.60)
2004	15.99 (± 32.39)
2005	15.77 (± 31.55)
2006	15.00 (± 31.68)
2007	17.00 (± 31.16)
2008	16.66 (± 31.90)
2009	15.63 (± 31.55)
2010	15.60 (± 31.70)
2011	16.42 (± 32.04)
Predictors	
Lake depth (m)	41.57 (± 22.32)
Sea lamprey (count)	162,799.30 (± 40,434.98)
Lake upwelling (count)	0.33 (± 0.60)
Harvest of top predators (kg)	782,001.70 (± 1,241,306)
Zooplankton density (count/m^2)	92,844.98 (± 46,854.28)
Cumulative degree days > 10˚C (count)	2,752.27 (± 77.58)

[†]For each year, "Value" summarizes the raw (observed) mean (± SD) number of total fish caught; whereas, for the model predictors, it summarizes the raw (observed) mean (± SD) of each variable.

Table A2.4. Observed annual mean (± SD) number of total fish caught at the southern Lake Huron zone, during 1998-2011. Refer to Table 2.1 for other variable descriptions.

Year	**Value**[†]
1998	292.37 (± 628.25)
1999	277.70 (± 611.43)
2000	285.02 (± 643.33)
2001	268.56 (± 599.91)
2002	276.13 (± 613.23)
2003	271.73 (± 604.44)
2004	272.78 (± 611.92)
2005	272.36 (± 609.13)
2006	275.83 (± 615.02)
2007	272.87 (± 611.36)
2008	278.63 (± 624.14)
2009	271.90 (± 610.18)
2010	274.93 (± 617.30)
2011	277.65 (± 622.11)
Predictors	
Lake depth (m)	31.94 (± 17.29)
Sea lamprey (count)	162,799.30 (± 40,434.98)
Lake upwelling (count)	0.01 (± 0.03)
Harvest of top predators (kg)	782,001.70 (± 1,241,306)
Zooplankton density (count/m^2)	92,844.98 (± 46,854.28)
Cumulative degree days > 10˚C (count)	3,072.19 (± 104.55)

[†]For each year, "Value" summarizes the raw (observed) mean (± SD) number of total fish caught; whereas, for the model predictors, it summarizes the raw (observed) mean (± SD) of each variable.

Figure A2.1. Similarities quantitatively characterized between fish communities sampled across four zones in Lake Huron during 1998-2011. We aggregated zonal fish communities and represented their row-wise dissimilarities based on the Bray-Curtis distance metric in R's *vegan* package. "CLH," "ENC," "SGB," and "SLH" represent the four zones: central Lake Huron, eastern North Channel, southern Georgian Bay, and southern Lake Huron, respectively. (A) Pairwise differences in community means per group (i.e., zone), including 95% confidence limits—based on a familywise-error rate defined by Tukey's Honest Significant Difference test. (B) Boxplots displaying the interquartile ranges (i.e., lower whisker, 25% quantile, 50% quantile [median; dark line], 75% quantile, upper whisker, and any extreme values [points]) of row-wise distances to community centroids. (C) Community ellipsoids displayed by their first and second Principal Coordinate Analysis (PCoA) axes, wherein zonal labels reside at their community centroids, and lighter (central) lines connect to the vertices of ellipsoid boundaries.

A

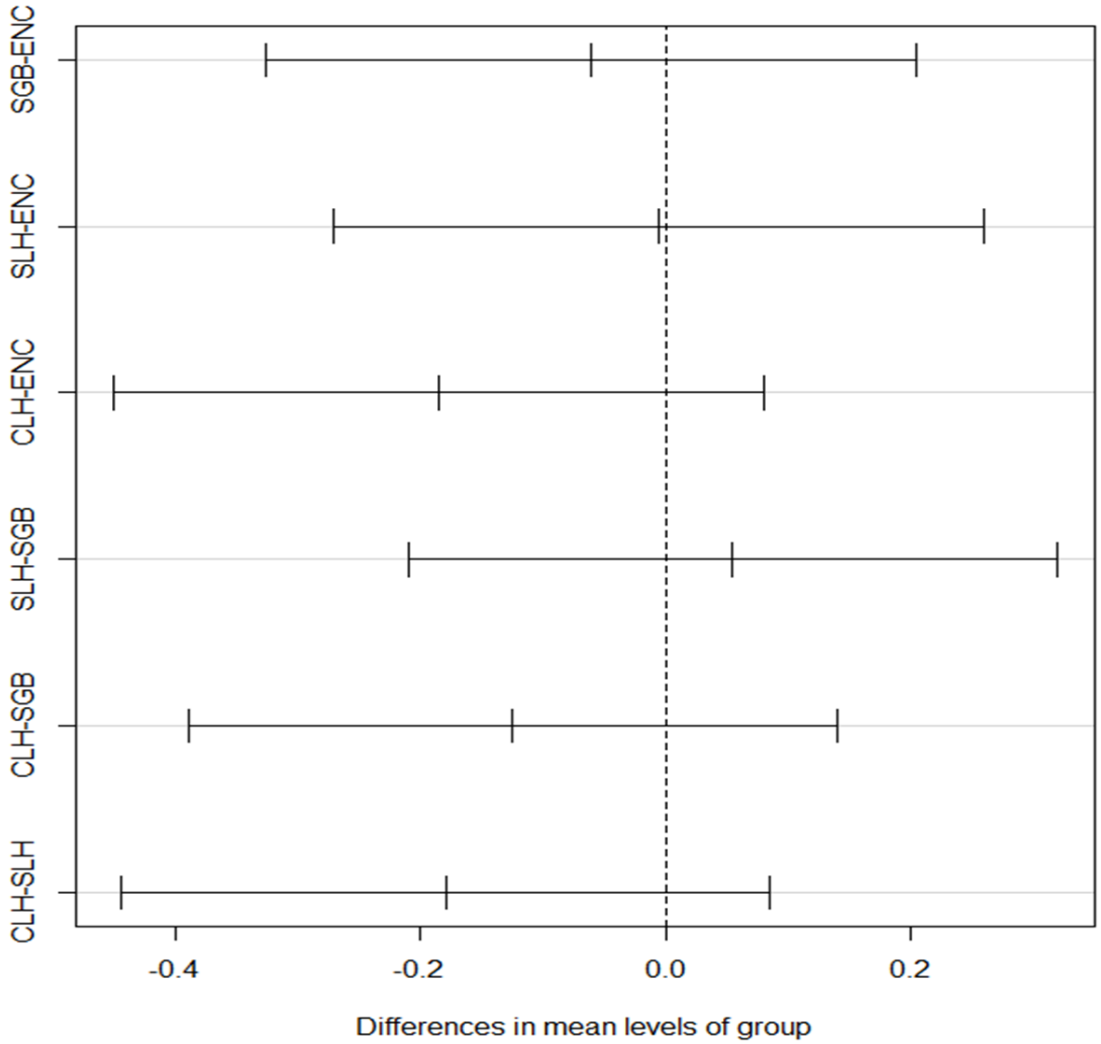


Figure A2.1. (cont'd)

B

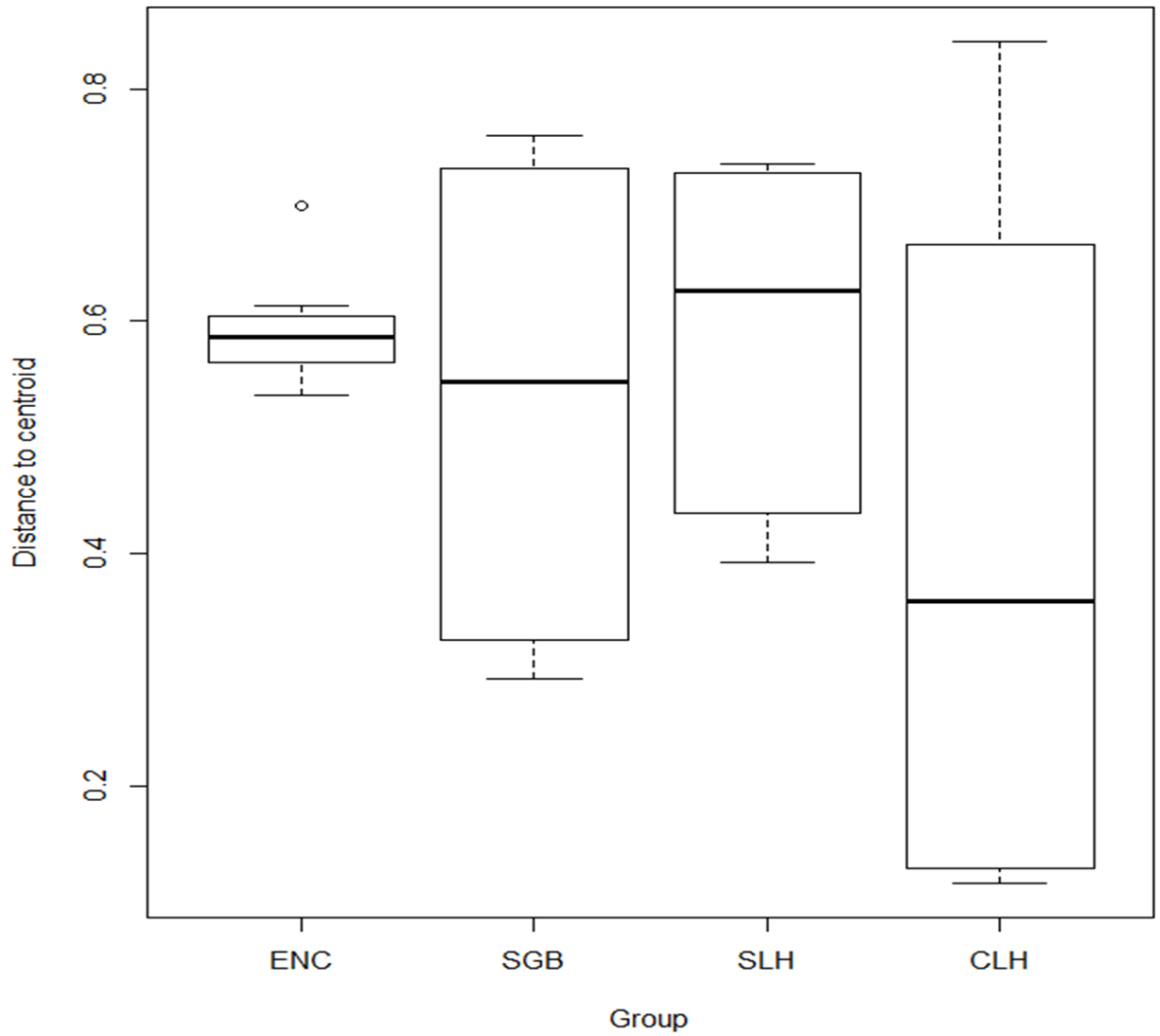


Figure A2.1. (cont'd)

C

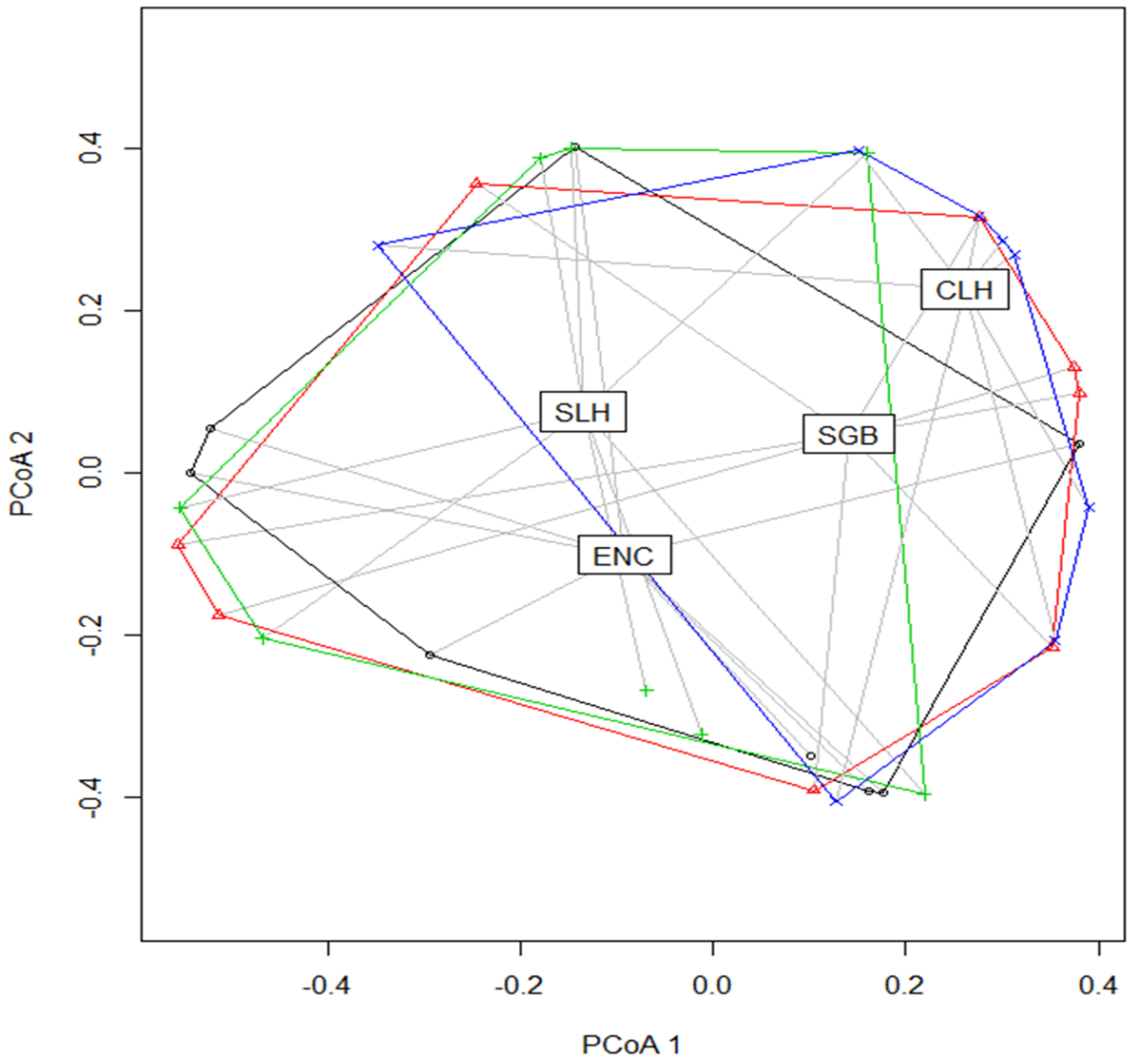


Figure A2.2. Predicted dynamics from the top-ranked dynamic factor analysis model estimated with one latent trend and the number of sea lamprey as a predictor and fit to multi-species fish abundance in the eastern North Channel zone during 1998-2011. Predictions are displayed as standardized abundance (N; i.e., y-axis) by time and were calculated by multiplying the matrix of factor loadings for individual species by the vector of annual latent trend estimates. Each plot notes the species and value of the model's relative mean-squared-error, a measure of absolute model fit, per species. The model is summarized in Table 2.2. Note that only nine species were observed in this zone.

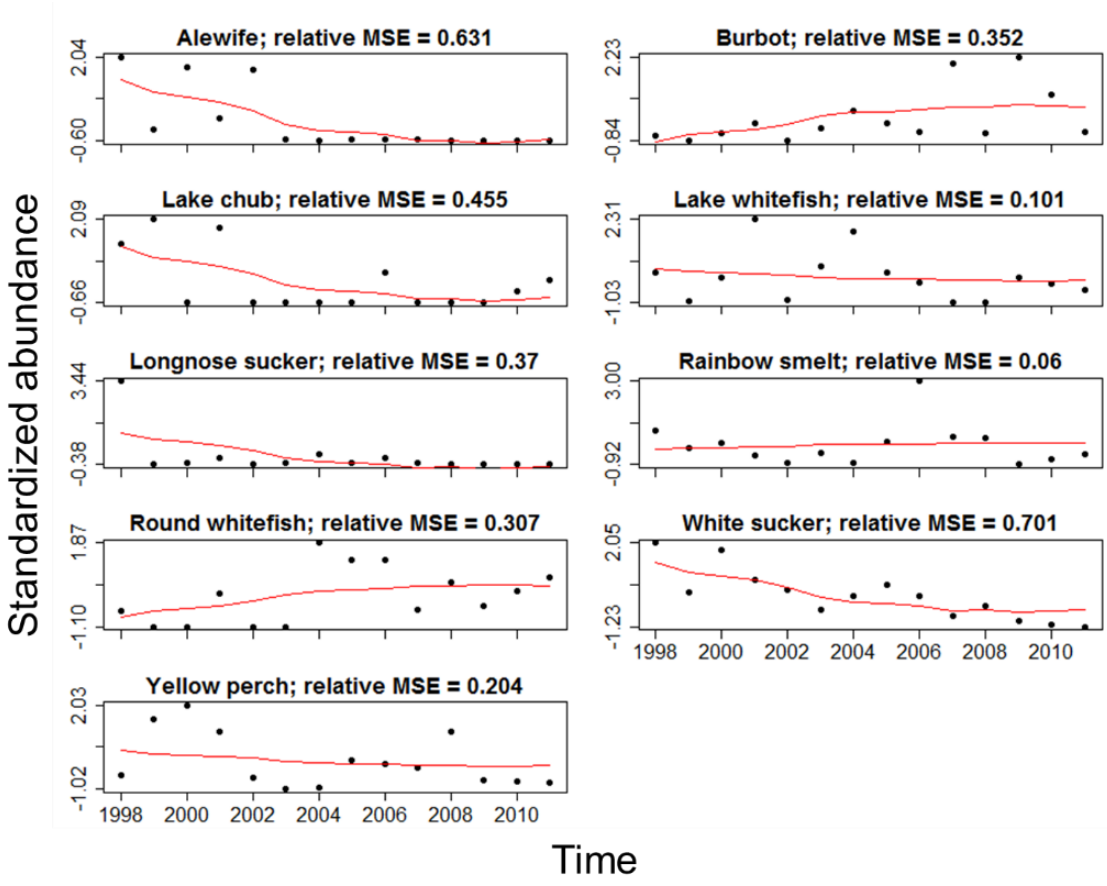


Figure A2.3. Predicted dynamics from top-ranked dynamic factor analysis models estimated with one latent trend and the number of upwelling days as a predictor and fit to multi-species fish abundance in the southern Georgian Bay zone during 1998-2011. The model is summarized in Table 2.5. Refer to Figure A2.2 for description of predicted values' calculation.

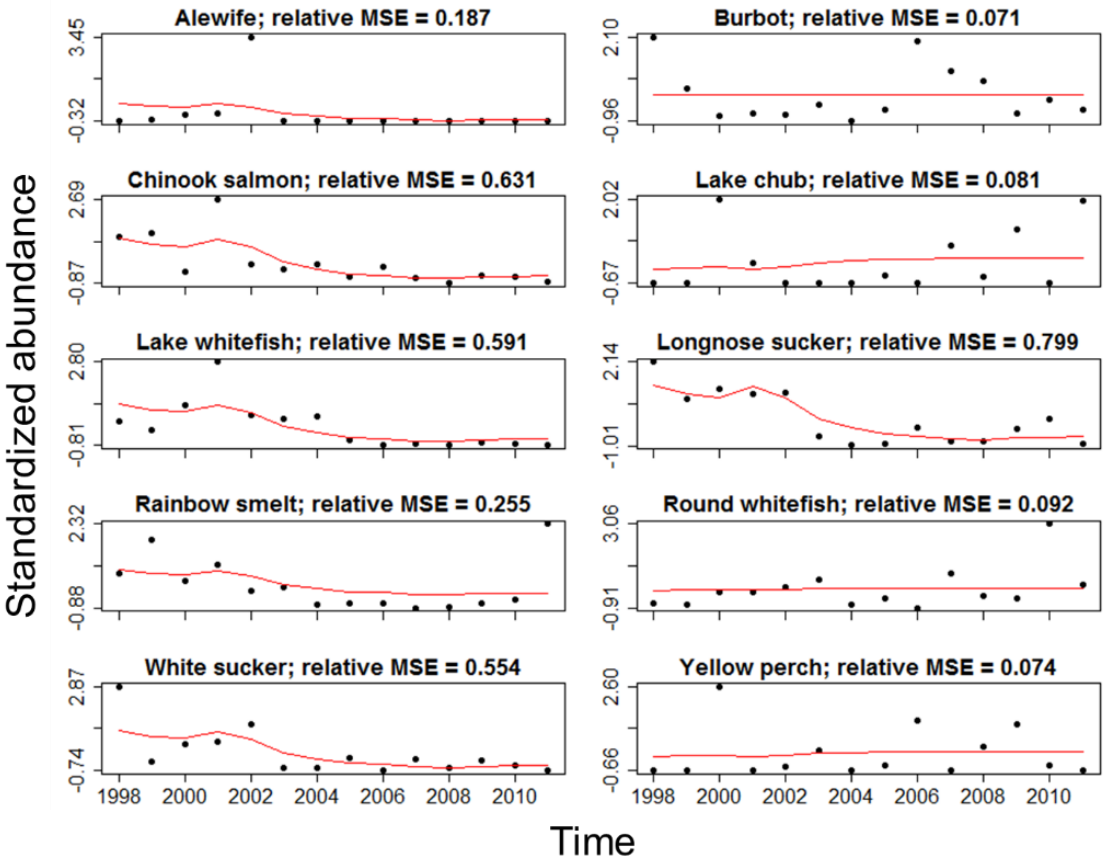


Figure A2.4. Predicted dynamics from a dynamic factor analysis model estimated with two latent trends and the cumulative degree days > 10˚C, number of upwelling events, and number of sea lamprey as predictors and fit to multi-species fish abundance in the central Lake Huron zone during 1998-2011. The model is summarized in Table 2.8. Refer to Figure A2.2 for description of predicted values' calculation.

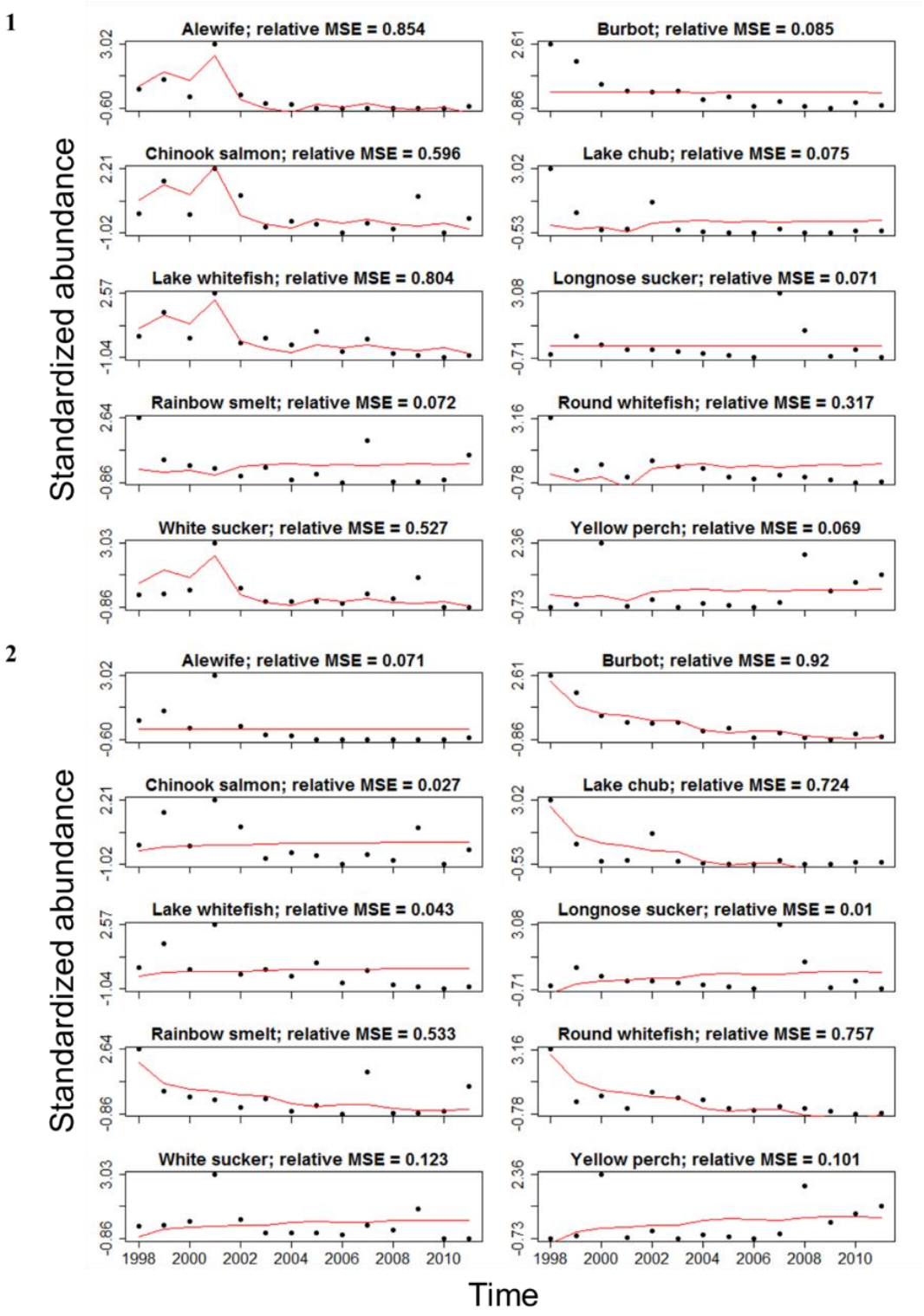
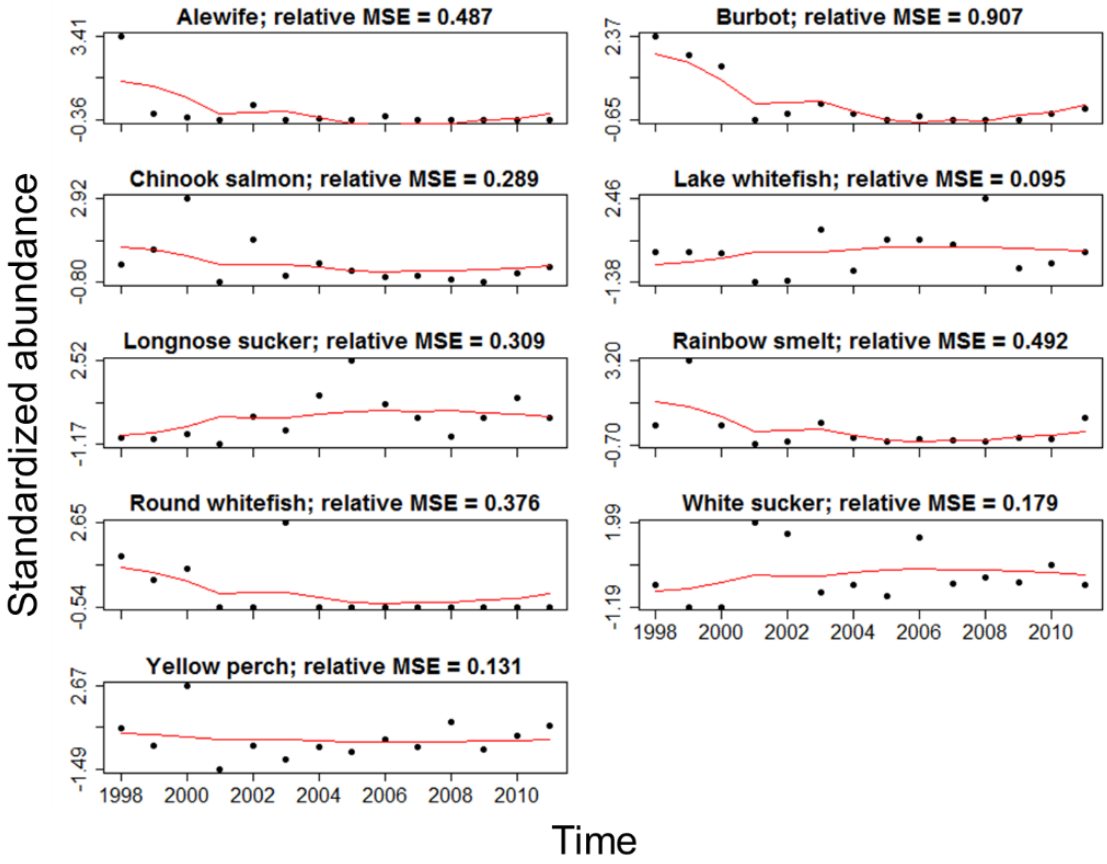


Figure A2.5. Predicted dynamics from top-ranked dynamic factor analysis models estimated with one latent trend and the number of sea lamprey as a predictor and fit to multi-species fish abundance in the southern Lake Huron zone during 1998-2011. The model is summarized in Table 2.11. Refer to Figure A2.2 for description of predicted values' calculation. Note that only nine species were observed in this zone.



REFERENCES

REFERENCES

Arthington, A. H., N. K. Dulvy, W. Gladstone, and I. J. Winfield. 2016. Fish conservation in freshwater and marine realms: status, threats and management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 26:838-857.

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., and B. R. Silliman. 2011. The value of estuarine and coastal ecosystem services. *Ecological Monographs* 81:169-193.

Baselga, A. 2017. Partitioning abundance-based multiple-site dissimilarity into components: balanced variation in abundance and abundance gradients. *Methods in Ecology and Evolution* 8:799-808.

Baselga, A. and C. D. L. Orme. 2012. betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution* 3:808-812.

Baselga, A., D. Orme, S. Villeger, J. de Bortoli, and F. Leprieur. 2018. betapart: Partitioning beta diversity into turnover and nestedness components. R package version 1.5.1. <https://CRAN.R-project.org/package=betapart>. Accessed Aug 2018.

Bence, J. R. and L. C. Mohr (Eds.). 2008. The state of Lake Huron in 2004. Great Lakes Fisheries Commission, Special Publication 08-01.

Bhagat, Y., and C. R. Ruetz. 2011. Temporal and fine-scale spatial variation in fish assemblage structure in a drowned river mouth system of Lake Michigan. *Transactions of the American Fisheries Society* 140:1429-1440.

Boulton, A. J., Ekebom, J., and G. M. Gislason. 2016. Integrating ecosystem services into conservation strategies for freshwater and marine habitats: a review. *Aquatic Conservation: Marine and Freshwater Ecosystems* 26:963-985.

Burnham, K. P. and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, Second Edition. Springer-Verlag, New York, NY.

Cambridge, M. L., A. M. Breeman, S. Kraak, and C. van den Hoek. 1987. Temperature responses of tropical to warm temperate *Cladophora* species in relation to their distribution in the North Atlantic Ocean. *Helgoländer Meeresuntersuchungen* 41:329-354.

Connerton, M., J. Lantry, M. Walsh, M. E. Daniels, J. Hoyle, J. Bowlby, J. H. Johnson, et al. 2014. Offshore pelagic fish community. Great Lakes Fisheries Commission, Technical Publication no. 14-01.

Darwall, W., K. Smith, D. Allen, M. Seddon, G. M. Reid, V. Clausnitzer, and V. J. Kalkman. 2009. Freshwater biodiversity: a hidden resource under threat. Pages 1-12 *in* The 2009

Review of The IUCN Red List of Threatened Species, J.-C. Vié, C. Hilton-Taylor and S.N. Stuart (Eds.). International Union for Conservation of Nature, Gland, Switzerland.

Davis, B., R. Baker, and M. Sheaves. 2014. Seascape and metacommunity processes regulate fish assemblage structure in coastal wetlands. *Marine Ecology Progress Series* 500:187-202.

De Bie, T., L. de Meester, L. Brendonck, K. Martens, B. Goddeeris, D. Ercken, H. Hampel, et al. 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecology Letters* 15:740-747.

DesJardine, R. L., T. K. Gorenflo, R. N. Payne, and J. D. Schrouder. 1995. Fish-community objectives for Lake Huron. Great Lakes Fisheries Commission, Special Publication 95-1.

Dobiesz, N. E. and N. P. Lester. 2009. Changes in mid-summer water temperature and clarity across the Great Lakes between 1968 and 2002. *Journal of Great Lakes Research* 34:371-384.

Dobiesz, N. E., D. A. McLeish, R. L. Eshenroder, J. R. Bence, L. C. Mohr, M. P. Ebener, T. F. Nalepa, et al. 2005. Ecology of the Lake Huron fish community 1970-1999. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1432-1451.

Dobiesz, N.E. 2003. An evaluation of the role of top piscivores in the fish community of the main basin of Lake Huron. Ph.D. dissertation, Michigan State University, East Lansing, MI, USA.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, et al. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 81:163-182.

Edsall, T. A. and M. N. Charlton. 1997. Nearshore waters of the Great Lakes. State of Lakes Ecosystem Conference 1996. EPA-905-R-97-015a. U.S. Environmental Protection Agency, Washington, DC, USA.

Environmental Systems Research Institute (ESRI). 2012. ArcGIS v 10.1. ESRI Inc., Redlands, CA, USA.

Erős, T., P. Sály, P. Takács, A. Specziár, and P. Bíró. 2012. Temporal variability in the spatial and environmental determinants of functional metacommunity organization: stream fish in a human-modified landscape. *Freshwater Biology* 57:1914-1928.

Farjalla, V. F., D. S. Srivastava, N. A. C. Marino, F. D. Azevedo, V. Dib, P. M. Lopes, A. S. Rosado, et al. 2012. Ecological determinism increases with organism size. *Ecology* 93:1752-1759.

Fetzer, W. W., B. M. Roth, D. M. Infante, D. F. Clapp, R. M. Claramunt, D. G. Fielder, D. K. Forsyth, et al. 2017. Spatial and temporal dynamics of nearshore fish communities in Lake Huron. *Journal of Great Lakes Research* 43:319-334.

Gamble, A. E., T. R. Hrabik, D. L. Yule, and J. D. Stockwell. 2011a. Trophic connections in Lake Superior Part II: the nearshore fish community. *Journal of Great Lakes Research* 37:550-560.

Gamble, A. E., T. R. Hrabik, J. D. Stockwell, and D. L. Yule. 2011b. Trophic connections in Lake Superior Part I: the offshore fish community. *Journal of Great Lakes Research* 37:541-549.

Giller, P. S., Covich, A. P., Ewel, K. C., Hall Jr, R. O., and D. M. Merritt. 2004. Vulnerability and management of ecological services in freshwater systems. Pages 137-159 i*n* Sustaining Biodiversity and Ecosystem Services in Soils and Sediments, D. H. Wall (Ed.). Island Press, Washington, DC, USA.

Hecky, R. E., R. E. H. Smith, D. R. Barton, S. J. Guilford, W. D. Taylor, M. N. Charlton, and T. Howell. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 61:1285-1293.

Heino, J., A. S. Melo, T. Siqueira, J. Soininen, S. Valanko, and L. M. Bini. 2015. Metacommuniyt organization, spatial extent, and dispersal in aquatic systems: patterns, processes, and prospects. *Freshwater Biology* 60:845-869.

Heino, J. 2013. The importance of metacommunity ecology for environmental assessment research in the freshwater realm. *Biological Reviews* 88:166-178.

Holmes, E. E. 2010. Derivation of the EM algorithm for constrained and unconstrained multivariate autoregressive state-space (MARSS) models. Technical report, Fisheries Division, National Oceanic and Atmospheric Administration, Seattle, WA, USA.

Holmes, E. E., E. J. Ward, and K. Wills. 2012. MARSS: Multivariate autoregressive state-space models for analyzing time-series data. *The R Journal* 4:11-19.

Holmes, E., E. Ward, and K. Wills. 2018. MARSS: Multivariate Autoregressive State-Space Modeling. R package version 3.10.10. <https://CRAN.R-project.org/package=MARSS>. Accessed Aug 2018.

Holyoak, M., M. A. Leibold, N. M. Mouquet, R. D. Holt, and M. F. Hoopes. 2005. Metacommuninites: a framework for large-scale community ecology. Pages 1-31 *in* Metacommunities: Spatial Dynamics and Ecological Communities, M. Holyoak, M. A. Leibold, and R. D. Holt (Eds.). University of Chicago Press, Chicago, IL, USA.

Hui, F. K. C., S. Taskinen, S. Pledger, S. D. Foster, and D. I. Wharton. 2015. Model-based approaches to unconstrained ordination. *Methods in Ecology and Evolution* 6:399-411.

Ivan, L. N., D. G. Fielder, M. V. Thomas, and T. O. Höök. 2014. Changes in the Sagniaw Bay, Lake Huron, fish community from 1970 to 2011. *Journal of Great Lakes Research* 40:922-933.

Ivan, L. N., T. O. Höök, M. V. Thomas, and D. G. Fielder. 2011. Long-term and interannual dynamics of walleye and yellow perch in Saginaw Bay, Lake Huron. *Transactions of the American Fisheries Society* 140:1078-1092.

Janetski, D. J. and C. R. Ruetz III. 2015. Spatiotemporal patterns of fish community composition in Great Lakes drowned river mouths. *Ecology of Freshwater Fish* 24:493-504.

Kao, Y., S. A. Adlerstein, and E. S. Rutherford. 2016. Assessment of top-down and bottom-up controls on the collapse of alewives (*Alosa pseudoharengus*) in Lake Huron. *Ecosystems* 19:803-831.

Larson, J. H., A. S. Trebitz, A. D. Steinman, M. J. Wiley, M. C. Mazur, V. Pebbles, H. A. Braun, and P. W. Seelbach. 2013. Great Lakes river mouth ecosystems: scientific synthesis and management implications. *Journal of Great Lakes Research* 39:5134-524.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601-613.

Ludsin, S. A., M. W. Kershner, K. A. Blocksom, R. L. Knight, and R. A. Stein. 2001. Life after death in Lake Erie: nutrient controls drive fish species richness, rehabilitation. *Ecological Applications* 11:731-746.

Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an ecological resource. *American Zoologist* 19:331-343.

Mathews, W. J. and E. Marsh-Mathews. 2016. Dynamics of an upland stream fish community over 40 years: trajectories and support for the loose equilibrium concept. *Ecology* 97:706-719.

McCormick, M. J. and G. L. Fahnenstiel. 1999. Recent climatic trends in nearshore water temperatures in the St. Lawrence Great Lakes. *Limnology and Oceanography* 44:530-540.

Mouquet, N. and M. Loreau. 2003. Community patterns in source-sink metacommunities. *American Naturalist* 162:544-557.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, et al. 2019. vegan: Community ecology package. R package version 2.5-6. <https://CRAN.R-project.org/package=vegan>. Accessed Aug 2019.

Ovaskainen, O., D. B. Roy, R. Fox, and B. J. Anderson. 2016. Uncovering hidden spatial structure in species communities with spatially explicit joint species distribution models. *Methods in Ecology and Evolution* 7:428-436.

Owens, R. W., R. O'Gorman, T. H. Eckert, and B. F. Lantry. 2003. The offshore fish community in southern Lake Ontario, 1972-1998. Pages 407-441 *in* State of Lake Ontario: Past, Present, and Future, M. Munawar (Ed.). Ecovision World Monograph Series, Aquatic Ecosystem Health and Management Society, Burlington, Ontario, CAN.

Padial, A. A., F. Ceschin, S. A. J. Declerck, L. de Meester, C. C. Bonecker, F. A. Lansac-Tôha, L. Rodrigues, et al. 2014. Dispersal ability determines the role of environmental, spatial, and temporal drivers of metacommunity structure. *PLoS One* 9:e111227.

Postel, S.L. and Carpenter, S.R. 1997. Freshwater Ecosystem Services. Pages 195-214 *in* Nature's Services, G. Daily (Ed.). Island Press, Washington, DC, USA.

R Core Development Team. 2020. R Statistical Software v. 4.0.2. R Foundation for Statistical Computing, Vienna, Austria.

Rennie, M. D., M. P. Ebener, and T. Wagner. 2012. Can migration mitigate the effects of ecosystem change? Patterns of dispersal, energy acquisition and allocation in Great Lakes lake whitefish (*Coregonus clupeaformis*). *Advances in Limnology* 63:455-476.

Riley, S. C. (Ed.). 2013. The state of Lake Huron in 2010. Great Lakes Fisheries Commission, Special Publication 13-01.

Schallenberg, M., de Winton, M. D., Verburg, P., Kelly, D. J., Hamill, K. D., and D. P. Hamilton. 2013. Ecosystem services of lakes. Pages 203-225 *in* Ecosystem services in New Zealand: Conditions and Trends, J. Dymond (Ed.). Manaaki Whenua Press, Lincoln, New Zealand.

Seelbach, P. W., L. R. Fogarty, D. B. Bunnell, S. K. Haack, and M. W. Rogers. 2013. A conceptual framework for Lake Michigan coastal/nearshore ecosystems, with application to Lake Michigan Lakewide Management Plan (LaMP) objectives. Report 2013-1138, U.S. Geological Survey, Reston, VA, USA.

Shurin, J. B., K. Cottenie, and H. Hillebrand. 2009. Spatial autocorrelation and dispersal limitation in freshwater organisms. *Oecologia* 159:151-159.

Soininen, J. 2014. A quantitative analysis of species sorting across organisms and ecosystems. *Ecology* 95:3284-3292.

Stoffels, R. J., K. R. Clarke, and D. S. Linklater. 2014. Temporal dynamics of a local fish community are strongly affected by immigration from the surrounding metacommunity. *Ecology and Evolution* 5:200-212.

Thorson, J. T., J. N. Ianelli, E. A. Larsen, L. Ries, M. D. Scheuerell, C. Szuwalski, and E. F. Zipkin. 2016. Joint dynamic species distribution models: a tool for community ordination and spatio-temporal monitoring. *Global Ecology and Biogeography* 25:1144-1158.

Thorson, J. T., M. D. Scheuerell, A. O. Shelton, K. E. See, H. J. Skaug, and K. Kristensen. 2015. Spatial factor analysis: a new tool for estimating joint species distributions and correlations in species range. *Methods in Ecology and Evolution* 6:627-637.

Tikhonov, G., L. Duan, N. Abrego, G. Newell, M. White, D. Dunson, and O. Ovaskainen. 2020. Computationally efficient joint species distribution modeling of big spatial data. *Ecology* 101:e02929.

Trebitz, A. S., J. C. Brazner, N. P. Danz, M. S. Pearson, G. S. Peterson, D. K. Tanner, D. L. Taylor, et al. 2009. Geographic, anthropogenic, and habitat influences on Great Lakes coastal wetland fish assemblages. *Canadian Journal of Fisheries and Aquatic Sciences* 66:1328-1342.

Urban, M. C. 2004. Disturbance heterogeneity determines freshwater metacommunity structure. *Ecology* 85:2971-2978.

Uzarski, D. G., T. M. Burton, M. J. Cooper, J. W. Ingram, and S. T. A. Timmermans. 2005. Fish habitat use within and across wetland classes in coastal wetlands of the five Great Lakes: development of a fish-based Index of Biological Intregrity. *Journal of Great Lakes Research* 31:171-187.

Vanderploeg, H. A., J. R. Leibig, T. F. Nalepa, G. L. Fahnenstiel, and S. A. Pothoven. 2010. Dreissena and the disappearance of the spring phytoplankton bloom in Lake Michigan. *Journal of Great Lakes Research* 36:50-59.

Walker, S. C. and D. A. Jackson. 2011. Random-effects ordination: describing and predicting multivariate correlations and co-occurrences. *Ecological Monographs* 81:635-663.

Wang, L., C. M. Riseng, L. A. Mason, K. E. Wehrly, E. S. Rutherford, J. E. McKenna, Jr., C. Castiglione, et al. 2015. A spatial classification and database for management, research, and policy making: The Great Lakes Aquatic Habitat Framework. *Journal of Great Lakes Research* 41:584–596.

Wehrly, K. E., J. E. Breck, L. Wang, and L. Szabo-Kraft. 2012. A landscape-based classification of fish assemblages in sample and unsampled lakes. *Transactions of the American Fisheries Society* 141:414-425.

Zuur, A. F. and G. J. Pierce. 2004. Common trends in northeast Atlantic squid time series. *Journal of Sea Research* 52:57–72.

Zuur, A. F., I. D. Tuck, and N. Bailey. 2003a. Dynamic factor analysis to estimate common trends in fisheries time series. *Canadian Journal of Fisheries and Aquatic Sciences* 60:542-552.

Zuur, A., R. Fryer, I. Jolliffe, R. Dekker, and J. Beukema. 2003b. Estimating common trends in multivariate time series using dynamic factor analysis. *Environmetrics* 14:665-685.

CHAPTER 3: REAPING WHAT WE SOW WHILE CONFRONTING RARITY: OCCUPANCY OF GRASSLAND-OBLIGATE BIRDS ASSOCIATES POSITIVELY WITH SET-ASIDE PROGRAM PLANTINGS IN SOUTHEAST MICHIGAN, USA

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Abstract

Farmland set-aside (ecological restoration) programs have the potential to benefit grassland-obligate wildlife, especially rare species. However, rare species are difficult to observe and may vary in response to set-aside restorations within different environmental contexts, including changes in broad- and fine-scale resources (e.g., vegetation) and conditions (e.g., patch connectivity). To quantify set-aside impacts to and identify conditions supportive of rare species, it is also necessary to account for observation errors associated with species rarity (e.g., imperfect detection) as well as multi-scale associations with land cover (e.g., landscape composition and configuration). We quantified grassland-obligate bird occupancy within Conservation Reserve Enhancement Program (CREP) restored grasslands during May-August 2005 and 2006 in southeast Michigan, USA. We compared vegetation composition between two CREP plantings, CP1 (i.e., non-native grasses and legumes) and CP23 (i.e., vegetation native to upland areas of restored wetlands), on former agricultural fields in 2006. We found that amount of bare ground and dead vegetation canopy cover differed between CP1 and CP23 fields, and we reliably observed seven grassland-obligate bird species across fields. We fit multi-species occupancy models for seven grassland-obligate bird species, and candidate models included linear effects of CREP plantings and effects of field- and landscape-level covariates while also accounting for imperfect species detection and survey year as a proxy for species-field

colonization dynamics. Based on the top-ranked model, marginal (mean) occupancy probabilities ranged from 0.43 (dickcissel, *Spiza americana*) to 0.88 (vesper sparrow, *Pooecetes gramineus*) with considerable uncertainty about occupancy across species. Marginal (mean) detection probabilities ranged from 0.17 (eastern kingbird, *Tyrannus tyrannus*) to 0.76 (bobolink, *Dolichonyx oryzivorus*) with little uncertainty about detection across species. Our analysis revealed positive associations of CP plantings with occupancy probability for bobolink (CP1), eastern meadowlark (*Sturnella magna*; CP23), and grasshopper sparrow (*Ammodramus savannarum*; CP23). Concurrent CREP and citizen-science surveys generated comparable diversity estimates based on rarefaction, indicating that our surveys reflect grassland bird occupancy across the region. This study describes preliminary responses of grassland-obligate bird occupancy at 14 set-aside (grassland restoration) fields varying in planting type, vegetation cover, and landscape context. Additional set-aside fields and plantings, observational surveys prior to set-aside initiation, and long-term monitoring of bird occupancy post-set-aside are necessary to fully evaluate impacts of set-aside (restored) lands on grassland-obligate bird occupancy and diversity. Such information will improve quantification of ecological-process error due to interspecies correlations and species-field colonization dynamics, providing more comprehensive descriptions of occupancy-detection processes in increasingly rare grassland-obligate birds and their restored habitats.

Introduction

Temperate grasslands are one of the most endangered ecosystems in the world, and > 70% of grasslands have been converted to agriculture in North America alone (Sampson et al. 2004, Ahlering et al. 2019). Land conversion negatively impacts temperate grasslands by reducing their area, frequency, and distribution. Other threats to temperate grasslands include changes in

historical fire frequency and intensity, increased livestock grazing, woody plant invasion, and climate change (Briggs et al. 2005, Ahlering et al. 2019). Additionally, remnant grasslands are largely fragmented and disconnected in North America, disrupting important biophysical processes (e.g., carbon sequestration) and reducing the likelihood of temperate grasslands persisting in the future (Noss et al. 1995, Leach and Givnish 1996). Moreover, farmland set-aside programs comprise one approach to ecological restoration aimed to help ameliorate the aforementioned impacts to grassland ecosystems in North America.

Farmland set-aside programs (e.g., the Conservation Reserve and Conservation Reserve Enhancement Programs, CRP and CREP, respectively) exist to increase the area, frequency, and distribution of native and non-native grasslands in the United States, which may help diminish or reverse declines in grassland wildlife (Herkert 2009). Both CRP and CREP are government programs administered as 10- to 15-year contracts that ensure annual cost-share and rental payments to farmers who remove highly erodible cropland from agricultural production, instead planting set-aside fields with grasses, trees, or other approved vegetation to benefit local wildlife, including grassland birds (United States Department of Agriculture [USDA] 2009, USDA Farm Service Agency 2010). The CRP is strictly a federal program while CREP is a partnership between federal and state governments, including additional partners such as tribal governments and private organizations in several cases (USDA Farm Service Agency 2010). Furthermore, as competition between set-aside programs and agricultural markets (e.g., crop-biofuel production; Secchi and Babcock 2007, Searchinger et al. 2008, Fargione et al. 2009) increases worldwide, it is imperative that conservation biologists and land managers evaluate and demonstrate benefits of set-aside (ecological restoration) practices to wildlife, especially rare (grassland-obligate) species.

Precipitous declines in quality and quantity of native grasslands negatively affects wildlife (Arenz and Joern 1996, Benedict et al. 1996, Corn and Peterson 1996, Rabeni 1996). However, considerable geographic variation exists in the effects of CREP on wildlife, owing to differences in local and regional climate, land use and land cover, and populations of humans and wildlife (Heard et al. 2000, Riffell et al. 2008). For example, Reiley and Benson (2020; i.e., based on field surveys conducted during 2012-2015 in Illinois, USA) found that many grassland bird species occurred in similar numbers across CREP planting types (e.g., riparian buffer, wetland restoration, hardwood tree, and permanent wildlife habitat). However, (a) only dickcissel (*Spiza americana*) density was higher at locations enrolled as permanent wildlife habitat, (b) changes in species density with increasing field age varied inconsistently among planting types, and (c) farmland set-aside benefits to grassland birds change over time (e.g., depending on initial planting type) while considerable similarity in field vegetation structure and bird communities may also manifest among fields with different plantings (Reiley and Benson 2020).

As another example, Pabian et al. (2013; i.e., based on roadway surveys conducted during 2001-2010 in Pennsylvania, USA) studied CREP fields involving other planting types (e.g., introduced [cool season] grasses and legumes, native [warm season] grasses, already established grasses, and filter strips with grasses). Specifically, they found that CREP plantings (a) positively affected five bird species (e.g., including eastern meadowlark, *Sturnella magna*) later in the study, (b) associated with abundance changes for the same five bird species throughout the study, (c) negatively affected three species (e.g., including vesper sparrow, *Pooecetes gramineus*), and (d) did not affect two species (e.g., including grasshopper sparrow, *Ammodramus savannarum*; Pabian et al. 2013). Additional findings suggested potential for increased benefits to grassland

bird occupancy and abundance at fields by installing (new) CREP plantings in locations that already include CREP-enrolled areas in the surrounding landscape (Pabian et al. 2013).

Although studies have quantified the responses of many grassland-facultative birds to federal- or state-administered set-asides, we currently lack understanding of how grassland-obligate birds, particularly those that are rare, respond to CREP set-aside farmlands. Grassland-obligate birds rely on intact native grassland habitat, and help maintain grasslands through seed dispersal (Knopf 1994, Herkert 1995). Unfortunately, Breeding Bird Survey (BBS) data indicate that grassland bird populations are consistently declining in North American birds (Sauer et al. 1995, Knopf 1996, Sauer et al. 2008, Sauer et al. 2017). For example, from 1980-2007 significant declines in four of ten grassland bird species inhabiting Michigan were documented—including vesper sparrow, eastern meadowlark, bobolink (*Dolichonyx oryzivorous*), and ring-necked pheasant (*Phasianus colchicus*). Over the same period, no grassland bird species population significantly increased (Sauer et al. 2008). These population trends have continued beyond 2007 (Sauer et al. 2017).

To our knowledge, few studies (Wisconsin Department of Agriculture, Trade and Consumer Protection 2004, Wentworth 2005, Wentworth et al. 2010, Wilson et al. 2010, Van Loan 2011) have evaluated characteristics of CREP planting mixes (i.e., whether seeded with native or non-native plants) and their potential associations with multi-species bird abundance or occupancy on set-aside farmlands, especially in the Great Lakes Plains Ecoregion (see Allen 2005). Administration of CREP involves multiple conservation practices (CP) resulting in designations such as CP1 (i.e., non-native vegetation), CP2 (i.e., native vegetation), or CP23 (i.e., wetland restoration) practices for participating fields. In the regional conservation district of

the current study, application of CP23 plantings includes native species typically found along upland areas surrounding wetlands, which essentially mimics conventional CP2 plantings.

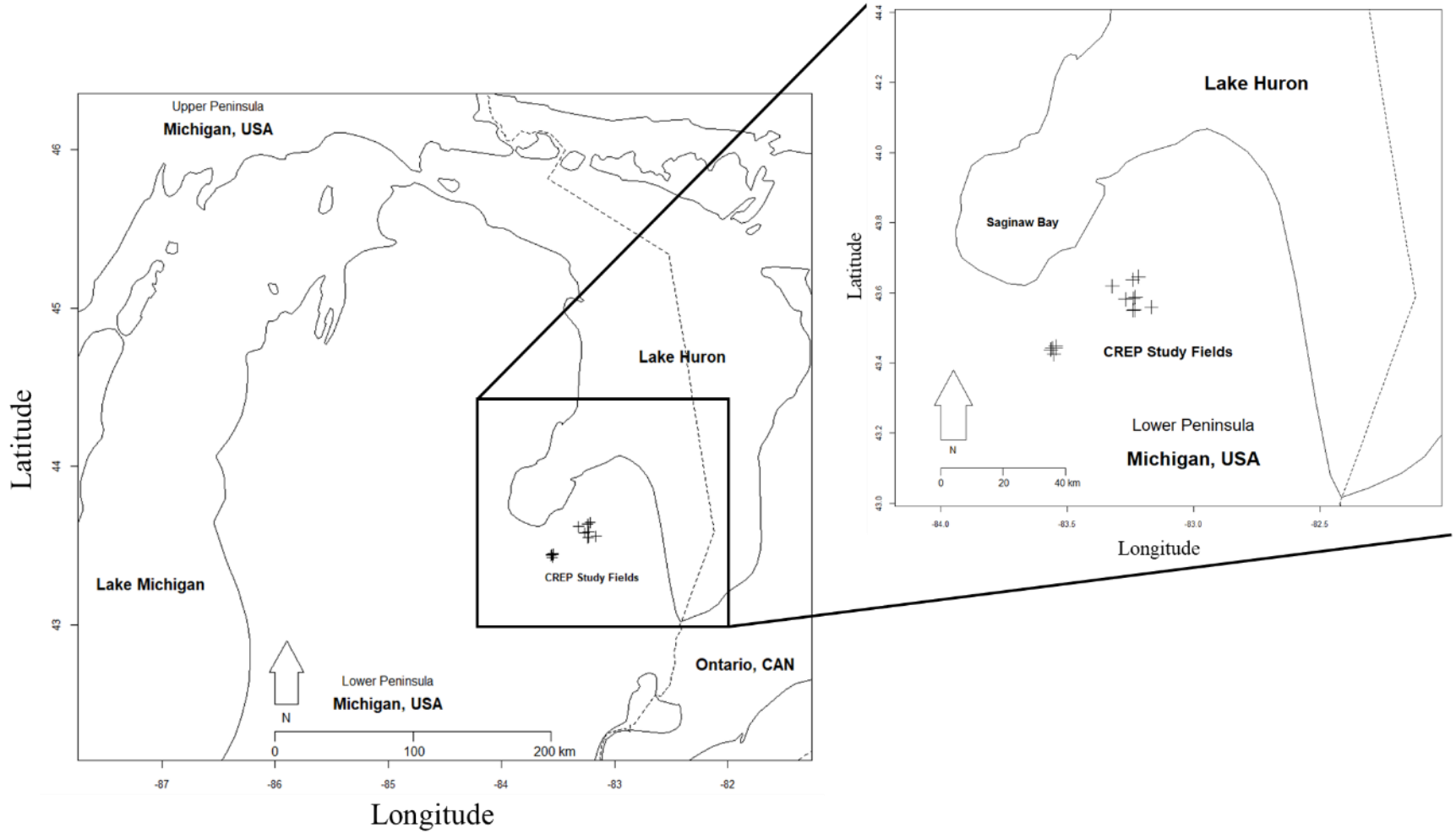
We posed the following questions and expectations: (1) how does vegetation composition vary between CREP-restored grasslands planted with either CP1 or CP23 plantings, where we expected that fields with higher forb and grass cover would promote higher grassland bird species occupancy, (2) do CP1 or CP23 plantings convey occupancy benefits to grassland-obligate birds while controlling for variation (e.g., percent cover types and surrounding landscape complexity) between study fields, where we expected that grassland bird species occupancy probabilities would be higher in CP23 than CP1 fields, (3) does landscape composition or configuration associate with grassland-obligate bird occupancy and at what extent(s), where we expected that landscape complexity at intermediate (i.e., > 400-m) extents would associate with grassland-obligate birds, and (4) how does grassland-obligate bird diversity compare between CREP fields and concomitant citizen-science records, where we expected that CREP fields would support higher numbers of grassland species than other areas in the surrounding landscape. To address these questions and expectations, we used multi-species occupancy models that incorporated environmental properties at multiple spatial extents, changing survey years, and imperfect species detection. Our work demonstrates utility of a multi-species framework toward elucidating diverse effects of conservation practices and multi-scale environmental properties on grassland-obligate birds as well as offer recommendations toward improvement of similar studies in the future.

Methods

Study area and planting practices

Our study occurred within the 8,219 km^2 Sandusky Lake Plain subsection of Michigan's southern Lower Peninsula, USA (Figure 3.1). The Sandusky Lake Plain consists of flat clay lake plain bordered by shoreline dunes and sand plain (Albert 1995). Prior to European settlement centuries ago, extensive wet and wet-mesic prairies occurred in areas outside of the coastal Great Lakes marshes of Saginaw Bay (Albert 1995). Today, such prairies occur only as small, fragmented, and disconnected remnants—systems generally residing on state-owned lands due to continued land conversion in the region, particularly for agriculture (Albert 1995).

Figure 3.1. Study area of 14 fields enrolled in the Conservation Reserve Enhancement Program from 2005-2006 in Michigan, USA.



Approximately 230 km^2 in the Sandusky Lake Plain sub-subsection (i.e., the Saginaw Bay, Lake Macatawa, and River Raisin watersheds) was enrolled in CREP grassland restoration at the time of this study (USDA Farm Service Agency 2007). Of the enrolled fields, we surveyed 14 (e.g., representing 13 landowners) ranging in size from 6.8 to 23.6 ha. All restored fields were planted in 2002, and seven fields were planted with CP23 forbs and native grasses over 100% of the field. The remaining seven fields were planted with CP1 non-native grasses and legumes on 70% of the field. In CP1 restored grasslands, the remaining 30% of the total area was planted with forbs and native grasses, which were planted to help provide winter shelter for local wildlife (USDA Natural Resources Conservation Service 2000a,b).

CP23 restored grasslands were planted with a seed mixture comprising 92% grasses and 8% forbs, which were tolerant of the herbicide Plateau® (BASF Corporation, Research Triangle Park, North Carolina, USA), an herbicide commonly applied by other landowners on neighboring croplands for weed management. Seed mixes were sowed at 7.3 kg/ha, as recommended (Voss 1972, USDA Natural Resources Conservation Service 2011). Three grass species were included in the native seed mixture in equal thirds: big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*), and little bluestem (*Schizachyrium scoparium*). Eighteen forb species (e.g., five native) were included in the native seed mixture. Black-eyed Susan (*Rudbeckia hirta*), crimson clover (*Trifolim incarnatum*), lance-leaf coreopsis (*Coreopsis lanceolata*), perennial flax (*Linum perenne lewisii*), and Siberian wallflower (*Erysiumum x marshallii*) each comprised 10% of the native forb seed mixture. Yellow coneflower (*Ratibida columnifera*), cosmos “sensation” mix (*Cosmos bipinnatus* variety), sulphur cosmos (*Cosmos sulphureus*), dame’s rocket (*Hesperis matronalis*), California poppy (*Eschscholzia californica*), and corn poppy “Shirley single” mix (*Papaver rhoeas* variety) each comprised 5% of the native

forb seed mixture. Shasta daisy "Alaska" (*Chrysanthemum x superbum*), perennial lupine (*Lupinus perennis*), prairie coneflower "Mexican hat" (*Ratibida columnifera* variety), plains coreopsis (*Coreopsis tinctoria*), perennial blanket flower (*Gaillardia aristata*), catchfly (*Silene armeria*), and purple coneflower (*Echinacea purpurea*) each comprised < 5% of the native forb seed mixture. Planted forb species native to Michigan consisted of black-eyed Susan, purple coneflower, yellow coneflower, lance-leaf coreopsis, and perennial lupine (Voss 1985, 1996, USDA Natural Resources Conservation Service 2011). Additionally, no native plant seeds included Michigan genotypes (J. Kratz, Tuscola County Conservation District, personal communication).

Non-native portions of CP1 fields were planted with a seed mixture comprising 46% non-native grasses and 54% non-native legumes. Seed mixes were sowed at 12.3 kg/ha, as recommended (Voss 1972, USDA Natural Resources Conservation Service 2011). Two grass species, orchardgrass (*Dactlyis glomerata*), and timothy (*Phleum pratense*), comprised equal parts of the non-native grass seed mixture while alfalfa (*Medicago sativa*) and red clover (*Trifolium pratense*) comprised equal parts of the non-native legume mixture. Within CREP-enrolled fields in our study area, CP23 fields resembled systems associated with wetland restoration in Michigan. As such, a small wetland was installed in each CP23 field during field establishment by severing field drain tiles as well as, if necessary, by creating a shallow depression in the soil. In CP23 fields, wetlands comprised generally < 3% of upland field area; however, the wetland in one field comprised ~10% of upland field area. We buffered each wetland by 25 m in CP23 fields and excluded these areas from our bird and vegetation surveys.

Data collection and preparation

We measured vegetation composition and structure using one randomly located sampling point per 0.4 ha in each study field, totaling between 17 and 59 locations per field, limited by field area. We collected vegetation data during the summer (15 May-14 August) breeding season in 2006. To measure vegetation cover, we centered a 50 × 25 cm Daubenmire frame on each selected location and identified all plant species within the frame, and we visually estimated percentage of the frame area occupied by bare ground, litter cover, and canopy cover (Daubenmire 1959). We also visually estimated cover of standing dead and living vegetation in the plant canopy and estimated proportion of grass, forb, and woody cover within the living canopy. Therefore, 100% of the Daubenmire plot area included % bare ground + % litter cover + % total canopy cover. Total canopy cover % = % dead canopy vegetation + % live canopy vegetation, and % live canopy vegetation = % grasses + % forbs + % woody plants.

To compare vegetation between and among CP1 and CP23 fields, we generated boxplots and evaluated mean differences in % cover measurements using one-way Analyses of Variance (ANOVA; Chambers et al. 1983). We evaluated differences in % cover (i.e., bare ground, dead, forb, grass, litter, and total) as a function of planting type (i.e., CP1 v. CP23). We produced boxplots of raw % cover variables and implemented ANOVAs using a familywise error rate adjusted with Tukey's honest significant difference in the "glht" function of the "multcomp" package in R version 4.0.2 (Hothorn et al. 2008, R Core Development Team 2020).

We counted multiple grassland-obligate and -facultative bird species at fields using line-transect sampling (Edwards et al. 1981). In each field, we surveyed the total area (i.e., except for wetlands and their associated buffers in CP23 fields) every 14 days during 1 June-14 August in 2005 (i.e., n = 5 replicate visits to each field) and during 15 May-14 August in 2006 (i.e., n = 6

replicate visits to each field). Transects ran the length of every field, and we initiated the first transect 25 m from a randomly selected field corner and then surveyed subsequent transects at 50 m intervals across the width of each field. This design allowed us to sample the bird community with a sampling intensity proportional to field size. On a given survey, one or two (dependent) observers walked transects and recorded every bird seen or heard to the species level, noting its general location upon detection (e.g., using field maps with aerial views). During each line-transect survey, observers recorded bird species presence and other contextual variables (e.g., date, time, field, transect, bird-location coordinates, individual number, species).

Whenever an individual or several bird(s) flushed, observers noted the new location that the bird(s) moved to avoid duplicate records of individuals. If a bird was observed and could not be identified to the species level, then it was recorded as unidentified. We later excluded all unidentified individuals from data analyses. Observers conducted most bird surveys between local sunrise and the 4 hours following; however, the three largest fields required up to 5 hours to survey post-sunrise, which largely depended on number of birds detected. Observers did not conduct transect surveys in the rain or whenever wind speeds exceeded 16 km/h (Millenbah et al. 1996). During the two weeks prior to data collection, we trained field observers (i.e., between two and four individuals per year) in local bird species identification and data collection.

We defined each survey season (i.e., summer 2005 and 2006) as the period between territory establishment and estimated dates of initial flight by first young-of-the-year. We used life history information from species accounts in Birds of the World and All About Birds online archives to estimate the expected dates (Cornell Lab of Ornithology 2019, Billerman et al. 2020). For a subset of known grassland species inhabiting Michigan, we estimated date of initial flight by first young-of-the-year as: bobolink, 17 June (Martin and Gavin 1995); dickcissel, 27 July

(Temple 2002); eastern meadowlark, 21 June (Lanyon 1995); grasshopper sparrow, 17 June (Vickery 1996); ring-necked pheasant, 27 June (Giudice and Ratti 2001); savannah sparrow (*Passerculus sandwichensis*), 1 July (Wheelwright and Rising 2008); sedge wren (*Cistothorus platensis*), 18 June (Herbert et al. 2001); and vesper sparrow, 1 July (Jones and Cornely 2002). Our line-transect surveys thus began on 1 June 2005 and 15 May 2006, and so we assumed that all species sampled had initiated territory establishment by those start dates.

Statistical analysis

We first converted multi-species abundances to detection and non-detection data to the field (spatial) level because we sought to estimate (a) species diversity and (b) species- and community-level bird responses to several field-level predictors. We also sought to evaluate associations of grassland-obligate birds (i.e., detected at fields) with surrounding landscape complexity (i.e., land cover composition and configuration). We only considered predictors with pairwise Pearson's $|r| < 0.60$, which limited collinearity among predictors in our candidate model set (Suzuki et al. 2008, Dormann et al. 2013; Table 3.1).

Table 3.1. Variables used to model multi-species occupancy of grassland-obligate birds surveyed during 2005-2006 in southeast Michigan, USA.

Variables	Definition	Spatial Extent	Source
Dependent			
Multi-species presence	Detection and non-detection observations based on replicated bird survey data.	Field	Current study[a]
Independent			
CREP[b] planting type	Indicator for CP1[b] (0) and CP23[b] (1) planting types.	Field	USDA[b]
Field age	Months since first planting.	Field	USDA
Field area	Area encompassing bird and vegetation surveys (ha).	Field	Current study
Field openness	Amount (ha) of open cover types within 5 km of surveyed field.	Field plus	2006 NLCD[c]
Forb cover	Variance in forb cover measured at randomized field locations.	Field	Current study
Grass cover	Variance in grass cover measured at randomized field locations.	Field	Current study
Landscape metrics[d]	Principal components of multiple landscape metrics.	Field plus	Current study

[a]Applied Forest and Wildlife Ecology Laboratory, Michigan State University, East Lansing, MI.
[b]CREP = Conservation Reserve Enhancement Program; CP1 = non-native plants; CP23 = native plants; USDA = United States Department of Agriculture Natural Resources Conservation Service.
[c]NLCD = National Land Cover Dataset (30-m resolution; Fry et al. 2012).
[d]Landscape metrics are described in Table 3.2. Landscape metrics calculated for 50-, 100-, 200-, 400-, 800-, 1600-, and 3200-m radial buffers centered on field centroids.

To describe grassland-obligate bird occupancy, we applied a single-season, multi-species occupancy model following Rota et al. (2016):

$$y_{ijk} \mid z_{ij} \sim Bernoulli(\boldsymbol{Z}_j\ ,\ p_{ijk})\ , \tag{3.1}$$

$$\boldsymbol{Z}_j \sim MVB(\psi_j)\ , \tag{3.2}$$

$$logit(\psi_j) = \beta_{0j} + \boldsymbol{\Psi_j}\beta_j +\ \varepsilon_j\ , \tag{3.3}$$

$$logit(p_{ijk}) = \alpha_{0j} + \boldsymbol{P_{ijk}}\alpha_j +\ \eta_j\ , \tag{3.4}$$

where y_{ijk} is the detection and non-detection (i.e., 1/0 scores) of species *i* at field *j* during replicate survey *k*, conditional on true species occupancy, which is distributed as a Bernoulli random variable with detection probability p_{ijk}. Latent (true) species occupancy $\boldsymbol{Z}_j = \{z_{1j}, z_{2j}, \dots, z_{Ij}\}$ is an *I*-dimensional vector of 1's and 0's indicating *I* species occupancy, which is modeled as a multivariate Bernoulli (MVB) random variable (sensu Rota et al. 2016) with logit-scale (estimated) species occupancy ψ_j at field *j* as a function of field-level (random) intercepts β_{0j}, field- and landscape-level covariates $\boldsymbol{\Psi_j}$ with a conformable vector of slope parameters β_j, and errors ε_j. Species-level detection probabilities p_{ijk} are logit-scale estimated as a function of field-level (random) intercepts α_{0j}, covariates $\boldsymbol{P_{ijk}}$ with a conformable vector of slope parameters α_j, and errors η_j. Finally, ψ_j is interpreted as the probability at which a species occupies field *j*, p_{ijk} is interpreted as the probability at which a species *i* is detected (i.e., per field *j* per replicate visit *k*), and logit-link-scale (linear) parameters β_{0j}, β_j, α_{0j}, and α_j are interpreted as the expected change in log odds for a 1-unit increase in associated covariates or, in the case of factor (categorical) effects, the log of odds ratio for a change between groups (e.g.,

CP23 and CP1, which is the reference level for CP planting type; Zipkin et al. 2010, Rota et al. 2016, Kéry and Royle 2016, 2021).

This hierarchical model structure thus includes field- and landscape-level effects to estimate multi-species occupancy, conditional on species presence, while also accounting for imperfect species detection and changes between survey years as a proxy for species-field colonization and extinction (e.g., multi-season models are not available in the "unmarked" package; Fiske and Chandler 2011). Model derived estimates include marginal occupancy and detection probabilities, which are species specific, as well as co-occupancy and conditional occupancy (and detection) probabilities, which are group specific (Rota et al. 2016, Kéry and Royle 2016, 2021). Co-occupancy characterizes estimated probabilities of groups of species cohabiting fields by CP planting type, and conditional occupancy and detection describes estimated probabilities for one species given the presence (or absence) of one or more species of a group cohabiting fields by CP planting type. Additionally, species groups were defined *a priori*—in our case habitat, foraging, nesting, or behavioral guilds. We thus report: (1) marginal occupancy and detection probabilities by species and CP planting, (2) co-occupancy probabilities by groups of species and CP planting, and (3) conditional occupancy and detection probabilities by groups of species and CP planting, where (i.e., for items 2 and 3) species groups are based on bird habitat, foraging, nesting, and behavioral guilds retrieved from the All About Birds (online) archive (Cornell Lab of Ornithology 2019).

In our candidate multi-species occupancy models, intercept estimates represented expected species occupancy probabilities at CP1 fields and survey year 2005 while controlling for covariates of interest and year 2006. The effect of CP23 thus represented mean deviation in species occupancy from CP1 fields (Table 3.1). We also considered field age (e.g., as a proxy for

vegetation maturity and potential plant interactions; Reiley and Benson 2020) and field openness (i.e., total area [ha] of open cover types within 5 km of field centroids, corresponding to search-radii lengths and estimated distances for dispersing grassland birds; Cava et al. 2016, Williams and Boyle 2018, 2019, Wolf et al. 2020, NatureServe 2021). Open cover types included barren, shrub/scrub, grassland/herbaceous, pasture/hay, and crop cover types as classified by the 2006 National Land Cover Dataset (Table 3.1; Fry et al. 2012). We treated cropland as an open cover type because the NLCD classification does not distinguish among crop types (e.g., corn, soybeans, wheat, and others, some of which being more open than closed [e.g., soybeans and wheat]). We considered variances in forb cover and grass cover within fields (Table 3.1). Previous research suggests that cover of bare ground, dead (standing) canopy, and litter are useful predictors of habitat selection and use by grassland birds (Fisher and Davis 2010), but each was highly (i.e., Pearson's $|r| > 0.60$) correlated with forb and grass cover estimates in this study. We also evaluated effects of principal components of landscape metrics (Table 3.2) describing land cover composition and configuration at multiple spatial extents (Table 3.1). We considered landscape characteristics proximate to CREP fields as primary drivers of habitat selection, influencing likelihood of field use by grassland birds (Bakker et al. 2002, Shahan et al. 2017).

Because factors affecting grassland bird habitat selection function at different spatial scales (Cunningham and Johnson 2006, Scholtz et al. 2017, Shahan et al. 2017), we quantified land cover patterns within 50-, 100-, 200-, 400-, 800-, 1600-, and 3200-m radii (i.e., circular buffers) around field centroids. In doing so, we assumed that field core areas would contain the highest-quality cover for grassland-obligate birds. This also allowed us to quantify land cover patterns at varying extents, representing different composition and configuration characteristics

in and around study fields. As a minimum spatial extent, we chose 50 m because it exceeded the resolution (i.e., 30-m) of our land use and land cover dataset—the 2006 National Land Cover Dataset (NLCD; Fry et al. 2012). As a maximum spatial extent, we chose 3200 m to represent broader landscape contexts associated with bird occupancy at individual fields (Cunningham and Johnson 2006). Deliberately, this extent was also shorter than the radial distance for quantifying field openness at 5 km around fields (Table 3.1). Our final group of model variables thus allowed evaluation of whether grassland bird occupancy responded to CREP planting type (i.e., management prescription), field age (i.e., proxy for vegetation maturity), variance in forb/grass cover (i.e., within-field vegetation structure), field openness (i.e., amount of nearby open habitats), or land cover composition and configuration (i.e., broader landscape characteristics).

We used the 2006 NLCD to quantify field openness at a 30-m spatial resolution (Fry et al. 2012). Because grassland-obligate birds associate strongest with open habitat types as well as proximate landscape characteristics (Cunningham and Johnson 2006, Scholtz et al. 2017, Shahan et al. 2017), we first reclassified the NLCD types (code) barren (31), shrub/scrub (52), grassland/herbaceous (71), pasture/hay (81), and crop (82) into an “open habitat” class. We reclassified remaining cover types (i.e., open water [11], developed [21], and deciduous forest [41]) into an “inhospitable matrix” class. To reclassify the 2006 NLCD, we used the “reclassify” function in R’s “raster” package version 3.3-7 in R version 4.0.2 (Hijmans 2020, R Core Development Team 2020). Because we also sought to characterize land cover composition and configuration of “open habitat” v. “inhospitable matrix” cover types, we computed raw and principal component quantities of numerous (correlated) landscape metrics expected to influence occurrence of grassland-obligate bird species (Bakker et al. 2002, Shahan et al. 2017).

To quantify land cover characteristics (Table 3.2), we used the "landscapemetrics" package version 1.5.0 in R version 4.0.2 (Hesselbarth et al. 2019, R Core Development Team 2020), which generates extent-defined (e.g., using buffers around study fields) composition and configuration metrics from raster datasets of land cover using FRAGSTATS version 4.2.1 (McGarigal et al. 2014). Contagion scores were invariant per field at finer spatial extents (e.g., 50-, 100-, 200-, and 400-m), because each extent contained a single cover type, and so we assumed 100% contagion scores in such cases. Euclidean nearest-neighbor distances were also inestimable at smaller spatial extents (e.g., based on a Queen's case neighborhood), and so we randomly sampled distances for qualified fields and scales assuming $Uniform(30, 50)$ in the absence of other information. We defined limits of these random draws using the spatial resolution of the NLCD (i.e., 30-m) and the smallest radius of our landscape buffers (i.e., 50-m).

Table 3.2. Metrics (McGarigal et al. 2014) used to represent cover type patterns surrounding Conservation Reserve Enhancement Program (CREP) fields in Michigan, based on the 2006 National Land Cover Dataset.

Metric	Abbreviation	Description
Patch Area	AREA_MN	Mean area (ha) across all patch types within a landscape.
Contagion	CONTAG	Connectedness (%) of patches within a landscape.
Edge Density	ED	Total edge length of a patch type divided by the total area (m/ha).
Euclidean Nearest Neighbor	ENN_MN	Mean distance (m) of patches to their nearest neighbor within a landscape.
Number of Patches	NP	Number of patches (count) within a landscape.
Patch Density	PD	Number of patches divided by total area (count per 100 ha).
Patch Richness	PR	Number of unique patch types (count) within a landscape.
Shannon Diversity index	SHDI	The negative sum, across all patch types, of the proportional abundance of each patch type multiplied by that proportion (unitless), based on total area.

In addition to retaining individual (raw) landscape metrics, we also applied a Principal Component Analysis (PCA) to reduce dimensionality of the metrics at each extent, independently. To do this, we used the "prcomp" function in R's "stats" package (R Core Development Team 2020). We confirmed that eigenvalues of the first two PC axes exceeded or approximately equaled the average eigenvalue across all PC axes using scree plots—visuals that describe variation in the matrix of landscape metrics (i.e., by PC axes) based on the Kaiser-Guttman procedure (Kaiser 1960). At each spatial extent (i.e., 50-, 100-, and so on), we retained two vectors of PC scores (i.e., PC1 and PC2) each whose factor loadings conveyed pairwise correlations between PC axes and individual landscape metrics. Finally, we estimated effects of PC1 and PC2 axes at different extents in a subset of our candidate models to evaluate the potential influence of land cover composition and configuration on grassland-obligate bird occupancy. If the PC of any landscape metrics (i.e., at a particular extent) appeared in a top-ranked model, then we used the PC's factor loadings (i.e., correlation coefficients describing landscape metric and PC-axis associations) to interpret land cover composition and configuration gradients quantified by each PC. We also report PCA bivariate and scree plots, one pair of plots per spatial extent (Figure B3.1).

With respect to candidate models considered (e.g., to formulate our multi-species occupancy [process-level] models), we considered all possible parameter combinations for which predictors did not exceed our pairwise correlation limit (i.e., Pearson's $|r| > 0.60$), and each candidate model had to generate fully identifiable parameters (e.g., given the limited number of study fields and species). Additionally, detection (observation-level) models always included a linear effect of surveyed field area for each replicate visit to CREP fields, comprising an index of survey effort. Data sparsity with respect to grassland-obligate bird species detection and non-

detection prohibited us from evaluating quadratic (nonlinear) or species-to-species and multi-predictor interactions, thus avoiding parameter non-identifiability.

We estimated 468 candidate models in total, which was largely influenced by two selected PCs of landscape metrics for each of seven spatial extents—a total number of candidate models also limited by restrictions on predictor collinearity (e.g., many PCs correlated across extents and sometimes with field-level CP or % cover types). To estimate candidate models, we used the maximum-likelihood-based "occuMulti" function in R's "unmarked" package version 1.0.1 in R version 4.0.2 (Fiske and Chandler 2011, R Core Development Team 2020). The "occuMulti" function can (a) incorporate covariates on discrete latent states (i.e., true species occupancy conditional on species presence), (b) control for interspecies correlations in occupancy (e.g., co-occurrence and competitive exclusion; Hui et al. 2015, Tobler et al. 2019), and (c) account for imperfect species detection by surveyors (e.g., final estimates become biased without incorporating imperfect detection; MacKenzie et al. 2002, MacKenzie et al. 2006, MacKenzie et al. 2009, Kéry and Royle 2016, 2021). Furthermore, the "occuMulti" function estimates single-season multi-species occupancy following Rota et al. (2016), and because dynamic multi-species models are neither available in "unmarked" nor advisable given only two years of data (e.g., insufficient to reliably estimate colonization and extinction between fields over time), we evaluated our candidate models using 2005 and 2006 data together and always controlled for year as a fixed effect on occupancy. This approach allowed us to consider whether CP effects differed among species and years after accounting for other covariates as well as imperfect detection (Fiske and Chandler 2011, Rota et al. 2016). Year effects also act as simple proxies for (implicit) species-field colonization and extinction between survey seasons.

Because our 2005 surveys lacked within-field measures of cover types (e.g., bare ground, dead canopy, forb, grass, litter, and total), we evaluated weather differences between 2005 and 2006 to help justify using identical cover measurements at fields between survey years. We assumed that barring direct manipulation of vegetation between years, temperature and precipitation were useful proxies of grassland plant respiration, net primary production, and growing season length (Risser et al. 1981, Knapp and Smith 2001, Ren et al. 2018). While amount of precipitation influences grassland vegetation height, temperature and soil conditions (i.e., along with precipitation) jointly influence plant species composition (UCMP 2007). We first retrieved monthly temperature (ºC) and precipitation (mm) data at a 4-km resolution from the 30-year Normals of the Parameter-elevation Regressions on Independent Slopes Model (PRISM; PRISM Climate Group 2004) across the extent of our study area. We chose to use the 4-km (resolution) data to understand changing weather patterns with assumed vegetation and associated land cover change on a broad spatial scale.

We summarized raster PRISM datasets of monthly mean temperature and total precipitation to their grand means across May-August 2005 and 2006, representing an average state for local weather and associated growing-season conditions during our two survey seasons (i.e., using R's "prism" package version 0.2.0 in R version 4.0.2; Hart and Bell 2015, R Core Development Team 2020). We then extracted values of seasonal mean temperature and precipitation at study fields using the "extract" function of R's "raster" package version 3.3-7 in R version 4.0.2 (Hijmans 2020, R Core Development Team). To assess differences between years, we generated boxplots of weather variables for fields by year and applied non-parametric (i.e., Wilcoxon signed-rank) paired two-sample *t*-tests to field-level (grand mean) estimates of summer temperature and precipitation. We chose to use a non-parametric test due to the limited

sample size (i.e., 14 fields). Producing the boxplots and conducting independent *t*-tests helped us evaluate our rationale for using identical vegetation measurements at fields between 2005 and 2006 in candidate models for multi-species occupancy.

In our candidate model set, we evaluated two null models, one intercept-only for both occupancy and detection, and another including intercept-only occupancy and a field surveyed area effect on detection. Null occupancy models imply that species do not assemble along common axes of environmental variation (i.e., assemble randomly), and such models provide simple contrasts with deterministic models estimating additional covariate effects on multi-species occupancy (Mihaljevic et al. 2015). To estimate observation (detection) models, we evaluated a linear effect of surveyed field area during each replicate survey visit (e.g., effects commonly used to estimate imperfect species detection as a function of the amount of area searched; Kéry and Royle 2016, 2021). To ensure model convergence, parameter identification, and estimation of parameter standard errors, we (a) excluded all interaction terms (i.e., covariate-to-covariate and species-to-species), (b) removed models that estimated standard errors exceeding 16 on the logit scale (i.e., 0.999 on the inverse-logit, or occupancy-rate, scale) for any parameter (e.g., comprising highly uncertain candidates due to sample size constraints on available degrees of freedom for multi-predictor [i.e., > 3] effects on multi-species occupancy), and (c) used Nelder-Mead optimization to evaluate models up to 100,000 total iterations. To expedite the model-fitting process, we *Z*-scored (i.e., standardized) each of our covariates, treated CP planting type as a factor (i.e., with CP1, indicator “0,” comprising the reference category), and estimated our candidate models in parallel using multiple computing processors on a high-powered computing cluster.

Across our candidate model set, we selected the top-ranked model using Akaike's (second-order) Information Criterion (i.e., models < 2.0 AICc of the top-ranked model were considered competing; Burnham and Anderson 2002). We chose not to model-average effects across competing models because of known biases and error propagation in conventional model-averaging approaches (Claeskens et al. 2016, Banner and Higgs 2017, Dormann et al. 2018), so we used the top-ranked model for inference (Burnham and Anderson 2002). We evaluated goodness-of-fit of the top-ranked model by only inspecting its Pearson residuals (Kéry and Royle 2016, 2021), particularly because MacKenzie and Bailey (2004) goodness-of-fit tests are not available for use with multi-species occupancy models in "unmarked" (Fiske and Chandler 2011). We checked for remaining spatial autocorrelation in our top-ranked model by examining multivariate spline correlations (i.e., pairwise-location [multi-species] residuals as a function of distance, analogous to a Mantel test) of model Pearson residuals using the "ncf" package version 1.2-9 in R version 4.0.2 (Moll et al. 2016, Moll et al. 2018, Bjornstad 2020, R Core Development Team 2020).

We were also interested in understanding how grassland (i.e., facultative and obligate) bird species diversity compared between our CREP study fields and other (non-CREP) areas in the region. We thus generated grassland bird species richness estimates at each study field and compared these estimates to broader-scale species richness estimates based on (spatially) nearby and (temporally) concurrent records of grassland birds collected by *e*Bird citizen scientists (Sullivan et al. 2009). To acquire count indices for estimating species richness from concurrent *e*Bird records, we used data retrieving and filtering functions available in the "auk" package version 0.4.1 in R version 4.0.2 (Strimas-Mackey et al. 2018, R Core Development Team 2020). We first downloaded publicly available *e*Bird records in North America and then filtered them

based on their occurrence (1) in Michigan, USA, (2) within the geographic bounding box of our CREP study fields, and (3) within 1-hr full checklists recorded between 06:00 and 11:00 during 15 May-14 August in 2005 and 2006 (i.e., coinciding with line-transect surveys at CREP study fields).

We estimated rarefied species richness from the filtered species-by-site matrices of abundance to control for measurement error in both our study and *e*Bird count records using the "vegan" package version 2.5-6 in R version 4.0.2 (Oksanen et al. 2019, R Core Development Team 2020). Rarefaction allowed us to adjust for sample (size) differences between our CREP surveys and filtered *e*Bird checklists (Sanders 1968, Hurlbert 1971), which thus permitted a fairer comparison of species richness estimates derived from our study fields and concurrent *e*Bird records. Based on subsamples of equal size, rarefied diversity metrics such as species richness can be computed and then compared between nearby related ecological systems, independent of differences in database sample size, record locations, or detection methods (Weiss et al. 2017).

To understand changes in species richness with increasing numbers of sample locations, we generated species-accumulation curves in "vegan" by applying rarefaction based on 10,000 permutations of input CREP field surveys and *e*Bird checklists (Gotelli and Colwell 2001, Chiarucci et al. 2008, Colwell et al. 2012). We report rarefaction curves for CREP study fields and *e*Bird locations in summer 2005 and 2006 based on one of nine (candidate) species accumulation models used to characterize species-area relationships (Dengler 2009). We report models that produced the lowest root-mean-squared error (RMSE) per dataset (i.e., CREP or *e*Bird) per year via nonlinear least squares regression—thus taking a data-driven approach to generate rarefaction curves. Candidate models estimated either Arrhenius, Gleason, Gitay,

Lomolino, Asymptotic, Gompertz, Michaelis-Menten, Logistic, or Weibull nonlinear accumulation using the "fitspecaccum" function in R's "vegan" package (Oksanen et al. 2019). Finally, we plotted mean (± SE) species richness against increasing numbers of sample locations for CREP study fields and *e*Bird checklists in 2005 and 2006, independently.

Results

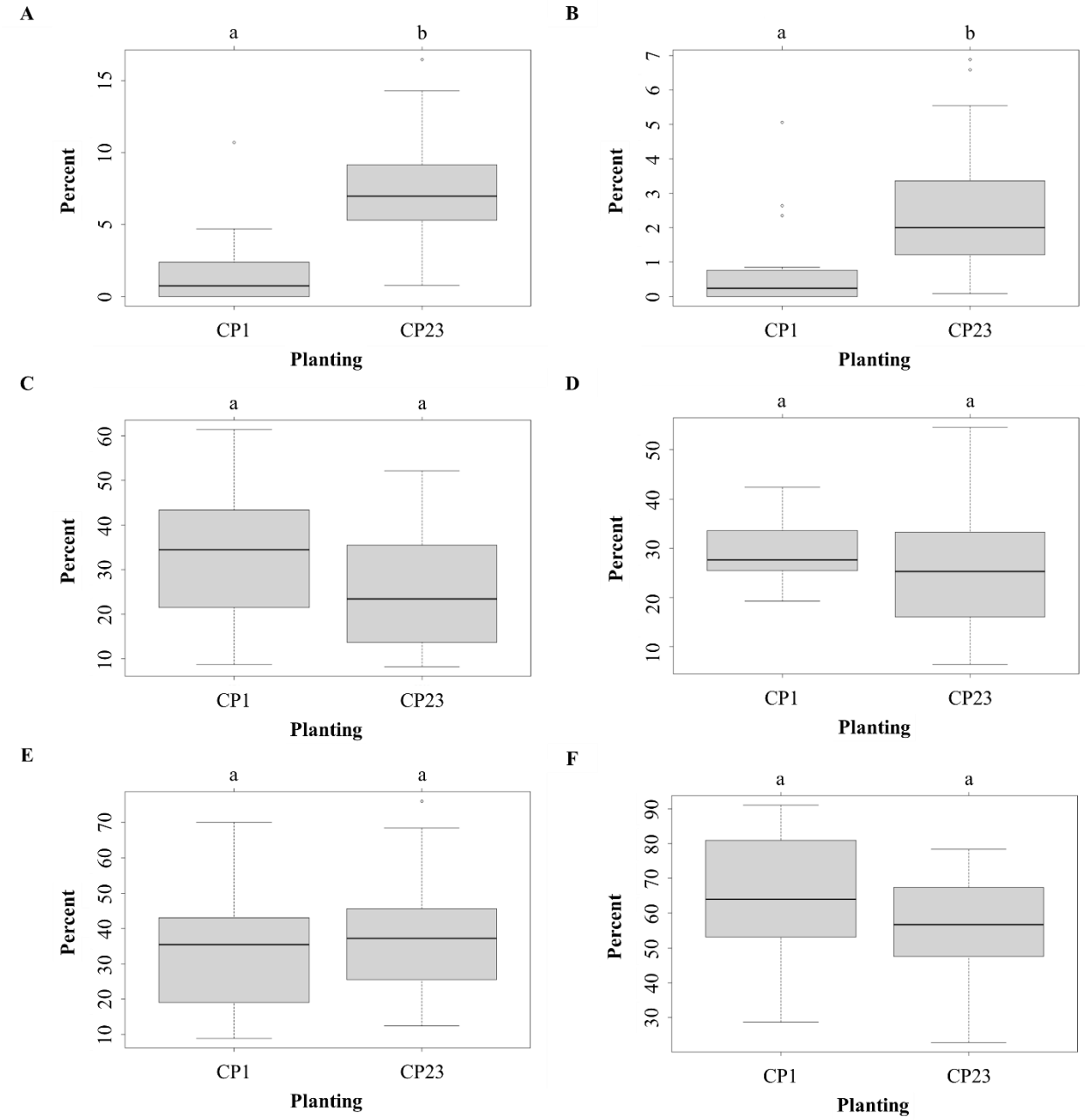
Grassland vegetation composition patterns across CREP fields

We recorded 69 plant species in this study: 60 recorded in CP23 (native) fields, and 37 recorded in (non-native) CP1 fields. Of the grand total, 32 species uniquely occurred in CP23 fields, including all planted native grasses. Nine species uniquely occurred in CP1 communities—mostly weedy, introduced species (e.g., burdock [*Artium* spp.], morning glory [*Ipomoea* spp.]. mustard [Cruciferae], ragweed [*Ambrosia* spp.] and spiny-leaf sow thistle [*Sonchus asper*]; Van Loan 2011). The most common grasses observed in CP23 fields (i.e., observed in ≥20% of vegetation sample plots) included big bluestem, indiangrass, and little bluestem, and the most common grasses observed in CP1 fields included orchardgrass, timothy, and annual ryegrass (*Lolium perenne*). Notably, ryegrass was not part of the original seed mix and likely established due to residual seed in (or invasion to) CP1 fields. The most common forbs observed in CP23 fields included several unplanted species such as dandelion (*Taraxacum* spp.), thistle (*Cirsium* spp.), black medick (*Medicago lupulina*), goldenrod (*Solidago* spp.), Queen Anne's lace (*Daucus carota*), and lettuce (*Lactuca* spp.), suggesting that some of the forb component of our CP23 seed mix did not establish. The most common forbs observed in CP1 fields included dandelion and thistle as well as alfalfa—an intentionally planted species.

Across fields, mean (± SD) total vegetation canopy cover was 60 (± 17%, range: 23-91%; Figure 3.2F), mean litter cover was 36 (± 17%, range 9-76%; Figure 3.2E), mean grass cover

was 28 (± 10%, range 6-55%; Figure 3.2D), and mean forb cover was 30 (± 15%, range 8-61%; Figure 3.2C). We did not detect significant differences in total vegetation canopy (Figure 3.2F), litter (Figure 3.2E), forbs (Figure 3.2C), or grass cover (Figure 3.2D) between CP1 and CP23 fields. However, mean (± SD) bare ground cover was 4 (± 4%, range 0-16%; Figure 3.2A) and mean dead canopy cover was 2 (± 2%, range 0-7%; Figure 3.2B), and both differed between CP plantings, with CP23 fields exhibiting more bare ground and standing dead vegetation than CP1 fields (i.e., albeit at much finer magnitudes than other cover types).

Figure 3.2. Cover type by Conservation Practice (CP) planting type: (A) bare ground, (B) dead, (C) forb, (D) grass, (E) litter, and (F) total vegetation cover on Conservation Reserve Enhancement Program (CREP) fields in southeast Michigan, 2006. Letters at the top of each graph denote significance between planting types based on Tukey-adjusted familywise error rates.



Weather and assumed vegetation and land cover patterns across CREP fields

We computed grand mean (± SD) precipitation of 84.46 (± 6.56 mm) and 84.90 (± 6.04 mm) during May-August 2005 and 2006, respectively, and grand mean (± SD) temperatures of 18.85 (± 0.20 ºC) and 18.79 (± 0.23 ºC) during May-August 2005 and 2006, respectively (Figure B3.2). Results of non-parametric (paired, two-sample) *t*-tests revealed that mean temperatures were greater in 2005 (Wilcoxon signed-rank paired $V = 100$, 13 [Satterthwaite-adjusted] df, $p < 0.01$) and mean precipitation did not differ between years (Wilcoxon signed-rank paired $V = 57$, 13 [Satterthwaite-adjusted] df, $p = 0.80$); however, precipitation was considerably more variable in 2005 (Figure B3.2). Because we found differences in mean temperature and variance of precipitation, each could have affected grassland vegetation phenology, composition, and structure at our study fields, thereby potentially reducing the validity of our assumption about similar weather and grassland vegetation and land cover between years. However, we note that boxplot profiles for temperature were generally comparable, and so the statistically significant difference in mean temperatures may not represent a biologically meaningful effect for vegetation and land cover between years.

Grassland-obligate bird occupancy and detection patterns across CREP fields

The surveyed (i.e., upland) area of CP23 fields ranged from 6.9-19.8 ha (median = 11.8, $\bar{x}$ = 12.6, SE = 1.9, $n = 7$) while surveyed area of CP1 fields ranged from 7.3-23.9 ha (median = 10.9, $\bar{x}$ = 12.3, SE = 2.1, $n = 7$). Between 2005 and 2006, 19 and 7% of detected birds were unidentified, respectively, and thus excluded from statistical models. In total, we observed 35 bird species, 12 of which included grassland obligates: bobolink, dickcissel, eastern kingbird (*Tyrannus tyrannus*), eastern meadowlark, grasshopper sparrow, Henslow's sparrow (*Ammodramus henslowii*), horned lark (*Eremophila alpestris*), northern harrier (*Circus cyaneus*),

ring-necked pheasant, savannah sparrow, sedge wren, and vesper sparrow. Four of these (i.e., dickcissel, grasshopper sparrow, Henslow's sparrow, and northern harrier) are listed as "species of greatest conservation need" by the Michigan Department of Natural Resources (MDNR 2015). We did not investigate occupancy patterns of savannah sparrows because we detected the species at every field at least once between replicate visits in 2005 and 2006. Because 23 other species associated with wetland, woodland, or other non-grassland (cover) types, and because we rarely encountered northern harrier, Henslow's sparrow, horned lark, or sedge wren (i.e., 1-3 detections were recorded between multiple visits at only one or two fields between seasons), we restricted our final analyses to seven grassland-obligate species (Table 3.3).

Table 3.3. Grassland-obligate bird species analyzed in our multi-species occupancy models. We retrieved data on habitat, foraging, nesting, and behavioral guilds from the Cornell Lab of Ornithology (2019). Included are bird common names, scientific names, and American Ornithological Society codes (Chesser et al. 2020) as well as nesting, foraging, and behavioral guilds (Cornell Lab of Ornithology 2019).

Species	**Foraging**	**Nesting**	**Behavior**
Bobolink (BOBO) *Dolichonyx oryzivorus*	Seeds	Ground	Ground forager
Dickcissel (DICK) *Spiza americana*	Seeds	Shrub	Ground forager
Eastern kingbird (EAKI) *Tyrannus tyrannus*	Insects	Tree	Aerial forager
Eastern meadowlark (EAME) *Sturnella magna*	Insects	Ground	Ground forager
Grasshopper sparrow (GRSP) *Ammodramus savannarum*	Insects	Ground	Ground forager
Ring-necked pheasant (RNPH) *Phasianus colchicus*	Insects and seeds	Ground	Ground forager
Vesper sparrow (VESP) *Pooecetes gramineus*	Insects	Ground	Ground forager

Multi-species grassland bird occupancy was best explained by CP planting type while controlling for survey year, which carried the majority of AICc weight (Table 3.4). This top-ranked model competed (i.e., < 2.0 ΔAICc) with a model that, in addition to survey year, included a fixed effect of the total number of patches around fields summarized at a 400-m extent, and both models were more informative than the null (intercept-only) occupancy and (intercept-only) detection models.

Table 3.4. Model selection table, including Akaike's (second-order) Information Criterion (AICc), ΔAICc, AICc weight, and number of parameters (*k*) for each candidate model reported. We report the top ten models of 468 total candidates. Candidate model refers to the occupancy predictor(s), and each candidate model included survey year while field surveyed area served as an observation-level (detection) predictor. See Tables 3.1 and 3.2 for descriptions of predictor variables.

Candidate Model	**AICc**	**ΔAICc**	**AICc Weight**	***k***
CP Type	693.48	0.00	0.50	35
Number of Patches at 400-m	694.38	0.91	0.32	35
LSM PC1 at 400-m	696.96	3.48	0.09	35
Patch Density at 1600-m	699.68	6.20	0.02	35
Contagion at 800-m	699.74	6.27	0.02	35
Number of Patches at 1600-m	700.12	6.64	0.02	35
Edge Density at 800-m	701.09	7.61	0.01	35
Edge Density at 1600-m	702.35	8.87	0.01	35
Shannon Diversity Index at 1600-m	703.88	10.40	0.00	35
Contagion at 1600-m	703.94	10.47	0.00	35
…	…	…	…	…

Based on the top-ranked model, occupancy probabilities at CP23-planted fields deviated positively from CP1-planted fields for eastern kingbird, eastern meadowlark, grasshopper sparrow, and ring-necked pheasant; however, most deviations were statistically insignificant, except for eastern meadowlark (p = 0.04) and grasshopper sparrow (p = 0.02), although we found marginal evidence for eastern kingbird (p = 0.08; Table 3.5). Occupancy probability

deviated negatively from CP1-planted fields for bobolink and vesper sparrow, but these deviations were not statistically significant. Additionally, bobolink occupancy was significantly (p = 0.04) and positively associated with CP1 plantings during 2005 while the remaining six species were not significantly associated with CP1 plantings. Bobolink, eastern kingbird, eastern meadowlark, grasshopper sparrow, and vesper sparrow had higher (while dickcissel and ring-necked pheasant had lower) occupancy probabilities in 2006 than 2005, but annual deviations in occupancy were not statistically significant after accounting for CP planting type. With respect to detection, increasing surveyed area (i.e., an index of survey effort) reduced likelihoods of observers detecting all species except for vesper sparrow, and eastern meadowlark detection significantly associated (p = 0.001) with increased effort while vesper sparrow detection was marginally important (p = 0.06; Table 3.5). With respect to statistical dependence in our observations, the top-ranked model adequately accounted for spatial autocorrelation in multi-species occupancy (i.e., Moran's $I \approx 0$; Figure B3.3), as evidenced by the 95% confidence intervals based on 10,000 bootstrap samples of each model's input data used to calculate and map patterns in the Pearson residuals

Table 3.5. Process- and observation-level effect estimates on the logit-link scale including associated point estimates and 95% confidence intervals for the top-ranked multi-species occupancy model. CP1 and CP23 comprise independent levels of the CP planting factor, of which CP1 is estimated in occupancy-level species-specific intercepts, and all other predictor variables comprise continuous covariates. Occupancy- and observation-level effects (i.e., for species-specific occupancy and detection rates, respectively) represent the expected change in log odds for a 1-unit increase in associated covariates. With respect to factors (e.g., CP planting type), effects correspond to the log of odds ratio for a change between groups (i.e., CP23 and CP1, the reference level). Factors and covariates, including raw landscape metric (LSM) and principal component (PC) quantities (and their spatial extents), are described in Tables 3.1 and 3.2. The top-ranked model is reported in Table 3.4. Bolded CIs indicate non-zero effects.

Process (Occupancy) Model			**Observation (Detection) Model**		
***Species* and Parameter**	**Estimate**	**95% CI**	***Species* and Parameter**	**Estimate**	**95% CI**
Bobolink			*Bobolink*		
Intercept (CP1, 2005)	1.848	**(0.058, 3.638)**	Intercept	1.151	**(0.733, 1.568)**
CP23	-1.342	(-3.268, 0.583)	Field Survey Area	-0.261	(-0.658, 0.136)
2006	0.193	(-1.612, 1.997)			
Dickcissel			*Dickcissel*		
Intercept (CP1, 2005)	-0.181	(-1.758, 1.396)	Intercept	-0.935	**(-1.826, -0.045)**
CP23	-0.037	(-1.917, 1.844)	Field Survey Area	-0.759	(-1.872, 0.355)
2006	-0.171	(-1.981, 1.639)			
Eastern kingbird			*Eastern kingbird*		
Intercept (CP1, 2005)	-1.640	(-4.003, 0.724)	Intercept	-1.591	**(-2.272, -0.909)**
CP23	2.317	(-0.318, 4.952)	Field Survey Area	-0.000	(-0.559, 0.559)
2006	1.551	(-1.041, 4.413)			
Eastern meadowlark			*Eastern meadowlark*		
Intercept (CP1, 2005)	-2.073	(-4.583, 0.441)	Intercept	-1.259	**(-1.855, -0.664)**
CP23	3.336	**(0.169, 6.504)**	Field Survey Area	-1.330	**(-2.144, -0.516)**
2006	1.694	(-1.219, 4.608)			
Grasshopper sparrow			*Grasshopper sparrow*		
Intercept (CP1, 2005)	-1.742	(-3.966, 0.483)	Intercept	-0.538	(-1.093, 0.017)
CP23	3.667	**(0.482, 6.852)**	Field Survey Area	-0.030	(-0.587, 0.527)
2006	0.474	(-2.481, 3.429)			

Table 3.5 (cont'd)

Ring-necked pheasant			*Ring-necked pheasant*		
Intercept (CP1, 2005)	2.422	(-0.350, 5.194)	Intercept	-0.627	**(-1.030, -0.225)**
CP23	0.467	(-1.706, 2.641)	Field Survey Area	-0.111	(-0.498, 0.275)
2006	-2.021	(-4.782, 0.740)			
Vesper sparrow			*Vesper sparrow*		
Intercept (CP1, 2005)	3.211	(-5.338, 11.761)	Intercept	-1.415	**(-1.908, -0.922)**
CP23	-1.997	(-10.444, 6.451)	Field Survey Area	0.416	(-0.011, 0.843)
2006	0.324	(-3.743, 4.391)			

Mean species (marginal) occupancy and detection probabilities varied between CP plantings, and uncertainty around occupancy estimates was high. Only eastern meadowlark and grasshopper sparrow occupancy differed significantly between CP planting types, and eastern kingbird, eastern meadowlark, grasshopper sparrow, and ring-necked pheasant exhibited higher (mean) occupancy probabilities in CP23 than CP1 fields (Figure 3.3A). Other species exhibited similar or lower (mean) occupancy probabilities between CP plantings, but those differences were not significant. Across CP plantings, bobolink was detected by observers more often than other species, and uncertainty around marginal detection estimates across CP plantings was lower than uncertainty around marginal occupancy estimates (Figure 3.3B).

Species co-detection estimates (i.e., grouped by guild) were non-identifiable across survey years and between CP plantings, but co-occupancy estimates were identifiable by guild, and mean co-occupancy probabilities for all species (i.e., grassland-habitat guild), ground foragers and nesters, granivores, insectivores, and shrub-tree nesters were low. Except for co-occupying granivores, all mean co-occupancy probabilities in CP23-planted fields exceeded those of CP1-planted fields across survey years; however, 95% confidence intervals consistently overlapped, and estimated uncertainty was highest for ground (nesting), granivorous (foraging), insectivorous (foraging), and shrub/tree (nesting) guilds between CP plantings (Figure 3.4).

Mean (conditional) occupancy estimates varied little between groups of species and CP plantings, and uncertainty around conditional occupancy estimates was high. Specifically, mean (conditional) occupancy was consistently high (i.e., > 0.75) at CP1 fields, consistently lower at CP23 fields, and exhibited considerable variation (e.g., SE range: 0.12-0.20) across CP plantings when considering bobolink occupancy given the presence of either (a) all other grassland species, (b) all other ground foragers, (c) all other ground nesters, or (d) all other granivores

(Figure 3.5A). Additionally, (e) dickcissel occupancy given the presence of all other shrub-tree nesters neared 50 and was similar between CP plantings; whereas, (f) eastern kingbird occupancy given the presence of other all other insectivores varied between CP plantings (e.g., conditional occupancy was higher at CP23 than CP1 fields). Uncertainty was consistently high (e.g., SE range: 0.12-0.20) across the six comparison groups between CP plantings. Mean (conditional) detection estimates also varied little between groups of species and CP plantings, but uncertainty around conditional detection estimates was low. Specifically, mean (conditional) detection was consistently high (i.e., > 0.75) across CP plantings when considering the four comparison groups with bobolink (i.e., items (a)-(d) above in terms of detection rather than occupancy). In contrast, conditional detection was low for both the shrub/tree (nesting) and insectivorous (foraging) comparison groups (i.e., items (e)-(f) above; Figure 3.5B). Uncertainty (SE) about conditional detection estimates ranged 0.05-0.10 across all six comparison groups.

In summary, probabilities of detection for grassland-obligate birds consistently exceeded 0.15, and bobolink was detected most often by observers. Additionally, occupancy probabilities for most species exceeded 0.50, which suggests that over half of a random sample of CREP fields should be occupied by grassland-obligate birds. However, such occupancy probabilities are also higher on CP23 than CP1 fields. Finally, when bobolink occur in either CP1 or CP23 fields, it is likely (e.g., ~0.75) that other ground foraging, ground nesting, and granivorous species also occur.

Figure 3.3. Marginal occupancy (A) and detection (B) estimates summarized by CP planting type and derived from the top-ranked model of multi-species grassland bird occupancy in southeast Michigan, 2005-2006.

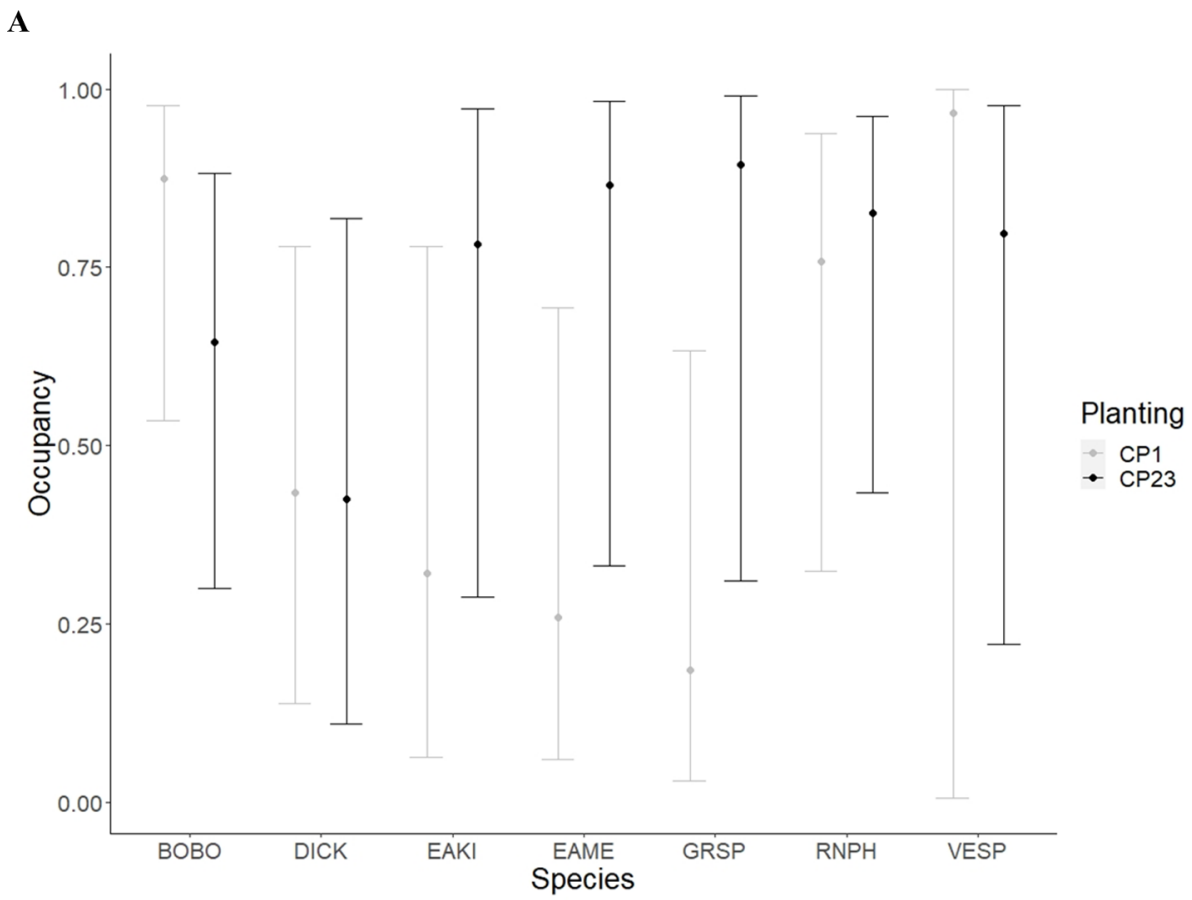


Figure 3.3 (cont'd)

B

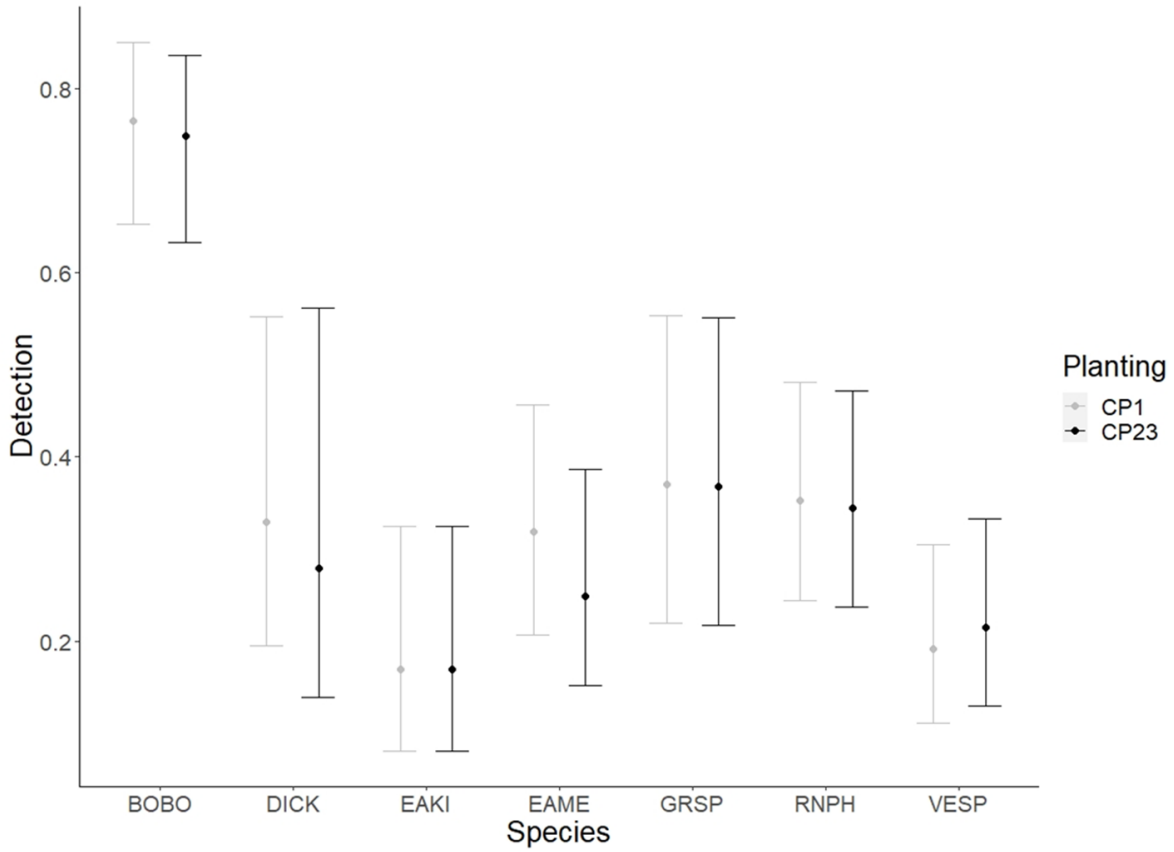


Figure 3.4. Co-occupancy estimates summarized CP planting type and derived from the top-ranked model of multi-species grassland bird occupancy in southeast Michigan, 2005-2006. Co-detection estimates were inestimable for most pairs of species due to sparsity of co-observations and thus not reported. Group comparisons include: All, where co-occupancy is estimated for all grassland bird species; GFs, where co-occupancy is estimated for species belonging to the ground forager (behavioral) guild; GNs where co-occupancy is estimated for species belonging to the ground nester (nesting) guild; GVs where co-occupancy is estimated for species belonging to the granivorous (foraging) guild; IVs where co-occupancy is estimated for species belonging to the insectivorous (foraging) guild; and STNs where co-occupancy is estimated for species belonging to the shrub/tree nester (nesting) guild. Species-guild memberships are summarized in Table 3.3. Ring-necked pheasant is both granivorous and insectivorous, thus represented in GV and IV foraging guilds.

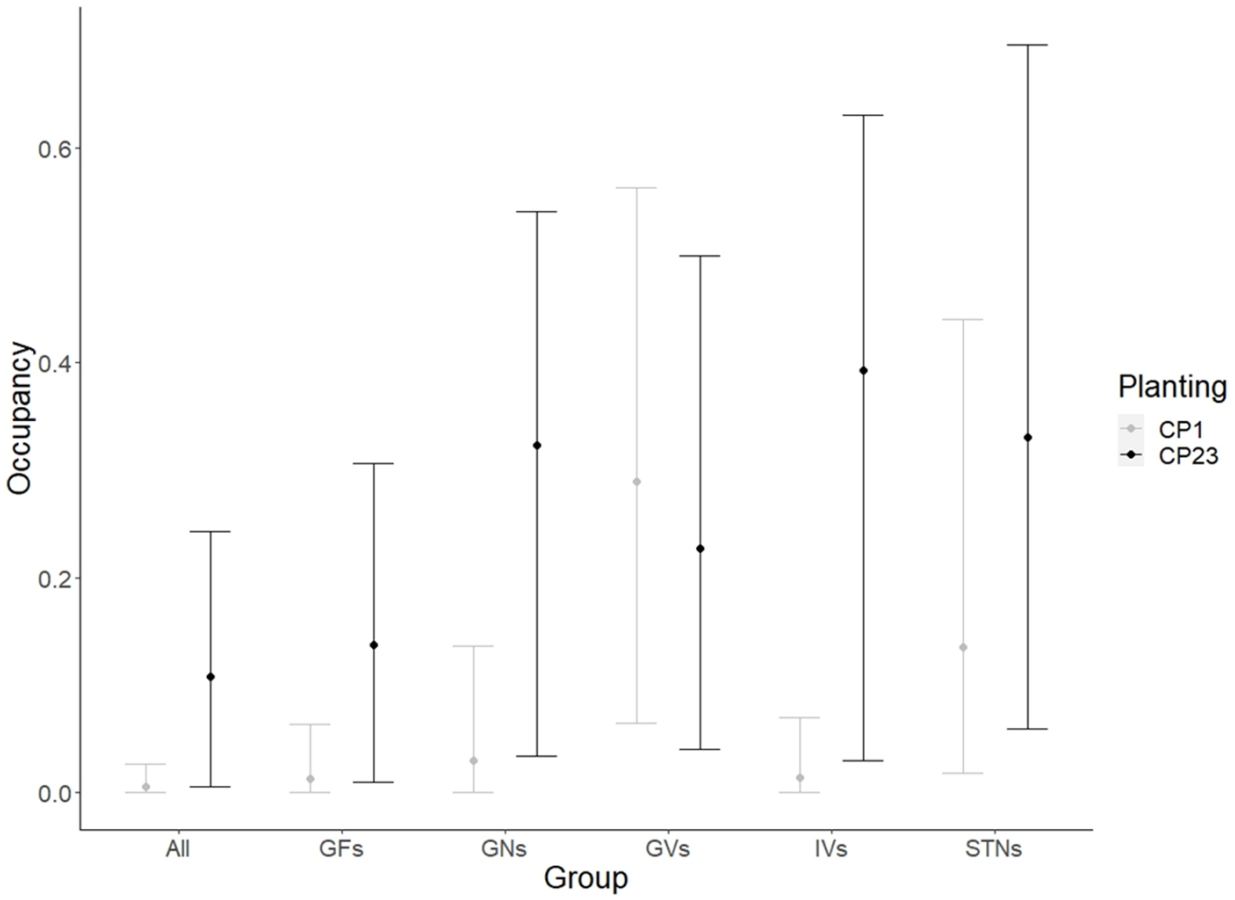


Figure 3.5. Conditional occupancy (A) and detection (B) estimates summarized CP planting type and derived from the top-ranked model of multi-species grassland bird occupancy in southeast Michigan, 2005-2006. Group comparisons include: BOBO | All, where bobolink occupancy and detection is conditional to presence of all other species; BOBO | GFs, where bobolink occupancy and detection is conditional to presence of all other species belonging to the ground forager (behavioral) guild; BOBO | GNs where bobolink occupancy and detection is conditional to presence of all other species belonging to the ground nester (nesting) guild; BOBO | GVs where bobolink occupancy and detection is conditional to presence of all other species belonging to the granivorous (foraging) guild; DICK | STNs where dickcissel occupancy and detection is conditional to presence of all other species belonging to the shrub/tree nester (nesting) guild; and EAKI | IVs where eastern kingbird occupancy and detection is conditional to presence of all other species belonging to the insectivorous (foraging) guild. Species-guild memberships are summarized in Table 3.3. Ring-necked pheasant is both granivorous and insectivorous, thus represented in GV and IV foraging guilds.

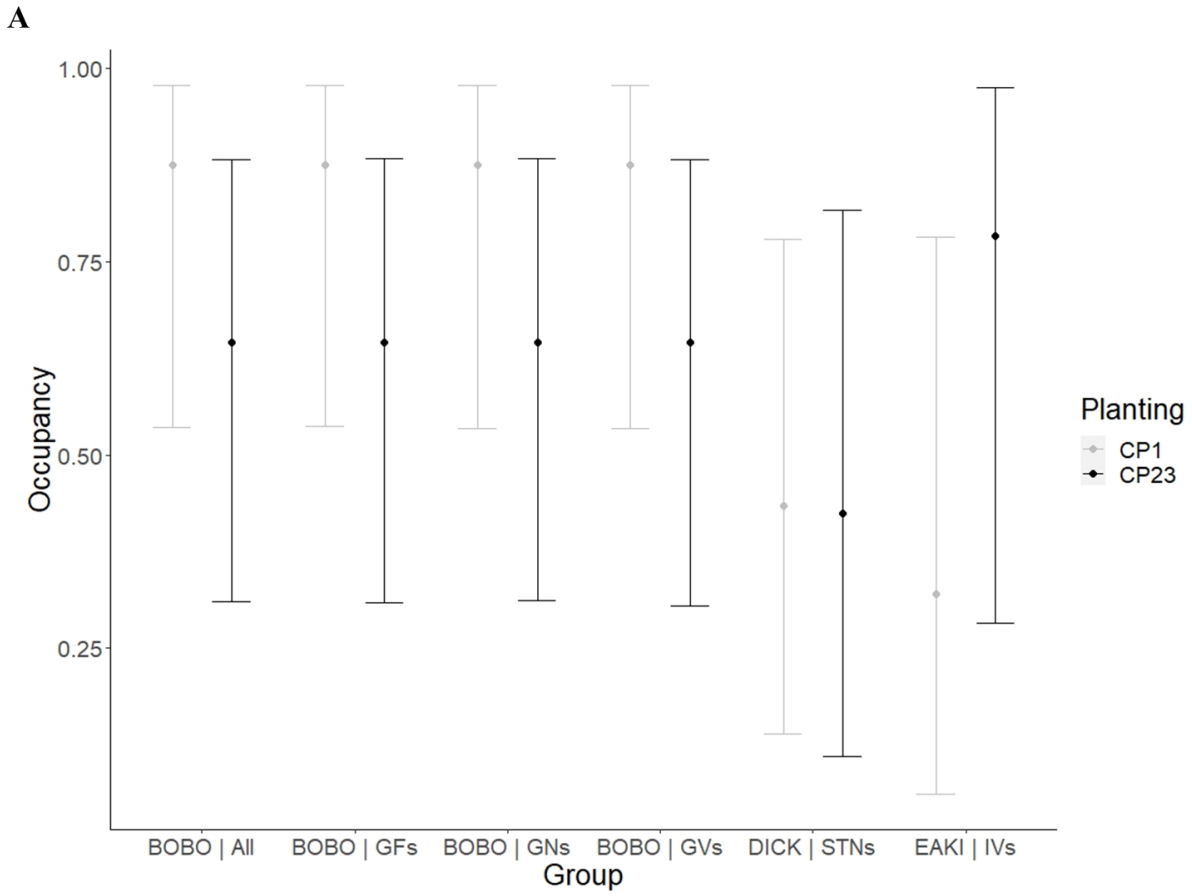
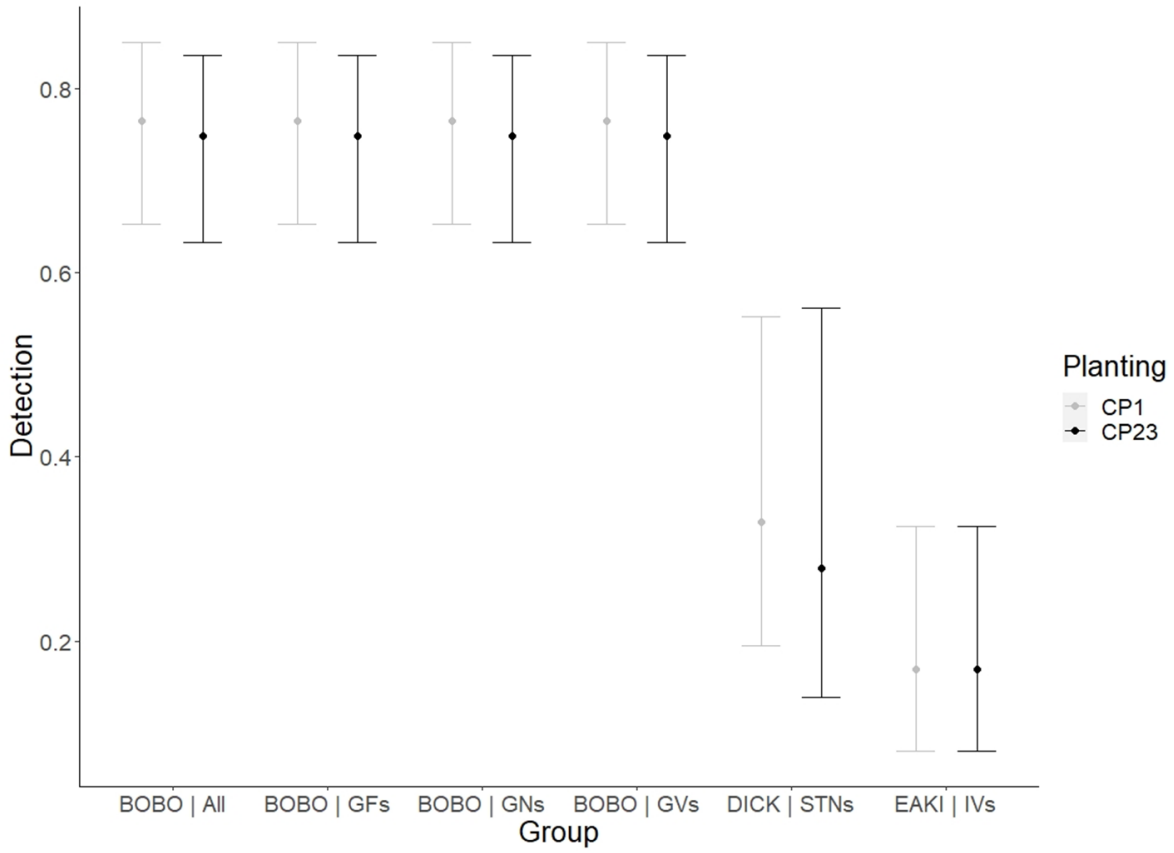


Figure 3.5 (cont'd)

B



Modeled species-accumulation curves using rarefaction to estimate species richness revealed few differences between CREP study fields and *e*Bird citizen-science records during May-August, 2005-2006. In 2005, our CREP survey sample included count data on 35 grassland (i.e., facultative and obligate) bird species recorded by two observers (i.e., sampling in teams of 1-2) across 14 fields (Figure B3.4A), and the *e*Bird sample of nearby checklist locations included count data on four grassland (i.e., facultative and obligate) bird species recorded by five observers (i.e., sampling individually) across four locations (Figure B3.4B). In 2006, our CREP survey sample included count data on 13 grassland species recorded by five observers (i.e., in teams of 1-5) across 14 fields (Figure B3.4A), and the *e*Bird sample included count data on 11 grassland species recorded by nine observers (i.e., in teams of 1-3) across 44 locations (Figure B3.4B). At half of the total number of locations surveyed between both datasets, mean (rarefied) species richness approached ten and 12 unique species at seven CREP fields in 2005 and 2006, respectively; whereas, mean (rarefied) species richness approached three and 12 unique species at two and 44 *e*Bird locations in 2005 and 2006, respectively. Mean (± SD) performance (i.e., RMSEs) of species-accumulation models equaled 0.024 (± 0.004) and 0.020 (± 0.005) across CREP and *e*Bird surveys, respectively, and most top models followed Weibull-estimated growth, except for *e*Bird samples collected during May-August 2005, multi-species count records that followed Lomolino-estimated growth; although the total number of locations sampled was small.

Discussion

Set-aside practices such as planting different CP seed mixes in CREP-restored grasslands conveys a limited number of benefits to grassland-obligate birds in southeast Michigan, including increased vegetation diversity and essential nesting and foraging habitats. While non-native CP1 and native CP23 plantings influenced vegetation composition, native CP23 plantings

did not have a consistently positive impact on species within the grassland-obligate bird community, contrary to our *a priori* expectations. After accounting for survey year, bobolink occupancy was higher on non-native CP1 fields, whereas eastern meadowlark and grasshopper sparrow occupancy was higher on CP23 plantings. Planting type was not important to dickcissel, eastern kingbird, ring-necked pheasant, and vesper sparrow occupancy probability. CREP planting types, therefore, appear to benefit a subset of grassland-obligate bird species inhabiting restored grasslands, and choice of planting type for grassland-obligate bird conservation depends on the focal species of interest.

CREP-restored grasslands enhance vegetation diversity, benefiting grassland-obligate birds

We expected that CREP (restored grassland) fields with higher forb and grass cover (e.g., captured by field-level variances in % cover types) would promote higher occupancy for grassland-obligate bird species, but top-ranked model results did not support this notion. Instead, vegetation surveys revealed that native (CP23) fields consistently contained higher (plant) species richness of both grasses and forbs than in non-native (CP1) fields, with CP23 fields containing > 1.5 times more plant species than CP1 fields. However, only (mean) cover of bare ground and dead vegetation differed between CP plantings across fields. Other vegetation variables, including % total, forb, grass, and litter cover did not differ between CP23 and CP1 fields. We explicitly tested forb and grass cover in multi-species occupancy models and these variables, relative to other cover types, were not important predictors of grassland-obligate bird occupancy.

We detected 12 (i.e., of 15 potentially occurring) grassland (i.e., facultative and obligate) bird species at CREP-restored grasslands in Michigan (Sauer et al. 1995, Sauer et al. 2008, Sauer et al. 2017). Only seven of 12 species observed were regularly detected and thus amenable to

multi-species occupancy analysis. For example, Henslow's sparrow was detected during only one visit at one field in 2005 as well as during one visit between only two fields in 2006, making this species rare in our dataset. Horned lark and northern harrier detections and non-detections followed a similar pattern to Henslow's sparrow rarity between survey years. Therefore, results from this study are limited to approximately < 50% of the grassland bird species that could occupy Michigan CREP-restored grasslands.

We predicted that CP23 fields would convey occupancy benefits to grassland-obligate bird species rather than CP1 fields, and we found this was true for eastern meadowlark and grasshopper sparrow. Bobolink occupancy was greatest in CP1 fields, likely owing to its known association with hayfields (Bollinger 1988, Bollinger and Gavin 1992, Bakker and Higgins 2009). CP1 seed mixes in our study contained > 50% white alfalfa and red clover—plant species common to hayfields in the midwestern USA (USDA 2009, USDA Farm Service Agency 2010). Eastern meadowlark occupancy was greatest at CP23 fields, across which grass and litter cover varied considerably more than (or equal to) CP1 fields—producing cover conditions that promote selection and use by eastern meadowlark (Wiens and Rotenberry 1981). Grasshopper sparrow occupancy was also greatest at CP23 fields, likely owing to significantly higher bare ground cover in such fields. While increased occurrence of drier (upland) plant species also influences occupancy of grasshopper sparrow (Wiens 1973a,b), we neither measured nor accounted for such characteristics in candidate occupancy models. While our results suggest initial occupancy benefits to grassland-obligate birds from CREP-restored grasslands, it is essential to acknowledge that other aspects of conservation success exist (e.g., enhanced nest success, increased population productivity, and stabilized or increasing abundance over time)—aspects which we did not address in the current study.

Moreover, range of CREP field sizes (e.g., CP1 = 7.3-23.9 ha, CP23 = 6.9-19.8 ha) was perhaps too small to impact grassland-obligate bird species richness. Total native (plant) area between CP1 and CP23 fields may also have been limiting to local bird diversity. For instance, CP1 native areas were generally smaller (e.g., < 34% of total field area) than in CP23 fields, and many CP1 areas may have been too small to attract numerous grassland bird species. Furthermore, estimated breeding territory size for grasshopper sparrow ranges from 0.85-1.4 ha (Vickery 1996), and the native portion of some CP1 fields was < 0.85 ha in our study. This design limitation underscores the importance of field size when considering designs of future studies evaluating grassland bird species occupancy (Ribic et al. 2009). Regardless, native portions of CP1 fields likely increased attractiveness of such plantings to some grassland bird species—notably, bobolink and to a lesser (i.e., statistically insignificant) extent ring-necked pheasant in the current study.

In addition to CREP administration (i.e., CP1 and CP23 plantings) and area-associated impacts to species occupancy probabilities, patterns in vegetation development at CP23 fields may also be an important determinant of grassland-obligate bird occupancy and abundance. Specifically, some grassland-obligate birds (e.g., bobolink and grasshopper sparrow) prefer a mosaic of bare ground and diverse vegetation structure to help facilitate ground foraging and nest access (Fisher and Davis 2010). Furthermore, native vegetation is often preferred as habitat canopy structure for many uses by grassland birds, which is likely because native vegetation tends to remain upright during winter into spring (USDA Natural Resources Conservation Service 2000a,b). Our vegetation surveys confirm that native (CP23) fields supported significantly higher amounts of standing dead vegetation cover than non-native (CP1) fields in southeast Michigan.

Observed grassland-obligate birds at CREP-restored grasslands included species known to have experienced consistent population declines across the Great Lakes region over the past decade (i.e., bobolink, dickcissel, eastern meadowlark, grasshopper sparrow, Henslow's sparrow, savannah sparrow, and vesper sparrow; Sauer et al. 2008, Sauer et al. 2017). Additionally, we documented one state endangered species (Henslow's sparrow; Norris 2014) and three other "species of greatest conservation need" (MDNR 2015). Therefore, even with relatively small fields (e.g., ranging 6.8-23.6 ha), our results showed that CREP grasslands provide essential habitat for some of the rarest grassland-obligate (bird) species in the Great Lakes region.

Comparable species diversity between concomitant CREP and eBird surveys

We expected that CREP-restored grasslands would support higher species richness of grassland-obligate birds compared to nearby locations surveyed by *e*Bird citizen scientists. We did not generate evidence to support this idea and caution that our results may be confounded with *e*Bird survey locations adjacent to other CREP-restored grasslands not part of the current study. Ignoring so few *e*Bird records on grassland-obligate birds collected during May-August 2005 (i.e., four grassland-obligate species reported across four sites), mean (rarefied) species richness estimates were largely equivalent between CREP and *e*Bird survey locations in 2006.

We used rarefaction to make CREP and *e*Bird surveys comparable, and most species accumulation curves were best explained by similar (i.e., Weibull) growth models, suggesting partial congruence in site-species accumulation patterns in southeast Michigan. However, while our 2005 and 2006 CREP surveys consistently included data collected from 14 fields, 2005 and 2006 *e*Bird surveys included data collected from four and 44 locations, respectively. In addition, total numbers of observers varied between survey years and datasets, and it is likely that associated level(s) of sampling independence and species-identification proficiency varied as

well. For example, 2005 and 2006 CREP surveys involved two and five unique observers, respectively; whereas, 2005 and 2006 *e*Bird surveys involved five and nine unique observers, respectively. CREP surveys in 2005 relied on data collection from either single (independent) or double (dependent) observers, and 2006 CREP surveys sometimes involved more than two (e.g., multiple dependent) observers collecting data in teams at individual fields over time. In contrast, *e*Bird citizen scientists consistently surveyed locations using either single (independent) or double (presumedly, dependent) observer approaches. Data collection discrepancies necessitate careful interpretation of CREP and *e*Bird species richness patterns based on rarefaction. Such discrepancies also highlight likely unaccounted for variation in observer detection in our multi-species occupancy models, but limited sample size precluded us from estimating observer-identity effects on detection between replicate visits to CREP fields.

Contextualization of results with previous research in restored-grassland systems

Other research suggests that species density may be a more reliable indicator of habitat quality for Nearctic and Palearctic birds (Bock and Jones 2004). For instance, Bock and Jones (2004) reviewed 109 peer-reviewed studies on 67 European and North American bird species and reported that habitats with higher species densities generally exhibited increased production (i.e., higher recruitment per capita per unit of land area). Occupancy estimates for grassland-obligate birds in our study thus provide a preliminary comparison of how native (CP23) and non-native (CP1) fields are functioning as grassland habitat; however, it cannot be overstated that it is important that future studies to explicitly generate and incorporate abundance indices or demographic data to evaluate habitat quality for (and distributional patterns) of focal bird species.

Moreover, previous research documented important population differences in grassland birds between native and non-native field types (Giuliano and Daves 2002); although, some CP-based evaluations reported species-specific results as variable as those of our own (Reiley and Benson 2020). Giuliano and Daves (2002) found that native warm-season grasslands, when compared to non-native cool-season grasslands, supported higher abundance and richness of bird species, including regionally declining populations of grasshopper sparrow and vesper sparrow. In contrast, other studies found few differences in species abundance between native and non-native vegetation, or studies found higher species abundance in non-native vegetation (i.e., confounded with field size; McCoy et al. 2001, Wentworth et al. 2010). In such studies, vegetation structure and composition of non-native fields differed from native (CP23) fields by being less diverse, including denser canopies, being poorly established, or becoming switchgrass (*Panicum virgatum)* dominated (i.e., dense stands of switchgrass comprise poor grassland bird habitat; Norment et al. 1999). Wentworth et al. (2010) demonstrated that at CREP fields in Pennsylvania, USA, grassland-obligate birds were rare, but found in higher abundance at fields of non-native, cool-season grasses than at fields of native, warm-season grasses. However, it is important to note that native grasslands in the Wentworth et al. (2010) study did not fully establish, and some fields were dominated by non-native grasses or other suboptimal vegetation (e.g., switchgrass), characteristics absent from our study of CREP fields.

In a study of Conservation Reserve Program (CRP) grasslands in Missouri, USA, McCoy et al. (2001) found that more grassland bird species occurred at higher abundances in non-native (CP1) fields than in native (CP2, permanent native grass) fields, which consisted of switchgrass monoculture, lower plant diversity, and higher canopy density. The opposite was true of CREP native (CP23) fields in our study, which were more diverse and less dense (i.e., including sparser

canopy cover and more visible bare ground) than non-native (CP1) fields. Cumulatively, these findings highlight the importance of planting mixed and fully established native fields toward enhancing grassland bird conservation. Furthermore, differences among CRP and CREP studies underscore shortcomings of reporting wildlife responses in the absence of vegetation data. When reporting grassland-obligate bird responses to a management prescription, like CP plantings administered via CREP, vegetation information is critical to ensure that plant-bird management goals are achieved.

Analysis limitations and research-management implications

Of 468 total candidate models, only 106 models produced fully identifiable parameters and standard errors. We suspect that parameter non-identifiability issues are explained by multiple possibilities. First, our sample size was small, involving evaluation of only seven (i.e., regularly detected) grassland-obligate bird species recorded during replicate survey visits to 14 study fields (i.e., equally split between two planting types) surveyed for two years. Such sample size limitations likely precluded most candidate models from estimating occupancy effects of interest with enough certainty, particularly contextual landscape variables determined informative in other studies (Bakker et al. 2002, Cunningham and Johnson 2006, Scholtz et al. 2017 Shahan et al. 2017).

Second, and also because of limited sample size, candidate models were unable to identify factor-covariate interaction effects or species-to-species interaction (e.g., competitive-exclusionary or co-occupancy) effects on multi-species occupancy, limitations that likely increased uncertainty around occupancy-level effects and derived estimates of species occupancy probabilities. We were also unable to directly estimate additional error variation in occupancy related to species-field colonization and extinction between survey years, which was due to

collecting only two years of survey data—a fundamental limitation prohibiting estimation of (as well as impacts to) colonization and extinction rates with any certainty. In addition to accounting for observation-process error due to imperfect species detection, incorporating ecological-process error due to species-field colonization dynamics helps reduce uncertainty around estimated effects and derived quantities, particularly in multi-species (hierarchical) models of occupancy or abundance (Kéry and Royle 2016, 2021).

It is also noteworthy that, while implicated in previous studies (Cunningham and Johnson 2006, Shahan et al. 2017), multi-extent landscape metrics (i.e., describing landscape context surrounding fields) did not significantly explain multi-species occupancy probabilities. In part, however, our work corroborates findings in Cunningham and Johnson (2006), who found that models of grassland (i.e., facultative [e.g., mainly wetland- or shrubland-associated] and obligate) bird occupancy involving only landscape-contextual factors rarely competed with models containing effects of proximate grassland factors in North Dakota, USA. Specifically, proximate-only models competed with landscape-only models for ~50% of total species studied (Cunningham and Johnson 2006). Such findings emphasized relevance of local habitat conditions, but surrounding landscape at broader extents also influenced occupancy for a subset of bird species studied (Cunningham and Johnson 2006). Moreover, best-explaining occupancy models for seven of 19 species (i.e., including bobolink and grasshopper sparrow) involved proximate factors (e.g., tree cover at 50 and 100 m from sample transects) and landscape-contextual factors (e.g., land cover composition and configuration metrics) summarized at a 1600-m extent (Cunningham and Johnson 2006). In the current study, landscape factors either competed with the top-ranked model (i.e., number of patches) or received partial data support (e.g., models with $2.0 \leq \Delta AICc \leq 10.0$ of the top-ranked model; Burnham and Anderson 2002),

particularly when considering land cover composition and configuration patterns at 400-, 800-, or 1600-m extents. This result partly supports our expectation that landscape complexity at intermediate spatial extents would associate with grassland-obligate bird occupancy.

In contrast, in grasslands of Minnesota and North and South Dakota, USA, Shahan et al. (2017) found that occupancy probabilities for eight of nine species (i.e., also including grassland-facultative and -obligate birds) were best explained by landscape-contextual factors (i.e., mostly land cover configuration variables), particularly at 3-4 km beyond grassland edges. Unlike the aforementioned studies, we only focused occupancy analysis on grassland-obligate bird species; therefore, underscoring an essential difference with previous studies. Additionally, we evaluated multi-species occupancy responses to changing field- and landscape-level variables over a short time (i.e., two years), limiting inference about species- and guild-level occupancy probabilities (Scholtz et al. 2017). With respect to our study of CREP-managed fields, increased total sample size (e.g., more fields surveyed and planted with CP1 or CP23 seed mixes), evaluated over longer time periods, landscape-contextual effects would likely be informative to multi-species occupancy evaluations of grassland-obligate birds in southeast Michigan and likely elsewhere.

Based on our results, we recommend that CP23 whole-field native plantings be used in favor of CP1 plantings despite higher costs associated with native seed mixes and specialized planting techniques necessary for successful native vegetation establishment. Although native (CP23) fields were often dominated by volunteer forb species in this study, special attention paid to planting techniques may improve establishment of native forbs and grasses (M. Sargent *personal communication*). Our results suggest that higher-quality native grasslands likely support more grassland-obligate birds than comparably sized areas of lower habitat quality (i.e., non-native grasslands). Furthermore, because grassland-obligate species exhibited varied responses to

CP plantings in our study, we suggest identifying species-specific objectives for future grassland-bird conservation strategies (Murray et al. 2008, Reiley and Benson 2020). In addition, increased number of set-aside fields and plantings, observational surveys prior to set-aside initiation, and long-term monitoring of bird occupancy post-set-aside are also necessary to fully evaluate impacts of set-aside lands on grassland-obligate bird occupancy and diversity.

In jurisdictions dominated by private lands, set-aside programs like CREP comprise important tools for ecological restoration in terms of conservation of grassland-obligate birds and other wildlife, providing new opportunities for establishing grassland-climate strongholds toward full-annual-cycle conservation of rare or imperiled species (Grand et al. 2019). Set-aside programs not only increase grassland connectivity (e.g., providing new movement corridors) and improve inhospitable-matrix permeability (e.g., decreasing patch isolation), contributing to broader restoration of degraded grassland landscapes and enabling system resilience in the face of global change. Specifically, non-native (restored) grasslands tend to (a) be less diverse and (b) poorly establish, (c) have denser canopies, or (d) become monocultures of suboptimal plant species (e.g., switchgrass; Norment et al. 1999, McCoy et al. 2001, Wentworth et al. 2010). In contrast, native (restored) grasslands tend to (a) be more diverse and (b) establish well in locations in which they evolved, (c) have less dense and more structurally diverse canopies, or (d) become polycultures of varied (cover) optimality (e.g., exhibiting differences in vegetated and non-vegetated cover, allowing birds to feed and nest at nearby locations; Fritcher et al. 2004). Such diverse characteristics of restored grasslands provide essential resources (e.g., nesting and foraging habitats) and conditions (e.g., varied vegetation structure) to specialized species including grassland-obligate birds, gradually benefiting their populations and leading to

heightened conservation success over time (McCoy et al. 2001, Wentworth et al. 2010, Pabian et al. 2013, Reiley and Benson 2020).

Furthermore, more targeted enrollment in CREP and CRP may also provide increased benefits to grassland-dependent wildlife (Pabian et al. 2013, Tanner and Fuhlendorf 2018). Attracting diverse ownership of set-aside lands likely conveys multi-species benefits as well, particularly beyond field- and landscape-level conditions (Ahlering et al. 2019). In addition, landowner responses to farmland set-aside incentives indicate that higher payments at the time of CREP enrollment increases program participation and retention rather than do small increases in annual payments over the term of the set-aside contract (Suter et al. 2008). Facing increased pressure from global food and biofuels markets (Secchi and Babcock 2007, Searchinger et al. 2008, Fargione et al. 2009), incentives for private landowner involvement in set-aside programs must be competitive and compelling. Numerous sources demonstrate the value and importance of CREP, CRP, and similar programs to humans and wildlife, management activities on private land that provide socioecological incentives for participants as well as long-term research studies. Notably, dedicated program administrators and participants ensure continuation and conservation successes of such programs for rare wildlife facing increased extralimital threats of climate change and continued land conversion to agriculture in the Anthropocene. In turn, conservation biologists and land managers must continue working to restore grassland ecosystems with the help of deliberate, extensive, and long-term farmland set-aside programs.

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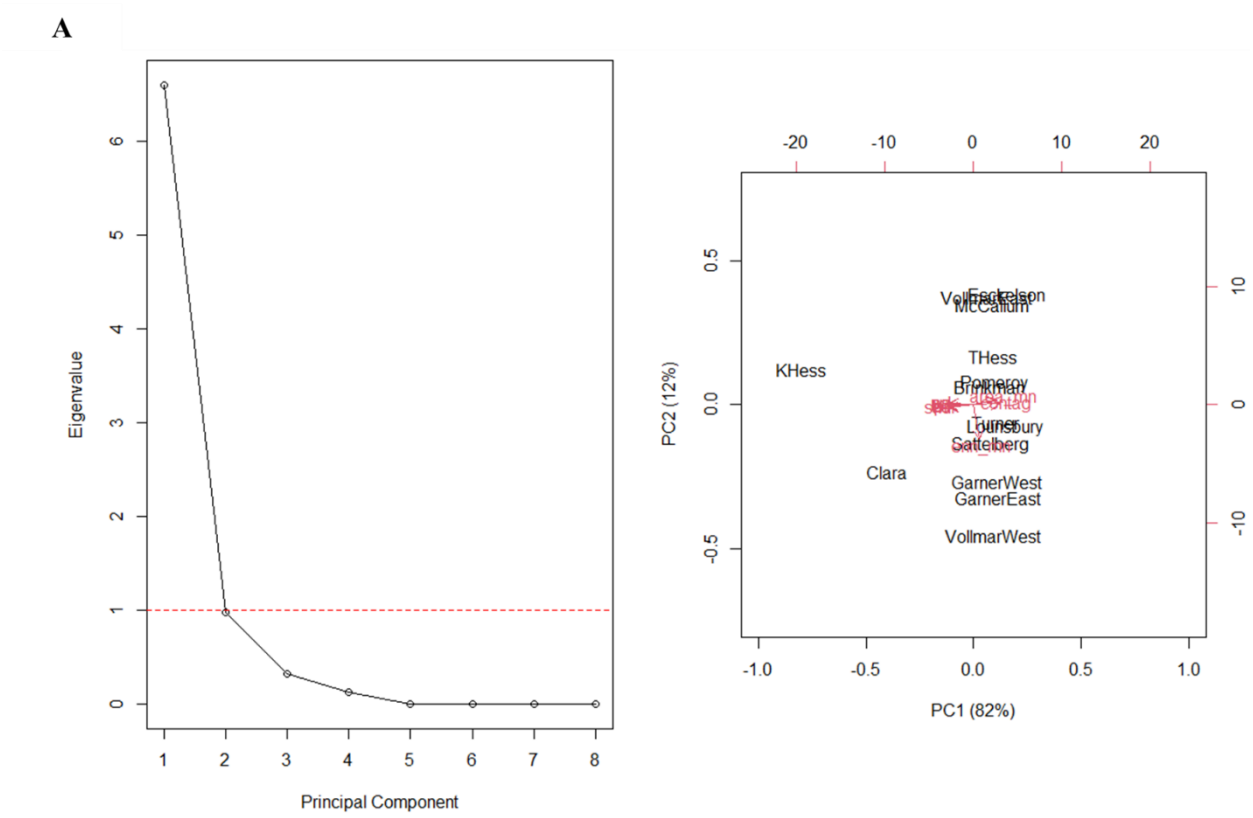
APPENDIX

Figure B3.1. Pairs of scree and bivariate (axis) plots derived from Principal Component Analyses, which we used to determine the number of principal component (PC) axes describing the most variation in multivariate gradients of eight (aggregate) landscape metrics summarized at multiple spatial extents surrounding study fields. We report the PCA results for multivariate metrics summarized at the following spatial extents: (A) 50-, (B) 100-, (C) 200-, (D) 400-, (E) 800-, (F) 1600-, and (G) 3200-m. We estimated metrics using the "landscapemetrics" package version 1.5.0 (Hesselbarth et al. 2019) and FRAGSTATS version 4.2.1 in R version 4.0.2 (McGarigal et al. 2014, R Core Development Team 2020). Mean eigenvalues (red dotted lines) are noted in scree plots, and factor loadings' vectors (red arrows) are noted in bivariate plots, one vector per landscape metric and displayed alongside study field-landowner surnames. Landscape metrics, including their names and identifying codes, are described in Tables 3.1 and 3.2.



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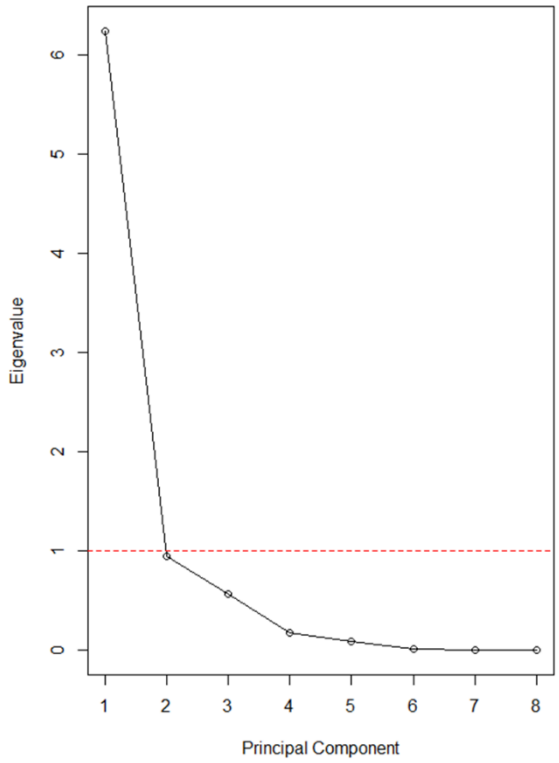

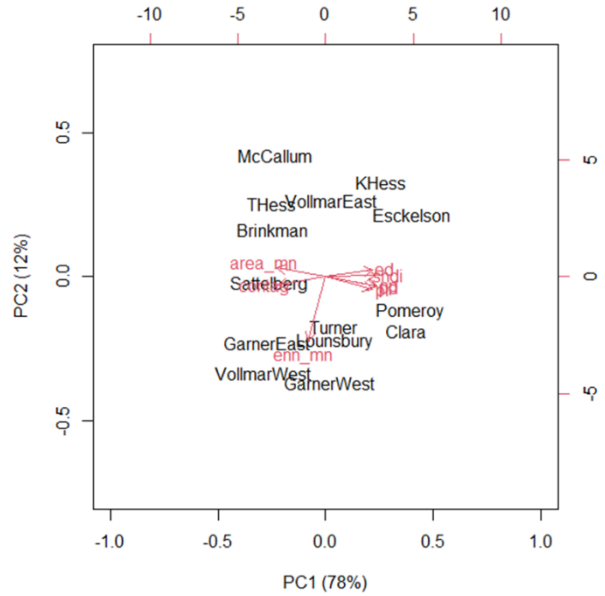

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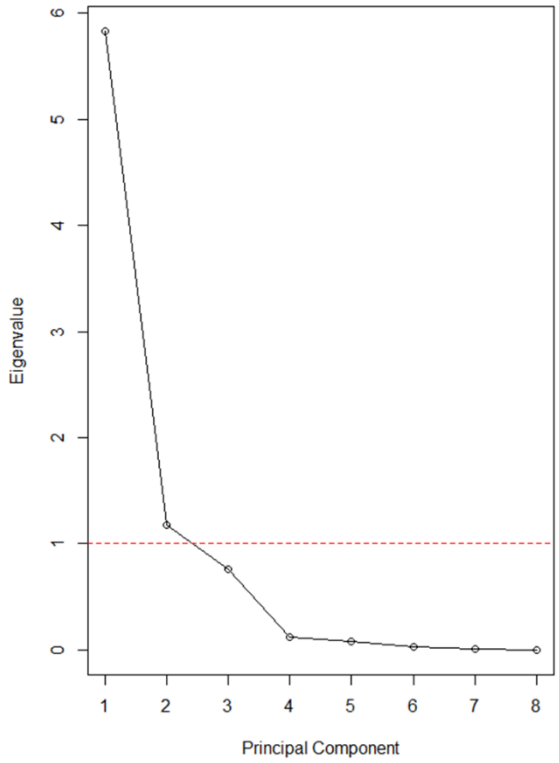

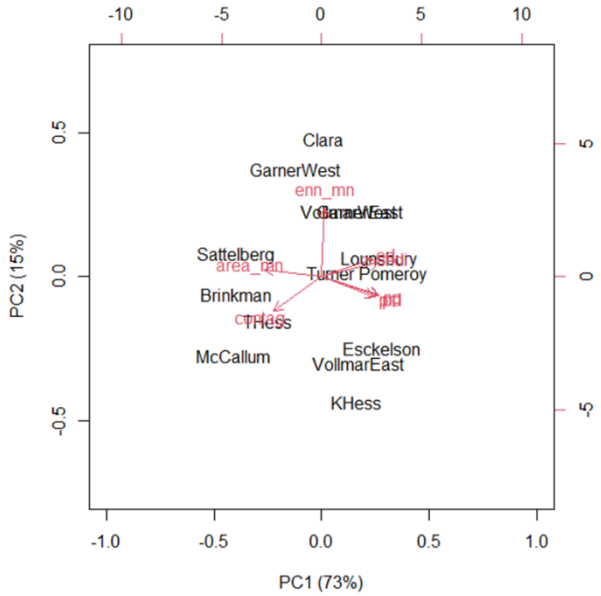

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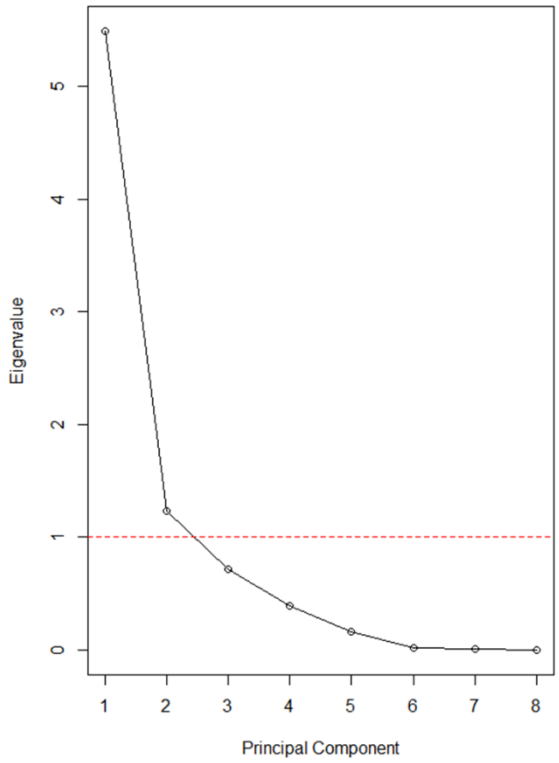

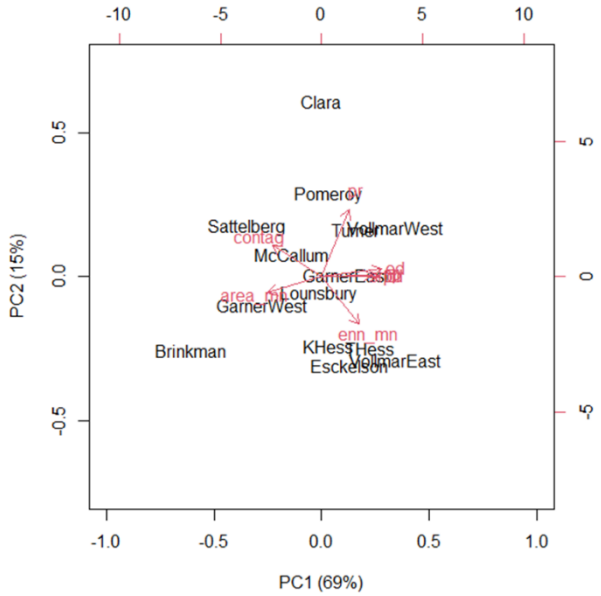

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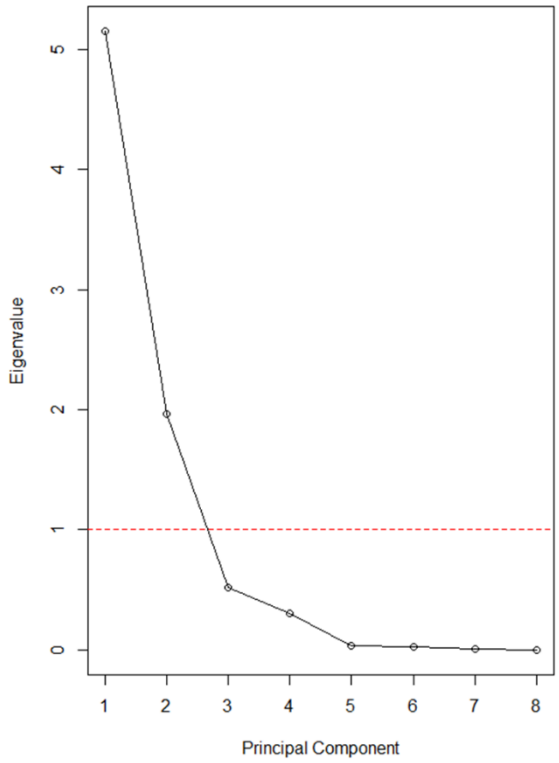

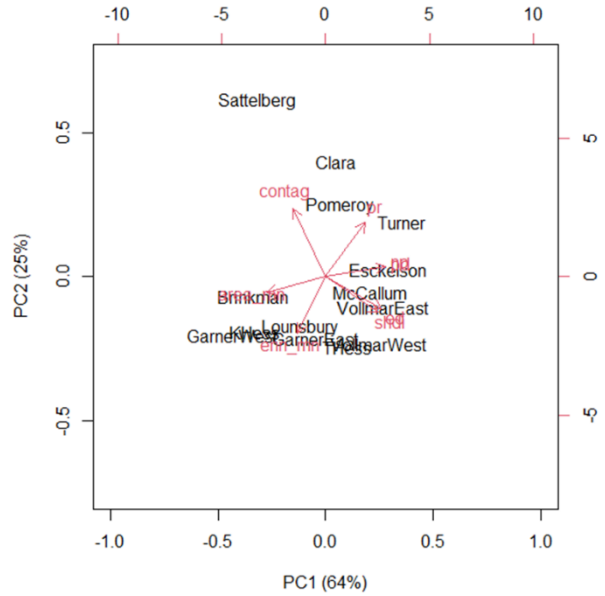

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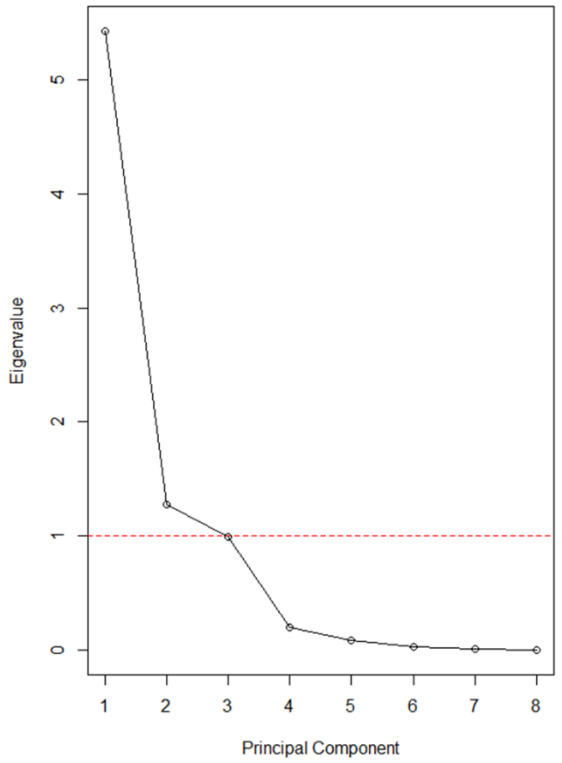

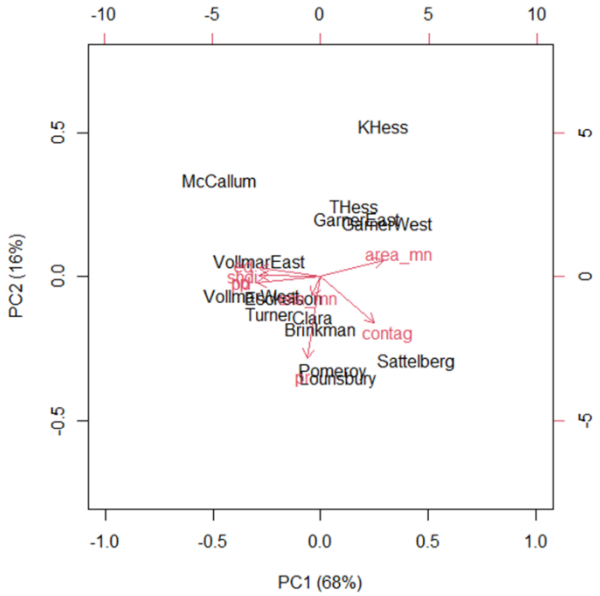

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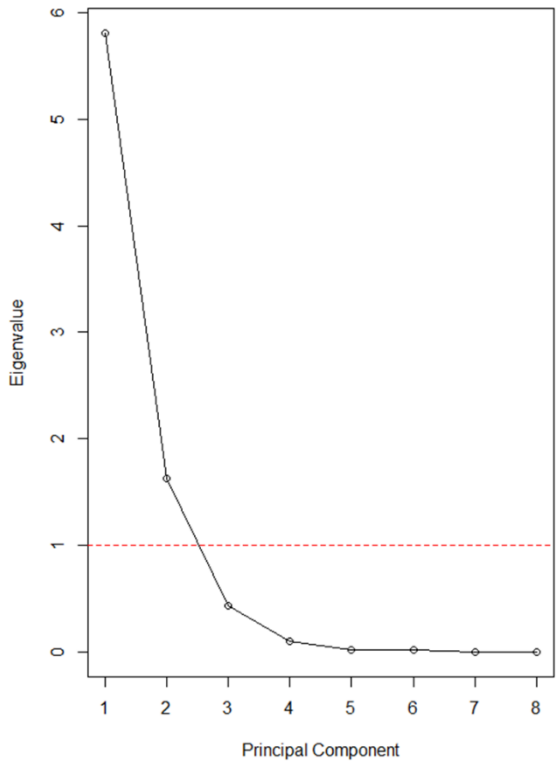


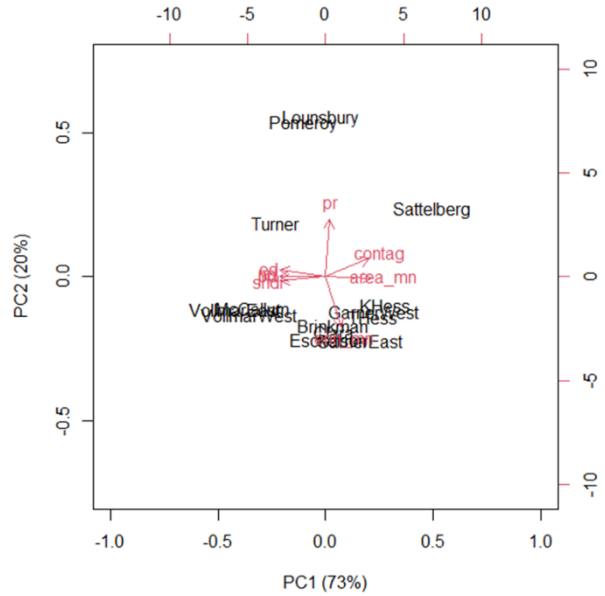


Figure B3.2. Grand mean (monthly total) precipitation and (monthly mean) temperature for southeast Michigan, summarized at study fields, during May-August 2005 and 2006, coinciding with grassland bird surveys. Error bars are defined by the 1.5 interquartile range of the data.

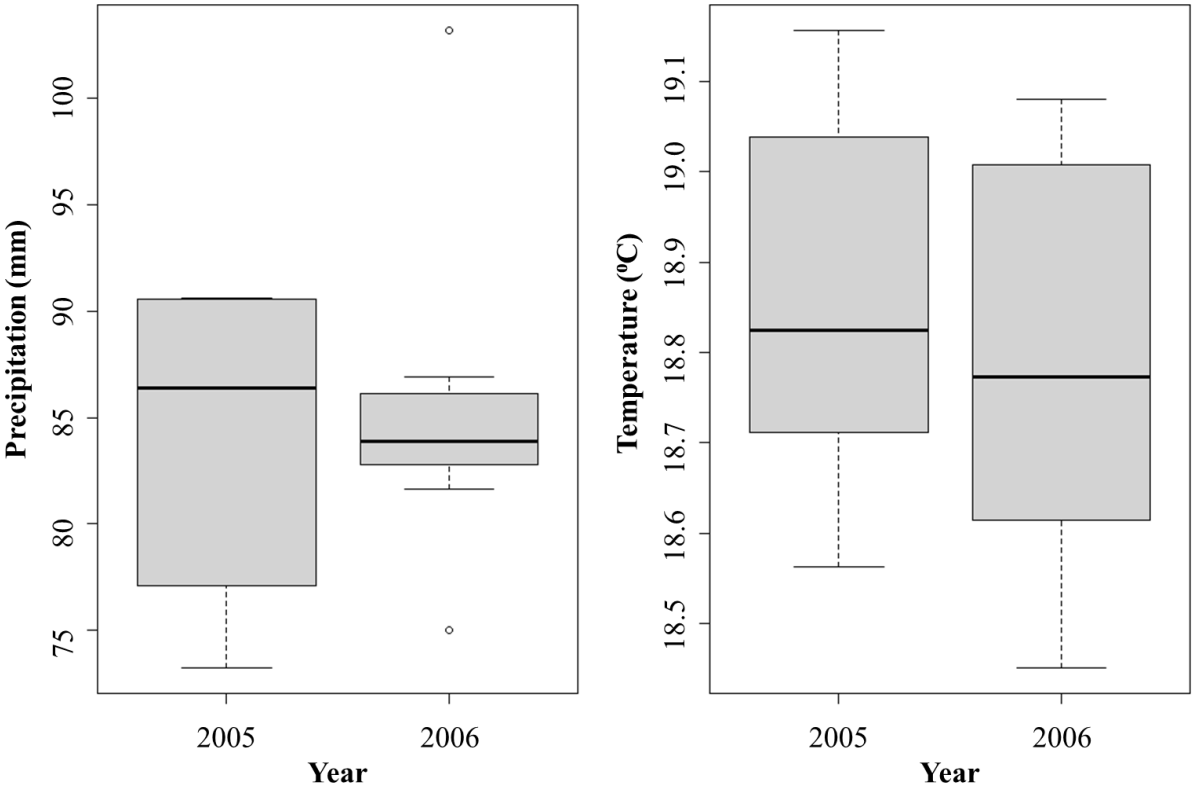


Figure B3.3. Spline correlations of multivariate Pearson residuals summarized across species and derived from the top-ranked model of multi-species grassland bird occupancy in southeast Michigan 2005-2006. Moran's *I* indicates the pairwise-location correlation coefficient as it changes with increasing distance of separation between CREP study fields, and the mean (solid line) and 95% confidence bands (gray) are displayed. Confidence bands consistently overlapping with Moran's *I* = 0 indicates that spatial autocorrelation in occupancy (i.e., across species and among study fields) is sufficiently accounted for by the top-ranked model.

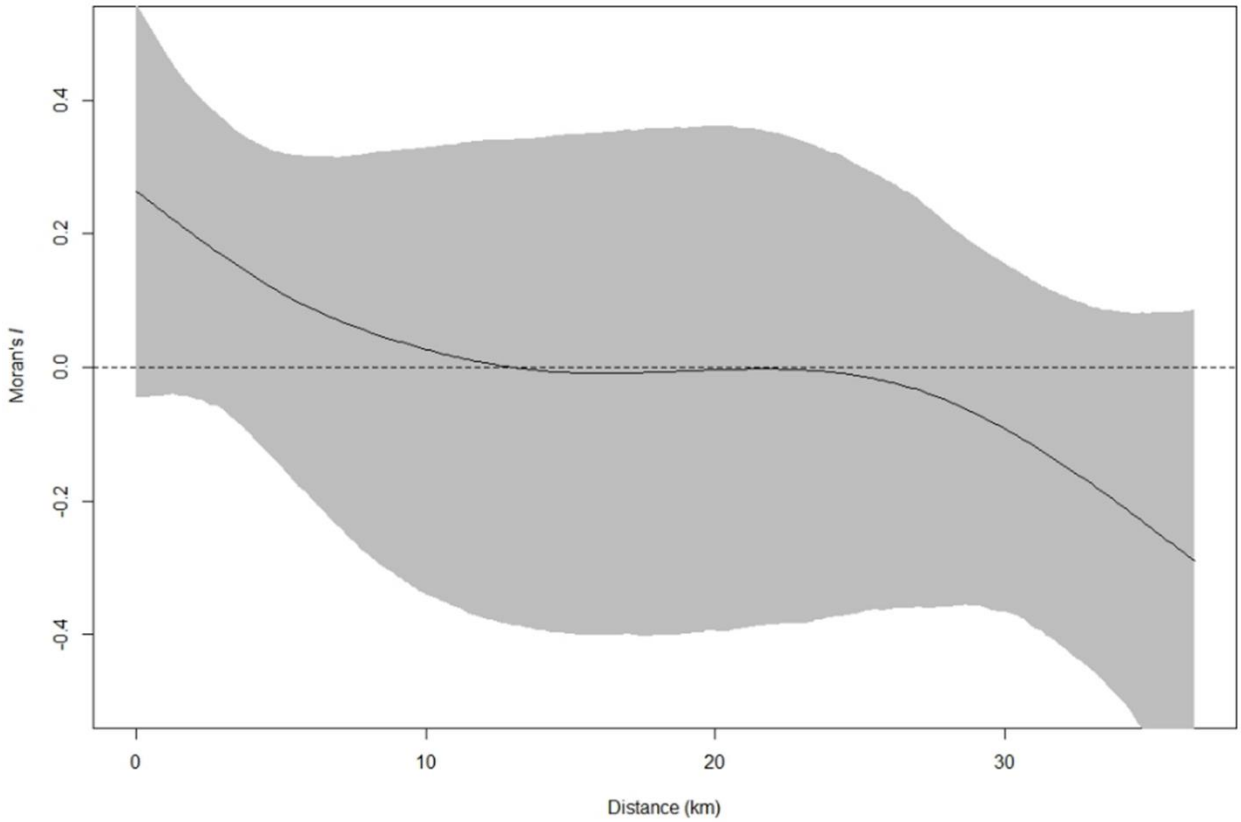


Figure B3.4. Accumulating (rarefied) richness of grassland-obligate bird species as a function of increasing numbers of sampling locations in southeast Michigan, 2005-2006. Richness scores (solid lines) are based on 10,000 permutations of input multi-species count datasets and estimated via nonlinear least squares regression. Best-fitting accumulation models (dotted lines) were determined based on each model's root-mean-squared error (RMSE), where lower scores indicate better fit. Species accumulation curves are displayed for May-August surveys at (A) CREP study fields and (B) *e*Bird citizen-science locations conducted in 2005 (blue) and 2006 (red).

A

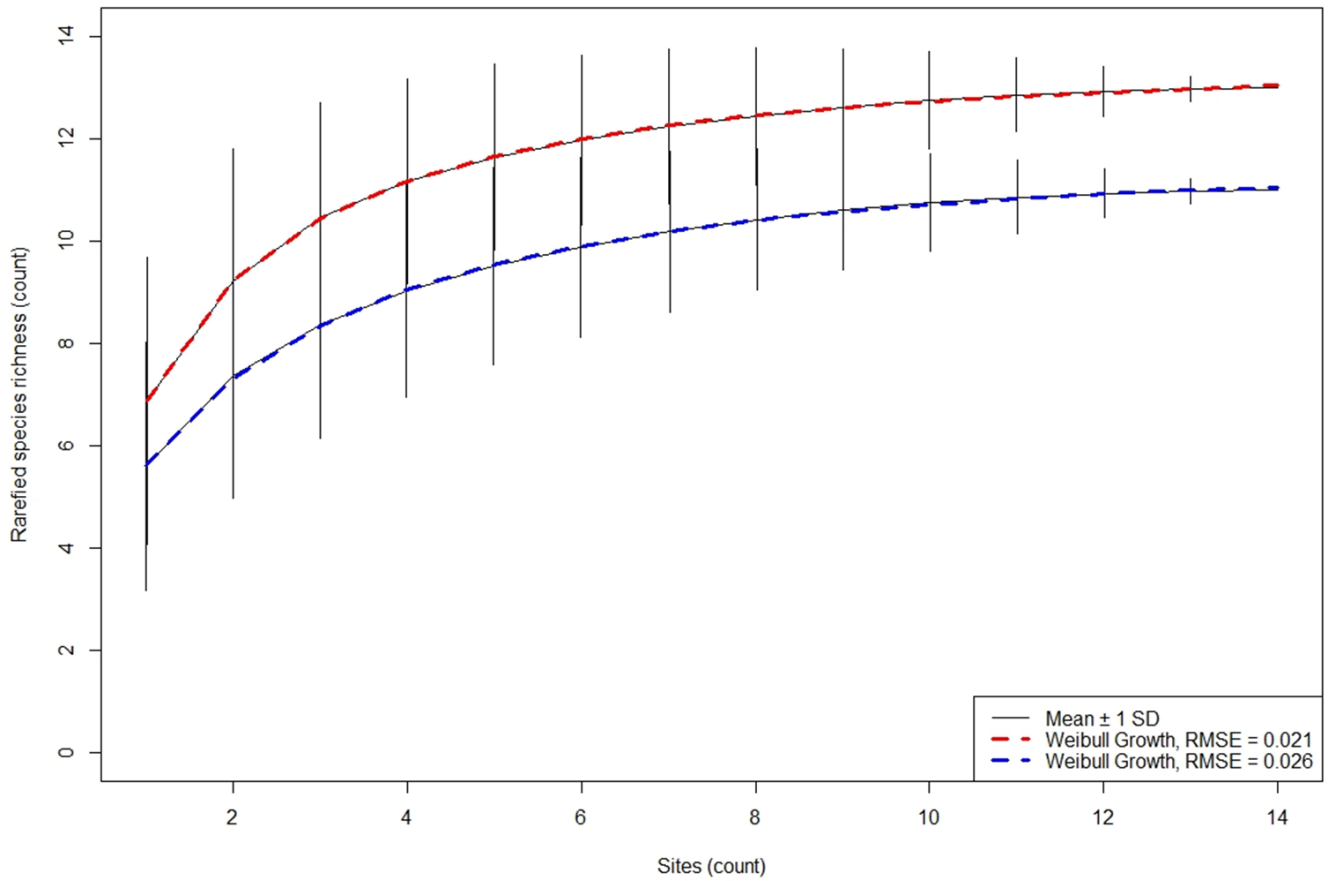
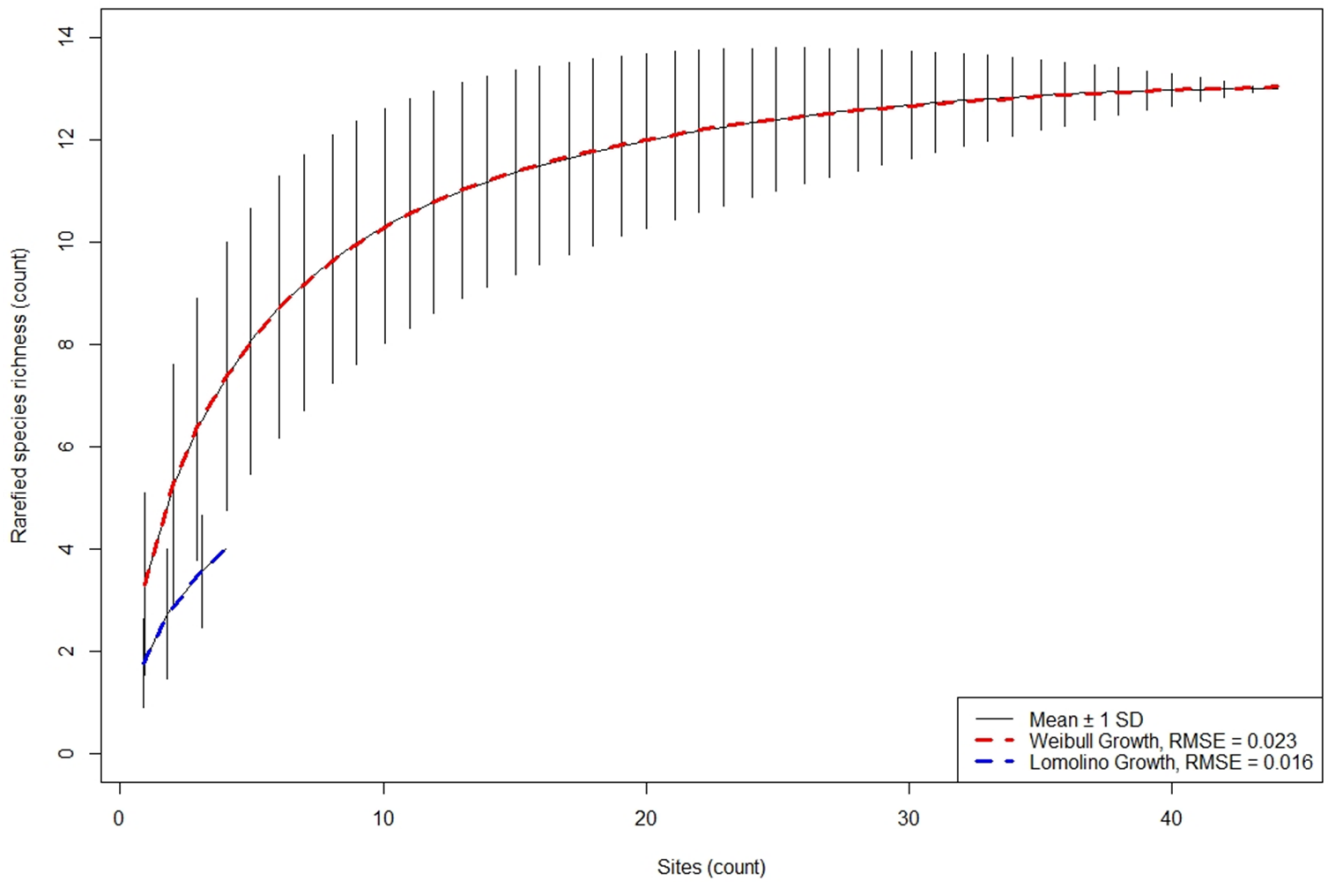


Figure B3.4 (cont'd)

B



REFERENCES

REFERENCES

Ahlering, M. A., D. H. Johnson, and L. H. Elliott. 2019. Land ownership and use influence grassland bird abundance. *Journal of Wildlife Management* 83:343-355.

Albert, D. A. 1995. Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working map and classification. U.S. Forest Service General Technical Report NC-178, North Central Forest Experiment Station, St. Paul, MN, USA.

Allen, A. W. 2005. The Conservation Reserve Enhancement Program. Pages 115-134 *in* Fish and Wildlife Benefits of Farm Bill Conservation Programs: 2000–2005 Update, J. B. Haufler (Ed.). The Wildlife Society Technical Review 05-2, Bethesda, MD, USA.

Arenz, C. L. and A. Joern. 1996. Prairie legacies: invertebrates. Pages 91-109 *in* Prairie Conservation: Preserving North America's Most Endangered Ecosystem, F. B. Samson and F. L. Knopf (Eds.). Island Press, Washington, DC, USA.

Bakker, K. K. and K. F. Higgins. 2009. Planted grasslands and native sod prairie: equivalent habitat for grassland birds? *Western North American Naturalist* 69:35-242.

Bakker, K. K., D. E. Naugle, and K. F. Higgins. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. *Conservation Biology* 16:1638-1646.

Banner, K. M. and M. D. Higgs. 2017. Considerations for assessing model averaging of regression coefficients. *Ecological Applications* 28:78-93.

Benedict, R. A., P. W. Freeman, and H. H. Genoways. 1996. Prairie legacies: mammals. Pages 149-166 *in* Prairie Conservation: Preserving North America's Most Endangered Ecosystem, F. B. Samson and F. L. Knopf (Eds.). Island Press, Washington, DC, USA.

Billerman, S. M., B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg (Eds.). 2020. Birds of the World (online). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://birdsoftheworld.org/bow/home>. Accessed Aug 2020.

Bjornstad, O. N. 2020. ncf: Spatial Covariance Functions. R package version 1.2-9. <https://CRAN.R-project.org/package=ncf>. Accessed Aug 2020.

Bock, C. E. and Z. F. Jones. 2004. Avian habitat evaluation: should counting birds count? *Frontiers in Ecology and the Environment* 2:403-410.

Bollinger, E. K. 1988. Breeding dispersion and reproductive success of bobolinks in an agricultural landscape. Dissertation, Cornell University, Ithaca, NY, USA.

Bollinger, E. K. and T. A. Gavin. 1992. Eastern bobolink populations: ecology and conservation in an agricultural landscape. Pages 497-506 *in* Ecology and Conservation of Neotropical Migrant Landbirds, J. M. Hagan III and D. W. Johnston (Eds.). Smithsonian Institution Press, Washington, DC, USA.

Briggs, J. M., A. K. Knapp, J. M. Blair, J. L Heisler, G. A. Hoch, M. S. Lett, and J. K. McCarron. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* 55:243-254.

Burnham, K. P. and D. R. Anderson. 2002. Model Selection and Multi-Model Inference, Second Edition. Springer-Verlag, New York, NY, USA.

Cava, J. A., N. G. Perlut, and S. E. Travis. 2016. Why come back home? Investigating the proximate factors that influence natal philopatry in migratory passerines. *Animal Behaviour* 118:39-46.

Chambers, J. M., W. S. Cleveland, B. Kleiner, and P. A. Tukey. 1983. Graphical Methods for Data Analysis. Duxbury Press, Boston, MA, USA.

Chesser, R. T., S. M. Billerman, K. J. Burns, C. Cicero, J. L. Dunn, A. W. Kratter, I. J. Lovette, et al. 2020. Sixty-first supplement to the American Ornithological Society's check-list of North American birds. *The Auk: Ornithological Advances* 137:ukaa030.

Chiarucci, A., G. Bacaro, D. Rocchini, and L. Fattorini. 2008. Discovering and rediscovering the sample-based rarefaction formula in the ecological literature. *Community Ecology* 9:121-123.

Claeskens, G., J. R. Magnus, A. L. Vasnev, and W. Wang. 2016. The forecast combination puzzle: a simple theoretical explanation. *International Journal of Forecasting* 32:754-762.

Colwell, R. K., A. Chao, N. J. Gotelli, S.-Y. Lin, C. X. Mao, R. L. Chazdon, and J. T. Longino. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology* 5:3-21.

Corn, P. S. and C. R. Peterson. 1996. Prairie legacies: amphibians and reptiles. Pages 125-134 *in* Prairie Conservation: Preserving North America's Most Endangered Ecosystem, F. B. Samson and F. L. Knopf (Eds.). Island Press, Washington, DC, USA.

Cornell Lab of Ornithology. 2019. All About Birds (online). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://www.allaboutbirds.org>. Accessed Aug 2019.

Cunningham, M. A. and D. H. Johnson. 2006. Proximate and landscape factors influence grassland bird distributions. *Ecological Applications* 16:1062-1075.

Daubenmire, R. F. 1959. A canopy cover method of vegetational analysis. *Northwest Science* 33:43-64.

Dengler, J. 2009. Which function describes the species-area relationship best? A review and empirical evaluation. *Journal of Biogeography* 36:728-744.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. García Marquéz, et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27-46.

Dormann, C. F., J. M. Calabrese, G. Guillera-Arroita, E. Matechou, V. Bahn, K. Bartoń, C. M. Beale, et al. 2018. Model averaging in ecology: a review of Bayesian, information-theoretic, and tactical approaches for predictive inference. *Ecological Monographs* 88:485-504.

Edwards, D. K., G. L. Dorsey, and J. A. Crawford. 1981. A comparison of three avian census methods. *Studies in Avian Biology* 6:170-176.

Fargione, J. E., T. R. Cooper, D. J. Flaspohler, J. Hill, C. Lehman, T. McCoy, S. McLeod, et al. 2009. Bioenergy and wildlife: threats and opportunities for grassland conservation. *BioScience* 59:767-777.

Fisher, R. J. and S. K. Davis. 2010. From Wiens to Robel: A review of grassland-bird habitat selection. *Journal of Wildlife Management* 74:265-273.

Fiske, I. J. and R. B. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43:1-23.

Fritcher, S. C., M. A. Rumble, and L. D. Flake. 2004. Grassland bird densities in seral stages of mixed-grass prairie. *Journal of Range Management* 57:351–357.

Fry, J. A., G. Xian, S. Jin, J. A. Dewitz, C. G. Homer, L. Yang, C. A. Barnes, et al. 2012. Completion of the 2006 National Land Cover Database update for the conterminous United States. *Photogrammetric Engineering and Remote Sensing* 77:858-864.

Giudice, J. H. and J. T. Ratti. 2001. Ring-necked pheasant (*Phasianus colchicus*) *in* The Birds of North America (online). A. Poole (Ed.). Cornell Lab of Ornithology, Ithaca, NY, USA. <http://bna.birds.cornell.edu/bna/species/176>. Accessed Sep 2010.

Giuliano, W. M. and S. E. Daves. 2002. Avian response to warm-season grass use in pasture and hayfield management. *Biological Conservation* 106:1-9.

Gotelli, N. J. and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in measurement and comparison of species richness. *Ecology Letters* 4:379-391.

Grand, J., C. Wilsey, J. X. Wu, and N. L. Michel. The future of North American grassland birds: incorporating persistent and emergent threats into full annual cycle conservation priorities. *Conservation Science and Practice* 1:e20.

Hart, E. M. and K. Bell. 2015. prism: Download data from the Oregon PRISM project. R package version 0.0.6. <https://CRAN.R-project.org/package=prism>.

Heard, L. P., A. W. Allen, L. B. Best, S. J. Brady, W. Burger, A. J. Esser, E. Hackett, et al. 2000. A comprehensive review of Farm Bill contributions to wildlife conservation, 1985-2000. W. L. Hohman, and D. J. Halloum (Eds.). U.S. Department of Agriculture Natural Resources Conservation Service, Wildlife Habitat Management Institute, Technical Report USDA/NRCS/WHMI-2000, Washington, DC, USA.

Herbert, J. R., D. E. Kroodsma, and J. P. Gibbs. 2001. Sedge wren (*Cistothorus platensis*) *in* The Birds of North America (online). A. Poole (Ed.). Cornell Lab of Ornithology, Ithaca, NY, USA. <http://bna.birds.cornell.edu/bna/species/176>. Accessed Sep 2010.

Herkert, J. R. 1995. An analysis of Midwestern breeding bird population trends: 1966-1993. *American Midland Naturalist* 134:41-50.

Herkert, J. R. 2009. Response of bird populations to farmland set-aside programs. *Conservation Biology* 23:1036-1040.

Hesselbarth, M. H. K., M. Sciaini,, K. A. With, K. Wiegand, and J. Nowosad. 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. R package version 1.5.0. *Ecography* 42:1648-1657.

Hijmans, R. J. 2020. raster: Geographic data analysis and modeling. R package version 3.3-7. <https://CRAN.R-project.org/package=raster>.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* 50:346-363.

Hui, F. K. C., S. Taskinen, S. Pledger, S. D. Foster, and D. I. Warton. 2015. Model-based approaches to unconstrained ordination. *Methods in Ecology and Evolution* 6:399-411.

Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52:577-586.

Jones, S. L. and J. E. Cornely. 2002. Vesper sparrow (*Pooecetes gramineus*) *in* The Birds of North America (online). A. Poole (Ed.). Cornell Lab of Ornithology, Ithaca, NY, USA. <http://bna.birds.cornell.edu/bna/species/176>. Accessed Sep 2010.

Kaiser, H. F. 1960. The application of electronic computers to factor analysis. *Educational and Psychological Measurement* 20:141-151.

Kéry, M. and J. A. Royle. 2016. Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance, and Species Richness in R and BUGS, Volume 1: Prelude and Static Models. Academic Press, Cambridge, MA, USA.

Kéry, M. and J. A. Royle. 2021. Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance, and Species Richness in R and BUGS, Volume 2: Dynamic and Advanced Models. Academic Press, Cambridge, MA, USA.

Knapp, A. K. and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291:481-484.

Knopf, F. L. 1994. Avian assemblages on altered grasslands. *Studies in Avian Biology* 15:247-257.

Knopf, F. L. 1996. Prairie legacies: birds. Pages 115-141 *in* Prairie Conservation: Preserving North America's Most Endangered Ecosystem, F. B. Samson and F. L. Knopf (Eds.). Island Press, Washington, DC, USA.

Knutson, M. G., G. Butcher, J. Fitzgerald, and J. Shieldcastle. 2001. Partners in Flight bird conservation plan for the upper Great Lakes Plain (physiographic area 16). U.S. Geological Survey, Upper Midwest Environmental Sciences Center in cooperation with Partners in Flight, La Crosse, WI, USA.

Lanyon, W. E. 1995. Eastern meadowlark (Sturnella magna) *in* The Birds of North America (online). A. Poole (Ed.). Cornell Lab of Ornithology, Ithaca, NY, USA. <http://bna.birds.cornell.edu/bna/species/176>. Accessed Sep 2010.

Leach, M. K. and T. J. Givnish. 1996. Ecological determinants of species loss in remnant prairies. *Science* 273:1555-1558.

MacKenzie, D. I. and L. L. Bailey. 2004. Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics* 9:300-318.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Academic Press, Burlington, MA, USA.

MacKenzie, D. I., J. D. Nichols, M. E. Seamans, and R. J. Gutiérrez. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology* 90:823-835.

Martin, S. G. and T. A. Gavin. 1995. Bobolink (*Dolichonyx oryzivorus*) *in* The Birds of North America (online). A. Poole (Ed.). Cornell Lab of Ornithology, Ithaca, NY, USA. <http://bna.birds.cornell.edu/bna/species/176>. Accessed Sep 2010.

Matteson, S., K. Kreitinger, G. Bartelt, G. Butcher, D. Sample, and T. Will. 2009. Partners in Flight bird conservation plan for the boreal hardwood transition (bird conservation region 12 - U.S. portion), version 1.0. <http://www.partnersinflight.org>. Accessed Nov 2010.

McCoy, T. D., M. R. Ryan, and L. W. Burger. 2001. Grassland bird conservation: CP1 vs. CP2 plantings in Conservation Reserve Program fields in Missouri. *American Midland Naturalist* 145:1-17.

McGarigal, K., S.A. Cushman, and E. Ene. 2014. FRAGSTATS: Spatial pattern analysis program for categorical and continuous maps, version 4.2.1. <http://www.umass.edu/landeco/research/fragstats/fragstats.html/>. Accessed Oct 2016.

Michigan Department of Natural Resources (MDNR). 2015. Michigan Wildlife Action Plan 2015-2025: Approach, Methods, and Survey Needs. Michigan Department of Natural Resources, Wildlife Division, Lansing, MI, USA. <https://www.michigan.gov/documents/dnr/wap_intro_ada_551377_7.pdf>. Accessed Jan 2020.

Mihaljevic, J. R., M. B. Joseph, and P. T. J. Johnson. 2015. Using multispecies occupancy models to improve the characterization and understanding of metacommunity structure. *Ecology* 96:1783-1792.

Millenbah, K. F., S. R. Winterstein, H. Campa, III, L. T. Furrow, and R. B. Minnis. 1996. Effects of Conservation Reserve Program field age on avian relative abundance, diversity and productivity. *Wilson Society Bulletin* 108:760-770.

Moll, R. J., J. D. Cepek, P. D. Lorch, P. Dennis, T. Robison, J. Millspaugh, and R. Montgomery. 2018. Humans and urban development mediate the sympatry of competing carnivores. *Urban Ecosystems* 21:765-778.

Moll, R. J., K. Kilshaw, R. A. Montgomery, L. Abade, R. D. Campbell, L. A. Harrington, J. J. Millspaugh, et al. 2016. Clarifying habitat niche width using broad-scale, hierarchical occupancy models: a case study with a recovering mesocarnivore. *Journal of Zoology* 300:177-185.

Murray, L. D., C. A. Ribic, and W. E. Thogmartin. 2008. Relationship of obligate grassland birds to landscape structure in Wisconsin. *Journal of Wildlife Management* 72:463-467.

NatureServe. 2021. NatureServe Explorer (online). NatureServe, Arlington, VA, USA. <https://explorer.natureserve.org/>. Accessed Mar 2021.

Nichols, J. D., L. L. Bailey, A. F. O'Connell, Jr., N. W. Talancy, E. H. Campbell Grant, A. T. Gilbert, E. M. Annand, et al. 2008. Multi-scale occupancy estimation and modeling using multiple detection methods. *Journal of Applied Ecology* 45:1321-1329.

Norment, C. J., C. D. Ardizzone, and K. Hartman. 1999. Habitat relations and birding biology of grassland birds in western New York. *Studies in Avian Biology* 19:112-121.

Norris, R. A. 2014. Special animal abstract for *Ammodramus henslowii* (Henslow's sparrow). Michigan Natural Features Inventory, Lansing, MI, USA.

Noss, R. F., E. T. Laroe, and J. M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. National Biological Service, U.S. Department of the Interior, Report Number 0611-R-01 (MF), Washington, DC, USA.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, et al. 2019. vegan: Community ecology package. R package version 2.5-6. <https://CRAN.R-project.org/package=vegan>. Accessed Aug 2019.

Pabian, S. E., A. M. Wilson, and M. C. Brittingham. 2013. Mixed responses of farmland birds to the Conservation Reserve Enhancement Program in Pennsylvania. *Journal of Wildlife Management* 77:616-625.

PRISM Climate Group. 2004. PRISM gridded climate data: 30-year Normals, 1981-2010. Northwest Alliance for Computational Science and Engineering, Oregon State University, Corvallis, OR, USA. <http://prism.oregonstate.edu>. Accessed Jan 2020.

R Core Development Team. 2020. R Statistical Software v. 4.0.2. R Foundation for Statistical Computing, Vienna, Austria.

Rabeni, C. F. 1996. Prairie legacies: fish and aquatic resources. Pages 111-124 *in* Prairie Conservation: Preserving North America's Most Endangered Ecosystem, F. B. Samson and F. L. Knopf (Eds.). Island Press, Washington, DC, USA.

Reiley, B. M. and T. J. Benson. 2020. Does conservation practice and site age influence vegetation structure and avian abundance in restored fields? *Wildlife Society Bulletin* 44:684-694.

Ren, S., X. Chen, W. Lang, and M. D. Schwartz. 2018. Climatic controls of the spatial patterns of vegetation phenology in midlatitude grasslands of the northern hemisphere. *Journal of Geophysical Research: Biogeosciences* 123:2323-2336.

Ribic, C.A., R. R. Koford, J. R. Herkert, D. H. Johnson, N. D. Niemuth, D. E. Naugel, K. K. Bakker, et al. 2009. Area sensitivity in North American grassland birds: patterns and processes. *The Auk: Ornithological Advances* 126:233-244.

Riffell, S., D. Scognamillo, and L.W. Burger. 2008. Effects of the Conservation Reserve Program on northern bobwhite and grassland birds. *Environmental Monitoring and Assessment* 146:309-323.

Risser, P. G., C. E. Birney, H. D. Blocker, S. W. May, W. J. Parton, and J. A. Wiens. 1981. The True Prairie Ecosystem. US/IBP Synthesis Series 16. Hutchinson Ross Publishing Co., Stroudsburg, PA, USA.

Rota, C. T., M. A.,Ferreira, R. W. Kays, T. D. Forrester, E. L. Kalies, W. J. McShea, A. W. Parsons, et al. 2016. A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution* 7:1164-1173.

Sampson, F. B., F. L. Knopf, and W. R. Ostlie. 2004. Great Plains ecosystems: past, present, and future. *Wildlife Society Bulletin* 32:6-15.

Sanders, H. L. 1968. Marine benthic diversity: a comparative study. *American Naturalist* 102:243-282.

Sauer, J. R., B. G. Peterjohn, S. Schwartz, and J. E. Hines. 1995. The grassland bird home page, version 95.0. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD, USA. <http://www.mbr-pwrc.usgs.gov/bbs/grass/grass.htm>. Accessed May 2010.

Sauer, J. R., J. E. Hines, and J. Fallon. 2008. The North American Breeding Bird Survey, results and analysis 1966-2007, version 5.15.2008. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD, USA. <http://www.mbr-wrc.usgs.gov/bbs/bbs.html>. Accessed Nov 2010.

Sauer, J. R., K. L. Pardieck, D. J. Ziolkowski, Jr., A. C. Smith, M.-A. R. Hudson, V. Rodriguez, H. Berlanga, et al. 2017. The first 50 years of the North American Breeding Bird Survey. *The Condor: Ornithological Applications* 119:576-593.

Scholtz, R., J. A. Polo, S. D. Fuhlendorf, and G. D. Duckworth. 2017. Land cover dynamics influence distribution of breeding birds in the Great Plains, USA. *Biological Conservation* 209:323-331.

Searchinger, T., R. Heimlich, R. A. Houghton, F. X. Dong, A. Elobeid, J. Fabiosa, S. Tokgoz, et al. 2008. Use of U.S. croplands for biofuels increases greenhouse gases through emissions from land-use change. *Science* 319:1238–1240.

Secchi, S. and B. A. Babcock. 2007. Impact of high corn prices on Conservation Reserve Program acreage. *Iowa Ag Review* 13:4-7.

Shahan, J. L., B. J. Goodwin, and B. C. Rundquist. 2017. Grassland songbird occurrence on remnant prairie patches is primarily described by landscape characteristics. *Landscape Ecology* 32:971-988.

Strimas-Mackey, M, E. Miller, and W. Hochachka. 2018. auk: eBird Data Extraction and Processing with AWK. R package version 0.4.1. <https://cornelllabofornithology.github.io/auk/>.

Sullivan, B. L., C. L. Wood, M. J. Iliff, R. E. Bonney, D. Fink, and S. Kelling. 2009. *e*Bird: a citizen-based bird observation network in the biological sciences. *Biological Conservation* 142:2282-2292.

Suter, J. F., G. L. Poe, and N. L. Bills. 2008. Do landowners respond to land retirement incentives? Evidence from the Conservation Reserve Enhancement Program. *Land Economics* 84:17-30.

Suzuki, N., D. H. Olson, and E. C. Reilly. 2008. Developing landscape habitat models for rare amphibians with small geographic ranges: a case study of Siskiyou Mountains salamanders in the western USA. *Biodiversity and Conservation* 17:2197-2218.

Tanner, E. P. and S. D. Fuhlendorf. 2018. Impact of agri-environmental scheme on landscape patterns. *Ecological Indicators* 85:956-965.

Temple, S. A. 2002. Dickcissel (*Spiza americana*) *in* The Birds of North America (online). A. Poole (Ed.). Cornell Lab of Ornithology, Ithaca, NY, USA. <http://bna.birds.cornell.edu/bna/species/176>. Accessed Sep 2010.

Tobler, M. W., M. Kéry, M., F. K. C. Hui, G. Guillera-Arroita, P. Knaus, and T. Sattler. 2019. Joint species distribution models with species correlations and imperfect detection. *Ecology* 100:e02754.

U.S. Department of Agriculture (USDA) Farm Service Agency 2010. Conservation Reserve Enhancement Program. U.S. Department of Agriculture Farm Service Agency, Washington, DC, USA. <http://www.apfo.usda.gov/FSA/webapp?area=home&subject=copr&topic=cep>. Accessed June 2010.

U.S. Department of Agriculture (USDA) Farm Service Agency. 2007. Conservation Reserve Program summary and enrollment statistics, fiscal year 2006. U.S. Department of

Agriculture Farm Service Agency, Washington, DC, USA. <http://www.fsa.usda.gov/ Internet/FSA_File/06rpt.pdf>. Accessed May 2010.

U.S. Department of Agriculture (USDA) Natural Resources Conservation Service. 2000a. Introduced grass planting: Conservation Reserve Enhancement Program, CREP CP-1. U.S. Department of Agriculture Natural Resources Conservation Service, Lansing, MI, USA. <http://www.michigan.gov/documents/mda_ CP-1_INTRODUCEDGRASS_9614_7.pdf>. Accessed May 2010.

U.S. Department of Agriculture (USDA) Natural Resources Conservation Service. 2000b. Native grass planting: Conservation Reserve Enhancement Program, CREP CP-2. U.S. Department of Agriculture Natural Resources Conservation Service, Lansing, MI, USA. <http://www.michigan.gov/documents/mda_CP-2_ NATIVEGRASS_9615_7.pdf>. Accessed May 2010.

U.S. Department of Agriculture (USDA) Natural Resources Conservation Service. 2011. The PLANTS database. National Plant Data Center, Baton Rouge, LA, USA. <http://plants.usda.gov>. Accessed Jan 2011.

U.S. Department of Agriculture (USDA). 2009. Conservation Policy: Land Retirement Programs. U.S. Department of Agriculture Farm Service Agency, Washington, DC, USA. <http://www.ers.usda.gov/Briefing/ConservationPolicy/ retirement.htm>. Accessed June 2010.

University of California Museum of Paleontology (UCMP). 2007. The grassland biome. University of California, Berkeley, CA, USA. <https://ucmp.berkeley.edu/exhibits/biomes/grasslands.php>. Accessed Jan 2020.

Van Loan, A. S. 2011. The conservation reserve enhancement program (CREP) and grassland bird conservation in Michigan. Dissertation, Michigan State University, East Lansing, MI, USA.

Vickery, P. D. 1996. Grasshopper sparrow (*Ammodramus savannarum*) *in* The Birds of North America (online). A. Poole (Ed.). Cornell Lab of Ornithology, Ithaca, NY, USA. <http://bna.birds.cornell.edu/bna/species/176>. Accessed Sep 2010.

Voss, E. G. 1972. Michigan flora: a guide to the identification and occurrence of the native and naturalized seed-plants of the state. Part I: gymnosperms and monocots. Cranbrook Institute of Science Bulletin 55 and University of Michigan Herbarium, Bloomfield Hills, MI, USA.

Voss, E. G. 1985. Michigan flora: a guide to the identification and occurrence of the native and naturalized seed-plants of the state. Part II: dicots (Saururaceae-Cornaceae). Cranbrook Institute of Science Bulletin 59 and University of Michigan Herbarium, Ann Arbor, MI, USA.

Voss, E. G. 1996. Michigan Flora: a guide to the identification and occurrence of the native and naturalized seed-plants of the state. Part III: dicots (Pyrolaceae-Compositae). Cranbrook

Institute of Science Bulletin 61 and University of Michigan Herbarium, Ann Arbor, MI, USA.

Weiss, S., Z. Z. Xu, S. Peddada, A. Amir, K. Bittinger, A. Gonzalez, C. Lozupone, et al. 2017. Normalization and microbial differential abundance strategies depend upon data characteristics. *Microbiome* 5:27.

Wentworth, K. 2005. Effects of local and landscape features on avian use and productivity on Pennsylvania Conservation Reserve Enhancement Program fields. Ph.D. Dissertation, The Pennsylvania State University, State College, PA, USA.

Wentworth, K. L., M. C. Brittingham, and A. M. Wilson. 2010. Conservation Reserve Enhancement Program fields: benefits for grassland and shrub-scrub species. *Journal of Soil and Water Conservation* 65:50-60.

Wheelwright, N. T. and J. D. Rising. 2008. Savannah sparrow (*Passerculus sandwichensis*) *in* The Birds of North America (online), A. Poole (Ed.). Cornell Lab of Ornithology, Ithaca, NY, USA. <http://bna.birds.cornell.edu/bna/species/176>. Accessed Sep 2010.

Wiens, J. A. 1973a. Interterritorial habitat variation in grasshopper and savannah sparrows. *Ecology* 54:877-884.

Wiens, J. A. 1973b. Pattern and process in grassland bird communities. *Ecological Monographs* 43:237-270.

Wiens, J. A. and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. *Ecological Monographs* 5:21-41.

Williams, E. J. and W. A. Boyle. 2018. Patterns and correlates of within-season breeding dispersal: a common strategy in a declining grassland songbird. *The Auk: Ornithological Advances* 135:1-14.

Williams, E. J. and W. A. Boyle. 2019. Causes and consequences of avian within-season dispersal decisions in a dynamic grassland environment. *Animal Behaviour* 155:77-87.

Wilson, A., M. Brittingham, and G. Grove. 2010. Association of wintering raptors with Conservation Reserve Enhancement Program grasslands in Pennsylvania. *Journal of Field Ornithology* 81:361-372.

Wisconsin Department of Agriculture, Trade and Consumer Protection. 2004. 2003 annual report: Wisconsin's Conservation Reserve Enhancement Program (CREP). Wisconsin Department of Agriculture, Trade and Consumer Protection, Madison, WI, USA.

Wolf, A. L., G. L. Slater, S. F. Pearson, H. E. Anderson, and R. Moore. 2020. Range-wide patterns of natal and breeding dispersal in the streaked horned lark. *Northwest Science* 94:31-43.

Zipkin, E. F., J. A. Royle, D. K. Dawson, and S. Bates. 2010. Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biological Conservation* 143:479-484.

CHAPTER 4: ALLOMETRIC SCALING FOR ESTIMATING RANGE-WIDE ABUNDANCE OF A COMMON FOREST BIRD ACROSS NORTH AMERICA

Abstract

Allometric scaling postulates that an ecological latent state (e.g., abundance) is related to the size of an organism; that is, traits like body mass constrain numerical limits on species abundance in response to the environment in space and time. State-space (hierarchical) models are powerful tools for describing ecological patterns and processes, yet few studies jointly evaluated the utility of body mass, traditional ecological covariates, and changing species abundance on broad scales. We quantified the relationship between species body mass and annual abundance from summer (i.e., May-August) Breeding Bird Survey (BBS) point counts of a common forest bird, red-eyed vireo (*Vireo olivaceus*), in North America from 2014 to 2018. We interpolated vireo body mass across the breeding range and acquired variables on climate and landscape complexity as macrogeographic controls on vireo abundance. In addition to a null model, we tested 12 candidate dynamic *N*-mixture models, half including mass-abundance scaling and other covariate effects while accounting for imperfect detection in the observation process, while also representing different hypotheses related to vireo population dynamics over time (e.g., logistic growth). The other six models did not include mass-abundance scaling. We found that models including body mass outperformed models based only on climate and landscape complexity for predicting spatially-explicit abundances. Derived estimates from the top-ranked model produced range-wide abundance patterns similar to those characterized by existing citizen-science products; however, patterns in our mapped estimates revealed previously unidentified hot and cold spots in abundance across the red-eyed vireo's range. This work demonstrates the utility of

dynamic (i.e., multi-season) allometric-scaling models for improving estimates of species abundance in an era of accelerated global change.

Introduction

Understanding how ecological processes function in human-altered ecosystems is critical to conservation. Species face several human-related threats to their persistence in space and time, including habitat loss and fragmentation (Bevers and Flather 1999, Bowers and Dooley, Jr. 1999, Mortelliti et al. 2014, Haddad et al. 2015, Newbold et al. 2015, Haddad et al. 2017), disease prevalence and transmission (Snäll et al. 2008), overharvest, decreased genetic diversity, and climate change (Jetz et al. 2007, Jarzyna et al. 2015, Urban 2015, Scheffers et al. 2016, Pörtner et al. 2021). Human-induced effects on animal populations operate across multiple spatiotemporal scales, with some impacts (e.g., climate change, land conversion) operating at global and continental extents.

Hence, a macro-scale perspective is important for assessing biotic assemblages over broad areas and times, particularly to understand ecological processes across scales (Brown and Maurer 1987, 1989, Heffernan et al. 2014, Zipkin et al. 2021). In addition, incorporating species traits into models explaining and predicting species' responses to environmental change is increasingly recognized as essential for functionally linking organisms to population and community structure and their dynamics in modern conservation (Messier et al. 2010, Blonder 2018, Zakharova et al. 2019), including ample opportunities to test theory-driven approaches to ecological restoration (Laughlin 2014, Meunier et al. 2017). However, while we do not lack data on organism traits (e.g., bird-banding data and the EltonTraits and Amniote Life History databases; Smith 2013, Wilman et al. 2014, Myhrvold et al. 2015, USGS Bird Banding Laboratory 2020), we do lack studies that simultaneously take a macro-scale approach and

incorporate trait-based ecology to predict and understand species responses to environmental change, particularly in terms of range-wide abundance.

Quantifying population trends (e.g., in abundance or demographic parameters over time) and environmental drivers can enhance understanding of impacts to species from various environmental factors including climate and landscape complexity (Jetz et al. 2007, Royle and Dorazio 2008, Jarzyna et al. 2015, Kéry and Royle 2016, 2021). In order to uncover robust relationships, however, it is essential to control for limiting processes such as survivorship, recruitment, and population growth, as well as measurement error including imperfect observer detection (Mokany et al. 2012, Pagel and Schurr 2012, Schurr et al. 2012, Newman et al. 2014). As environmental factors change, species traits also change to reflect those environmental conditions potentially linked to shifts in population descriptors (Brown and Maurer 1987, 1989). One such trait is species body mass, which is a trait sensitive to climate and land-use change (Sheridan and Bickford 2011, Oliveira et al. 2016, Keleman and Rehan 2020), and body mass also reflects species ecological role(s) and life-history characteristics (Pianka 1970, 1972). Body mass is also commonly used as a nonlinear explanatory variable of other species traits (e.g., linear dimensions) or population states (e.g., abundance), particularly quantifying how emergent properties scale with organism size (Carbone et al. 2007, White et al. 2007, Rossberg et al. 2008, Hechinger et al. 2011, Kendall et al. 2019). Allometric mass-abundance scaling equations for estimating population parameters have been debated in the ecological literature, and consensus on the value of mass-abundance scaling exponents remains unclear (Brown and Maurer 1986, Marquet et al. 2004, Hechinger et al. 2011, but see Hendriks 2007). This lack of consensus suggests that system measurement error is at play between discordant studies (Lovegrove 2000, Bokma 2004, Carroll et al. 2006, Bagchi et al. 2014, Kilmer and Rodríguez 2017).

Quantifying multiple sources of measurement error and uncertainty in ecological patterns and processes—including mass-abundance scaling relationships—is possible with state-space (hierarchical) models (Royle and Dorazio 2008, Kéry and Royle 2016, 2021). Common sources of measurement error and uncertainty in datasets and analyses include spatiotemporal autocorrelation, imperfect species detection, and scale-phenomenon mismatches. If this measurement error is not included, then the accuracy and precision of model parameters can be reduced. Hierarchical models that incorporate essential scales, predictor variables, nuisance parameters, and population-limiting processes often achieve the greatest realism and thus better predict latent (unobservable) ecological states such as species occupancy or abundance (Royle and Dorazio 2008, Hostetler and Chandler 2015, Bellier et al. 2016, Kéry and Royle 2016, 2021). In the context of predicting spatially-explicit species abundance patterns, to our knowledge, few studies have considered joint estimation of species allometry, traditional (linear) ecological covariates, and changing population dynamics in hierarchical models at continental extents (Kendall et al. 2019).

To incorporate such components in state-space models of ecological pattern and process at broad extents, first, numerous data on organisms are necessary. Compared to other taxonomic groups (e.g., mammals and reptiles), large amounts of georeferenced long-term data exist on bird species worldwide, particularly in North America (e.g., including multi-national and -decadal data sources; Robbins et al. 1986, Sullivan et al. 2009, Pardieck et al. 2014, Fink et al. 2020). Birds comprise an important and well-studied taxonomic group because many species are widespread geographically, making them useful indicators of ecosystem health (Septon et al. 1995, Padoa-Schioppa et al. 2005, Sergio et al. 2006, Solomou and Sfougaris 2015). Consistent with recent pervasiveness of negative human impacts on the environment, numerous bird species

have declined over the past 50 years in North America (Sauer et al. 2017, Rosenberg et al. 2019). Birds also fill important roles in ecosystems as local prey biomass, predators or scavengers, plant pollinators and seed or parasite dispersers, and many bird species serve as energy and biomass conduits to ecosystems between or within continents as long-distance migrants (Price 2002, Whelan et al. 2008, Whelan et al. 2015). In addition, numerous extrinsic factors presumably contribute to patterns of bird abundance and distribution.

Macrogeographic factors that influence species abundance and distribution are important for linking broad-scale environmental variation to population processes (Maurer and Taper 2002), especially bird populations which actively respond to landscape-level disturbances such as habitat loss and fragmentation (Smith et al. 2011, Haddad et al. 2015, Jarzyna et al. 2015). Potential macrogeographic constraints on bird distributions include precipitation, temperature, land cover, proximity to core of the species distribution, landscape composition and configuration, landform and elevation, resource competition with conspecifics or other species, and dispersal ability, particularly in the context of metapopulations (Hanski 1998a,b, González-Megías et al. 2005, Bahn et al. 2008, Hartfelder et al. 2020). When resources such as food, mates, or nesting habitats are clustered, many bird species tend to congregate during the breeding season, making them visually or audibly detectable by observers via point-counts (Ralph et al. 1995). Owing to broad ecological significance and relative ease of sampling, bird populations are readily surveyed with broad-scale monitoring programs.

We evaluated range-wide species abundance to macrogeographic drivers and spatially-explicit body mass for a common forest bird across North America, red-eyed vireo (*Vireo olivaceus*). We asked: (a) do allometric (mass-abundance) relationships and traditional (linear) ecological covariates inform state-space models of species abundance range-wide, where we

expected such models would perform better than models that excluded mass-abundance scaling, (b) what form of population dynamics (e.g., logistic growth) controls range-wide abundance over time, where we expected that density-dependent growth would be most informative, and (c) how do extrapolated model estimates of range-wide abundance compare to estimates informed by different broad-scale monitoring programs, where we expected that derived estimates would contrast those of other broad-scale programs, particularly in terms of identifying patterns in high and low (range-wide) abundance. To answer these questions, we: (1) filtered survey routes for count data on red-eyed vireos; (2) compiled multiple macrogeographic predictors, including spatially-explicit body mass, on a continental scale to relate to species count data; (3) quantified the influence of macrogeographic variables and mass-scaling relationships on species abundance; and (4) extrapolated abundance model predictions to the range extent. This work evaluates the utility of allometric-scaling relationships with both traditional (linear) predictor variables and classic population dynamics for a common bird species in North America. We believe this work helps advance understanding of the spatial organization of bird populations and establishes a framework potentially useful for evaluating spatial organization of other taxa at continental extents.

Methods

Model species, study area, and broad-scale data

Red-eyed vireo (hereafter REVI) is one of the most common forest songbirds in north-central and eastern North America (Figure 4.1). A Nearctic-Neotropical migrant, REVIs breed in the United States and Canada, and they overwinter in Central America and northwestern South America (Loria and Moore 1990, Sandberg and Moore 1996, Cimprich et al. 2020, Fink et al. 2020). Sexes are considered weakly dimorphic and socially monogamous, and primary food

sources include various insects foraged from forest canopy vegetation, especially caterpillars (James 1976, Robinson and Holmes 1982, Marshall et al. 2002, Marshall and Cooper 2004). Body size and associated mass of REVI varies clinally from east to west, with smaller individuals found in eastern North America (Ridgway 1904, Smith 2013, USGS Bird Banding Laboratory 2020). Previous research notes species mean (± SD) body mass of 15.00 ± 1.30 g (range: 11.10-19.80 g, *n* = 113 individuals) in adult males and 14.10 ± 1.26 g in adult females (range: 11.38–18.03 g, *n* = 111 individuals; Dunning, Jr. 1993).

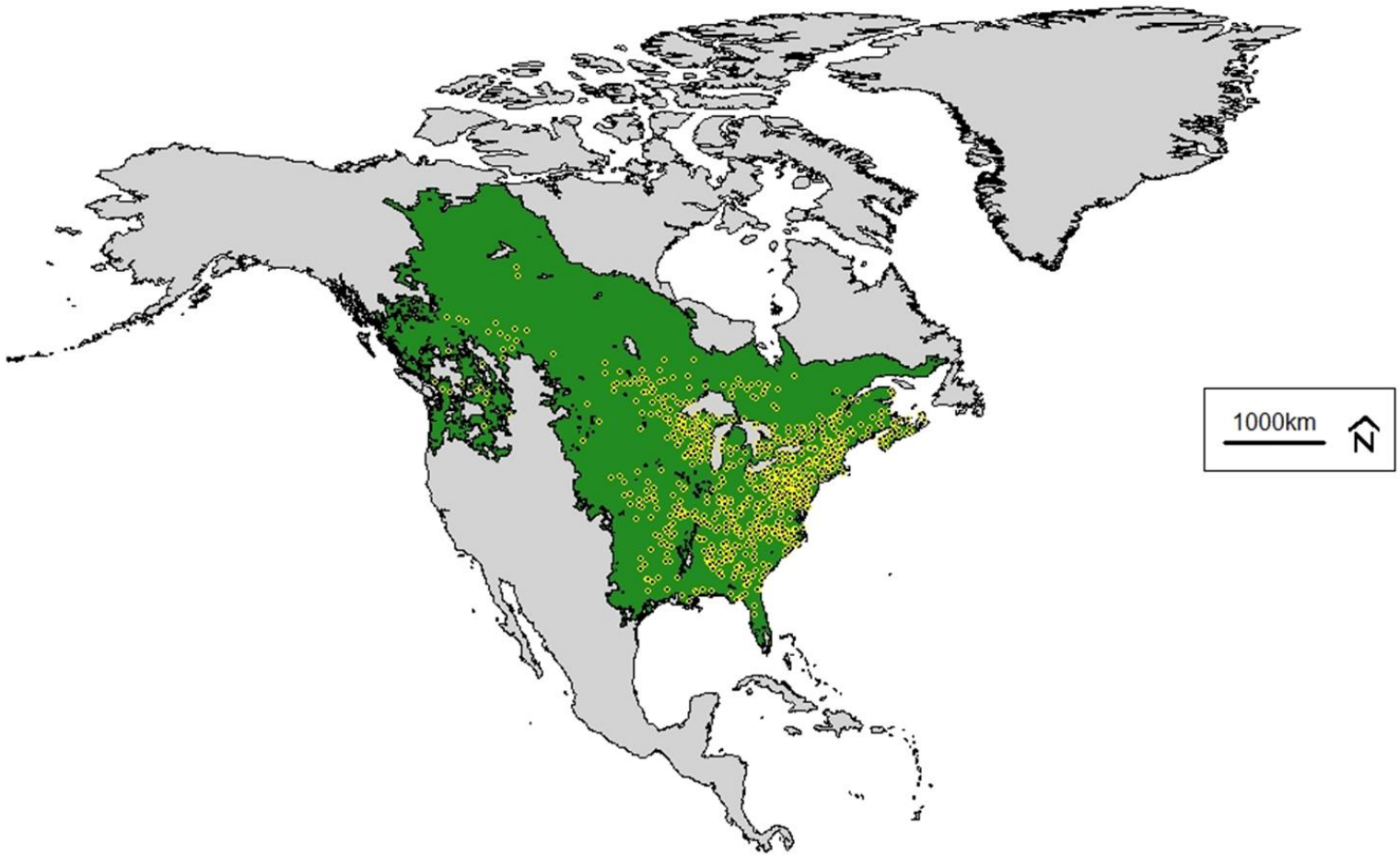
Range-wide, REVIs breed in deciduous and mixed deciduous-coniferous forests (Stewart and Aldrich 1952, Lawrence 1953, Southern 1958, Barlow and Rice 1977, Graber et al. 1985), including areas where understory shrubs are plentiful (Sutton 1949, Lawrence 1953, Southern 1958, James 1976). REVI can also be found near small openings in forest canopies (Tyler 1950, Southern 1958, Crawford et al. 1981). In southern pine (*Pinus* spp.) dominated areas, REVIs are commonly found in riparian areas, especially where hardwood trees are most abundant (Hamel 1992). In northern areas, REVIs are associated with alder (*Alnus* spp.) and aspen (*Populus* spp.) groves (Barlow and Power 1970), and in northern hardwoods and other deciduous forests (Tyler 1950, Graber et al. 1985, Cimprich et al. 2020). The REVIs are more abundant in core than periphery forest and range locations (Graber et al. 1985), and the species can also occur in human-dominated landscapes, including cities, residential areas, parks, cemeteries, and more—especially wherever large trees exist (Tyler 1950, Graber et al. 1985, Cimprich et al. 2020). Because of its commonness and ubiquity, REVIs are conducive to macroecological investigations (Brown et al. 1995).

The study area comprises the breeding range of REVI in continental North America, wherein most BBS routes are sampled in the lower 48 United States and several provinces of

Canada (Figure 4.1). The REVI breeding range spans areas with subarctic (i.e., north-central Canada), temperate (i.e., central and eastern USA), or sub-tropical conditions (i.e., Florida; Bolen 1998, Chapman and Bolen 2015). North-continental areas tend to be dominated by taiga and mixed subarctic forests, mid-continental areas contain row crop agriculture and mixed evergreen and deciduous forests, and southeast-continental areas include more wet temperate and tropical humid forests (i.e., in southern Florida; Bolen 1998, Chapman and Bolen 2015). Two major mountain ranges reside in North America, the Rocky Mountains in the west and Appalachian Mountains in the east.

One broad-scale monitoring program useful for macroecological analyses of species abundance and distribution is the North American Breeding Bird Survey (BBS). The BBS is a cooperative international monitoring program that started in 1965 and has been in continuous operation since (Robbins et al. 1986, Pardieck et al. 2014). The BBS is largely supported by citizen-scientists and professional biologists who collect data on bird communities observed along designated survey routes. Subsequently, the U.S. Geological Survey quality controls, archives, and distributes the data. These data are valuable because they include information on numerous species sampled across a broad spatial extent. The utility of nonlinear hierarchical models for describing bird communities using BBS data has been demonstrated (Smith and Edwards 2021), and so it follows that these data may also be conducive to an allometric-scaling (nonlinear and hierarchical) assessment of species abundance. Additionally, BBS data are collected annually, adding an important temporal dimension to associated analyses.

Figure 4.1. Red-eyed vireo (*Vireo olivaceus*) range (green; i.e., from *e*Bird; Fink et al. 2020) in North America and 759 Breeding Bird Survey (BBS) routes (start of route denoted with yellow points) along which observers recorded red-eyed vireos during the annual breeding season, 2014-2018. Stop-level survey counts, route-start locations, survey conditions, and associated run protocols were retrieved from the U.S. Geological Survey's Patuxent Wildlife Research Center (Pardieck et al. 2014).



Data collection and preparation

Contributors to the BBS record counts of REVIs (and other bird species) and other survey-relevant variables (e.g., start and stop times, cloud cover), via 3-min point-counts conducted every 0.80 km (i.e., ~0.5 mi) along established 39 km (i.e., ~24.5 mi) survey routes (i.e., roads). Data from a single route comprise 50 total stops, where observers record total number of unique individuals seen or heard within 400 m (i.e., ~0.25 mi) of each stop (e.g., recording birds to the species taxonomic level; Sauer et al. 1997, Pardieck et al. 2014). We downloaded count records from the BBS database from 2014 to 2018, corresponding to the spatiotemporal availability of independent variables of interest (Table 4.1). We filtered BBS data to only include routes surveyed in a program-consistent manner (i.e., using only survey routes that followed the standard monitoring protocol; Pardieck et al. 2014, Sauer et al. 2019). Finally, because the BBS data do not include coordinates of individual route-stop (point-count) locations (Pardieck et al. 2014), we summed REVI counts across the 50 stops, thus inference on REVI abundance is at the route level (Table 4.1; Hostetler and Chandler 2015).

To explain variation in the abundance-level (i.e., ecological process) of our candidate models, we retrieved REVI body mass and size records from the U.S. Geological Survey's Bird Banding Laboratory (BBL; Smith 2013). These data represent observations at bird-banding stations across REVI range in North America during 2014-2018 (Table 4.1; USGS Bird Banding Laboratory 2020). Bird-banding records included information about REVI body size, including mass (g), wing chord (mm), tarsus length (mm), and more; however, only body mass records were consistently measured by observers at most banding stations (e.g., less than a dozen records lacked species mass data). Consequently, as a proxy for body size, we used REVI body mass in allometric-scaling models. To characterize species body mass, we computed mean REVI body

mass for a banding location by pooling observations across all age and sex categories. We limited calculation of station-level means to the REVI breeding season (i.e., May-August), thereby excluding spring and autumn migration because REVI body masses are more dynamic during migration (Loria and Moore 1990). We estimated (expected) body mass for REVIs across their distribution by applying spatial variography and universal kriging to the geolocated mean body masses (Cressie 1993, Pebesma 2004, Cressie and Wikle 2011). As REVI body mass is known to vary clinally (Ridgway 1904, Smith 2013, USGS Bird Banding Laboratory 2020), we had a general idea on how the pattern from the final interpolation surface should look. After computing mean REVI body masses across age and sex classes at each banding station, we then universally kriged those masses, generating an interpolated surface of expected REVI mass

Table 4.1. Dependent and independent variables for analysis of red-eyed vireo abundance to body mass constraints, local weather, and forest, landscape, and core-periphery variables, including variable definition, spatial extent, and data source. Temporal variables were summarized annually or during the summer months (i.e., May-August). Spatial variables were either summarized to the starting location of survey routes or to a 39-km (circular) buffer surrounding them (i.e., because BBS route-stop locations were not available during the period of study).

Variable	Definition	Spatial Extent	Source(s)
Dependent			
Red-eyed vireo counts	Counts (discrete) of red-eyed vireos recorded via the Breeding Bird Survey, summed across stop locations within survey routes	Route	BBS[a]
Independent			
Body mass	Log-scale transformation of (interpolated) red-eyed vireo mean body masses (g) from individuals measured	100-km grid cell resolution of universally kriged body masses, measured at bird-banding stations during May-August 2014-2018, spatially extracted to survey route start locations	BBO[b], BBL[c]
Temperature	Annual (summer, May-August) maximum temperature (ºC)	1-km grid cell resolution of weather variables, spatially extracted to survey route start locations	Daymet[d]
Precipitation	Annual (summer, May-August) total precipitation (mm)	1-km grid cell resolution of weather variables, spatially extracted to survey route start locations	Daymet
Interaction	Product of annual (summer, May-August) total precipitation (mm) and maximum temperature (ºC)	1-km grid cell resolution of weather variables, spatially extracted to survey route start locations	Daymet
Canopy cover	Mean canopy cover (%) of forests surrounding survey routes	30-m grid cell resolution of canopy cover, bounded within a 39-km (radius) buffer around survey routes	GFCD[e]

Table 4.1 (cont'd)

Distance from range core	Straight-line distance (km) from survey route locations to the centroid of the red-eyed vireo's range	Route	*e*Bird[f]
Landscape metrics[g]	Aggregate landscape metrics describing context surrounding survey routes, summarized by their principal components	30-m grid cell resolution of land cover, bounded within a 39-km (radius) buffer around survey routes	NALCMS[h]

[a]BBS = Breeding Bird Survey; Environment Canada, Ottawa, ON, CAN and Patuxent Wildlife Research Center, U.S. Geological Survey, Laurel, MD, USA (Pardieck et al. 2014).
[b]BBO = Bird Banding Office, Environment Canada, Ottawa, ON, CAN
[c]BBL = Bird Banding Laboratory, U.S. Geological Survey, Reston, VA, USA (USGS Bird Banding Laboratory 2020).
[d]Daymet version 4.0 (2020), Distributed Active Archive Center, Oak Ridge National Laboratory, Oak Ridge, TN, USA (Thornton et al. 2020).
[e]GFCD = Global Forest Change Database version 1.7 (2019), University of Maryland, College Park, MD, USA (Hansen et al. 2013).
[f]*e*Bird Distribution and Abundance; Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA (Fink et al. 2020).
[g]Landscape metrics are described in Table 4.2. Principal components of landscape metrics were applied in the same candidate models because principal-component axes are orthogonal and thus uncorrelated.
[h]NALCMS = North American Land Change Monitoring System version 2.0 (2015); Commission for Environmental Cooperation (USA, CAN, and MEX; CEC 2015, Homer et al. 2017).

We first generated a sample variogram, using a Cressie-Hawkins correction for outlier measures as well as default binning, in the "variogram" function of the "gstat" package version 2.0-7 in R version 4.0.2 (Pebesma 2004, Gräler et al. 2016, R Core Development Team 2020). We then estimated the functional form of the sample variogram using the "autofitVariogram" function of the "automap" package version 1.0-14, which selects the best-fitting variogram model to the input data based on the lowest sum of squares' error (Hiemstra et al. 2009). We considered Bessel, circular, exponential, Gaussian, hole, linear, logarithmic, pentaspherical, periodic, spherical, spline, and wave variogram models (Cressie 1993, Pebesma 2004, Cressie and Wikle 2011). We then inserted the chosen model (i.e., based on the lowest sum of squares' error) and associated estimates of nugget, range, and partial sill to the "fit.variogram" function of the "gstat" package (Pebesma 2004, Gräler et al. 2016). Following estimation of spatial variography, we interpolated REVI body masses among locations using universal kriging with the "krige" function in the "gstat" package (Pebesma 2004, Gräler et al. 2016). Results of the interpolation produced a continuous surface of expected (mean) REVI body mass across its breeding range in North America at a 100-km spatial resolution. Finally, we confirmed whether the interpolated surface described the east-west clinal variation in REVI body mass as expected.

Because REVI feed primarily on insects (Marshall 2000, Marshall et al. 2002), especially caterpillars during the breeding season, we included continental estimates of precipitation, temperature, and their potential interaction to use as proxies for caterpillar biomass (Visser et al. 2006, Schöll et al. 2016), which is known to influence breeding density and territory size of forest birds (e.g., REVI territory size inversely correlates with the volume of foliage within a territory; Marshall and Cooper 2004). Beyond impacts to caterpillars, temperature and precipitation also have fitness impacts on breeding birds, particularly as phenological shifts in

vegetation and associated prey occur (McKellar et al. 2013, Imlay et al. 2018, Wysner et al. 2019). Consequently, we downloaded monthly (total) precipitation and (maximum) temperature during May-August 2014-2018 from the Daymet database (Thornton et al. 2020), which represents weather variables summarized at a 1-km spatial resolution across North America. To associate these data with BBS routes, we extracted grand mean total precipitation and maximum temperature to the starting location of each filtered BBS route using R's "raster" package version 3.3-7 (Hijmans 2020). We estimated an interaction of precipitation and temperature in REVI abundance models.

Forest-dependent species such as REVI positively associate with forest canopy area or cover (Crawford et al. 1981). To account for route-level variation in forest canopy in candidate models, we downloaded $10^{o} \times 10^{o}$ raster tiles of annual (mean) forest percent canopy cover at 30-m resolution for North America from the 2019 Global Forest Change database version 1.7 (Hansen et al. 2013), based on Landsat 8 Operational Land Imager instrument measurements from 2013 to present. Additionally, because the BBS database does not provide geographic coordinates of recent (i.e., 2014-2018) route-stop locations or route shapefiles (Pardieck et al. 2014, Hostetler and Chandler 2015), we could neither ascertain the location nor direction of survey route pathways, and so we circularly buffered each (geolocated) route start location by 39 km (i.e., the length of a BBS route). In doing so, we assumed that forest percent canopy cover summarized across the spatial extent of a BBS route at the start location would generally represent forest conditions along the route, and thereby be informative for REVI breeding density and total abundance. Within each route-specific 39-km (radius) buffer, we summarized the mean percent canopy cover across raster locations and then assigned values to BBS routes

using raster operations (e.g., the “extract” function, among others) in R’s “raster” package (Hijmans 2020).

The core-periphery hypothesis predicts that abundance, genetic variation, and associated fitness are likely highest at the core, rather than periphery, of a species geographic range—reflecting increased spatial isolation among individuals as well as the extent to which locations meet ecological niche requirements of species (Brown 1984, 1995, Brown et al. 1995). Therefore, we estimated distance between the start locations of filtered BBS routes and the estimated core (i.e., geographic centroid) of the breeding range for REVI in North America (e.g., derived from *e*Bird citizen-science data collected during 2005-2019; Fink et al. 2020). To do this, we used the “st_centroid” and “st_distance” functions of R’s “sf” package version 0.9-8 (Pebesma 2018). We were also interested in accounting for landscape context (e.g., spatial arrangement, composition, and diversity) in models of REVI abundance. To do this, we downloaded publicly available data from the 2015 North American Land Change Monitoring System (NALCMS), which describes 19 land cover types summarized at a 30-m spatial resolution (CEC 2015, Homer et al. 2017)—including multiple classes for shrublands and forests (i.e., cover types REVI commonly associate with; Cimprich et al. 2020). We first reclassified the level-2 cover types of the NALCMS raster into “REVI habitat” and “inhospitable matrix” classes (Table C4.1). To reclassify the 2015 NALCMS, we used the “reclassify” function in R’s “raster” package (Hijmans 2020).

Because we also sought to characterize landscape-level composition and configuration of “REVI habitat” v. “inhospitable matrix” cover types, we calculated principal component scores for numerous (i.e., highly correlated, pairwise-Pearson’s $|r| > 0.60$) landscape metrics (e.g., capturing land cover arrangement, composition, and diversity) expected to influence occupancy

and abundance of REVI. To quantify multiple landscape metrics describing areas surrounding filtered BBS routes, we used R's "landscapemetrics" package version 1.5.0 (Hesselbarth et al. 2019), which generates extent-defined (e.g., using circular buffers around starting locations of BBS routes) composition and configuration metrics from raster datasets of land cover using FRAGSTATS version 4.2.1 (McGarigal et al. 2014). Like our summaries of percent canopy cover, we quantified landscape metrics of interest at a 39-km spatial scale around filtered BBS routes using circular buffers (Table 4.2).

We next applied a Principal Component Analysis (PCA) to reduce the dimensionality of the BBS route (759 rows) by landscape metric (8 columns) matrix of correlated variables to generate composite landscape scores (i.e., principal component [PC] axes or eigenvectors) at the 39-km extent. To do this, we used the "prcomp" function in R's "stats" package (R Core Development Team 2020). Specifically, we conducted a PCA on the *Z*-scored (i.e., standardized) matrix of landscape metrics derived from our "REVI habitat" v. "inhospitable matrix" land cover dataset. We then assessed how many PC-axis eigenvalues exceeded or neighbored the average eigenvalue across all PC axes in scree plots—visuals useful for determining the number of PC axes that explain considerable variation in the matrix of landscape metrics—based on the Kaiser-Guttman procedure (Kaiser 1960). In total, we acquired three vectors of PC scores (i.e., PC1, PC2, and PC3) whose factor loadings conveyed pairwise correlations between PC axes and individual landscape metrics estimated using FRAGSTATS and R. Finally, we used estimates of the effects of the PC1, PC2, and PC3 axes in our models to interpret the influence of individual landscape metrics on REVI abundance using each PC's factor loadings (i.e., correlation coefficients describing landscape metric and PC-axis associations). We report the PCA bivariate and scree plots (Figure C4.1).

Table 4.2. Landscape metrics (see McGarigal et al. 2014) used to represent cover type patterns at 39-km (radius) buffers around Breeding Bird Survey (BBS) route starting locations distributed across North America, based on the 2015 North American Land Change Monitoring System (CEC 2015, Homer et al. 2017).

Metric	Abbreviation	Description
Patch Area	AREA_MN	Mean area (ha) across all patch types within a landscape.
Contagion	CONTAG	Connectedness (%) of patches within a landscape.
Edge Density	ED	Total edge length of a patch type divided by the total area (m/ha).
Euclidean Nearest Neighbor	ENN_MN	Mean distance (m) of patches to their nearest neighbor within a landscape.
Number of Patches	NP	Number of patches (count) within a landscape.
Patch Density	PD	Number of patches divided by total area (count per 100 ha).
Patch Richness	PR	Number of unique patch types (count) within a landscape.
Shannon Diversity index	SHDI	The negative sum, across all patch types, of the proportional abundance of each patch type multiplied by that proportion (unitless), based on total area.

For detection-level (i.e., observation process) covariates in our candidate models, and to account for variation in observer imperfect detection of REVI at filtered BBS routes, we estimated number of survey hours per route because REVI activity varies with rates of singing by other bird species (Ficken et al. 1974), as well as lengthening surveys from morning twilight to midday (Williamson 1971, Marshall and Cooper 2004). We first converted each survey's start and end (i.e., hour:minute Greenwich Mean Time) times to date-time vectors using the "as.POSIXct" function in R's "base" package and then calculated differences between start and end date-times in hours using the "difftime" function in R's "base" package (R Core Development Team 2020). The outcome of this process represented total survey effort by observers per route. Additionally, we assumed a small amount of observer lag (e.g., travel) time between 0.8-km spaced survey stops, and so we adjusted route-level (total) effort by subtracting: 49 moves (i.e., between 50 stops) multiplied by route-level (total) effort, adjusted by observers' average time spent between stops (i.e., total effort minus average time, where average time equal total effort minus the quotient of 150 minutes [i.e., 50 stops * 3-min point counts per stop] and 49 moves between 50 stops). Described formulaically: $Effort_{\ adjusted} = Effort_{\ total} - \left[49 * \left(Effort_{\ total} - \left(\frac{150}{49}\right)\right)\right]$, wherein $Effort_{\ adjusted}$ and $Effort_{\ total}$ are unique to each route-year and summarized in hours. We computed hours of adjusted survey effort per route-year and considered both linear and quadratic effects of effort in our models of REVI detection, which conveys that detection may change linearly or parabolically with lengthening survey effort (e.g., toward or away from periods of varied species activity; Marshall and Cooper 2004, Kéry and Royle 2016, 2021). Furthermore, too few BBS routes are actually surveyed > 2 times per year (Pardieck et al. 2014), and so our detection models are restricted to single-visit estimates, which has been previously tested with similar atlas datasets (Lele et al. 2012, Peach et al. 2017). While

negative bias in latent ecological states manifested in simulation studies of single-season (static), single-visit models (i.e., often due to violations of population closure assumptions or changing link functions for detection; Knape and Korner-Nievergelt 2015, 2016, Dennis et al. 2015, Sólymos and Lele 2016, Zipkin et al. 2014), multi-season (dynamic) single-visit models do not assume population closure between discrete (survey) time steps (i.e., primary periods; Dail and Madsen 2011), and dynamic model estimators become stable and efficient with large sample sizes as well as provide useful alternatives to naïve estimators of abundance (Sólymos et al. 2012).

Statistical analysis and comparisons with citizen-science products

To understand how mass-scaling (nonlinear) and other (linear) covariates inform modeled abundance estimates at a broad extent, we implemented single-species multi-season (dynamic) binomial *N*-mixture models to interannual counts of REVI at filtered BBS routes (Dail and Madsen 2011, Fiske and Chandler 2011, Hostetler and Chandler 2015). The dynamic *N*-mixture model comprises a generalized form of the binomial *N*-mixture model (Royle 2004), in that repeated primary and secondary sampling periods are involved in estimating ecological (abundance) and observational (detection) processes, respectively. While primary sampling periods (e.g., surveys between years) are considered open to births, deaths, immigration, and emigration, secondary sampling periods (e.g., repeat survey visits within years) are considered closed to such population-growth processes (Dail and Madsen 2011). Furthermore, dynamic *N*-mixture models may consider different mixture distributions (e.g., conventional or zero-inflated Poisson or negative binomial; Fiske and Chandler 2011) and apply various functions to account for interannual population dynamics (i.e., between primary periods) that allow for estimation of apparent survival, recruitment, immigration, carrying capacity, and maximum instantaneous

population growth, depending on choice of dynamics and including additional capacity to estimate such rates using covariates (Hostetler and Chandler 2015, Bellier et al. 2016).

Importantly, Dail and Madsen's (2011) model also assumes that a substantial portion of the study population returns to sampling locations between primary periods (i.e., the target species is site faithful), and REVIs exhibit high fidelity to their breeding sites over time (e.g., on average, > 65% of 147 individuals returned to the same [and dispersed little, 174.88 ± 41.69 m, from] territories between breeding seasons during 1996-1999 in West Virginia, USA; Marshall 2000, Marshall et al. 2002). Other REVI studies reported similar (high) site fidelities (i.e., relative to other neotropical migrant species) during the breeding season (Rice 1978, Roberts and Muir 1998). In addition, REVI breeding territories are compact (e.g., 0.39 ± 0.16 ha; Marshall 2000, Marshall and Cooper 2004), and thus able to reside within the total sampling area of a BBS route stop (i.e., > 500,000 m^2 based on $\pi * 400^2$, coinciding with the approximate point-count radius in meters; Pardieck et al. 2014). In light of the aforementioned, we believe that REVI territory fidelity and size satisfies Dail and Madsen's (2011) model assumption of sampling a large (e.g., > 50%) portion of the total number of unique individuals between successive primary periods.

The conventional dynamic *N*-mixture model (i.e., with absolute or constant population dynamics) resembles the following, after Dail and Madsen (2011):

$$N_{i1} \sim Poisson(\lambda_{i1}) \ , \tag{4.1}$$

$$log(\lambda_{i1}) = \beta_{0i1} + \boldsymbol{\Lambda_{i1}}\beta_{i1} + \ \varepsilon_{i1} \ , \tag{4.2}$$

$$S_{i,t+1} \sim Binomial(N_{it}, \varphi) \ , \tag{4.3}$$

$$R_{i,t+1} \sim Poisson(\gamma)\ , \tag{4.4}$$

$$N_{i,t+1} = S_{i,t+1} + R_{i,t+1}\ , \tag{4.5}$$

$$y_{ijt} \sim Binomial(N_{it} * p_{ijt})\ , \tag{4.6}$$

$$logit(p_{ijt}) = \alpha_{0ijt} + \boldsymbol{P_{ijt}}\alpha_{ijt} + \eta_{ijt}\ , \tag{4.7}$$

where y_{ijt} is the count of REVI at BBS route *i* during replicate survey visit (i.e., secondary period) *j* during survey year (i.e., primary period) *t* and distributed as a Binomial random variable with abundance N_{it} and detection probability p_{ijt}. Process-level latent (true) abundance N_{it} is estimated at route *i* during primary period *t* = 1 (i.e., year 2014, initializing the model) and distributed as a Poisson (e.g., or zero-inflated Poisson or negative binomial) random variable with site-level REVI abundance λ_{i1} estimated on the log scale at route *i* during primary period *t* = 1, as a function of route-level (random) intercepts β_{0i1}, covariates $\boldsymbol{\Lambda_{i1}}$ with a conformable vector of slope parameters β_{i1}, and errors ε_{i1}. Observation-level detection probabilities p_{ijt} are logit-scale estimated as a function of route- and visit-level (random) intercepts α_{0jt} during visit *j* and year *t*, covariates $\boldsymbol{P_{ijt}}$ with a conformable vector of slope parameters α_{ijt}, and errors η_{ijt}. For our purposes, *j* = 1 in this analysis because most BBS (i.e., protocol-compliant) routes are only sampled once per year—thus comprising a detection model structure for single-visit data (Lele et al. 2012, Peach et al. 2017). Additionally, $N_{i,t+1}$ is estimated for each consecutive year *t* + 1 (e.g., *t* = 1, 2, 3, 4 for years 2015, 2016, 2017, and 2018) based on binomially- and Poisson-distributed random variables $S_{i,t+1}$ (i.e., survivors) and $R_{i,t+1}$ (i.e., recruits or gains), respectively—including apparent survival rate φ and recruitment rate γ, implying absolute or constant population dynamics between years (Kéry and Royle 2016, 2021).

In the process (abundance) model, back-transformed covariate effects (i.e., from the estimated log scale) are exponentiated and considered event (incident) rate ratios such that every 1-unit increase in a covariate conveys an associated positive or negative (multiplicative) effect on (i.e., increase or decrease in) REVI abundance when valued either less than or greater than 1.0, respectively—log-scale coefficients equivalent to zero indicate no effect on the event-rate ratio scale (e.g., event-rate ratios comprise multiplicative effects on mean abundance; Hilbe 2011, Kéry and Royle 2016, 2021). In the observation (detection) model, back-transformed covariate effects (i.e., from the estimated logit scale) are inverse logit and interpreted as the expected change in log odds for a 1-unit increase in each covariate (Kéry and Royle 2016, 2021). Finally, multiple parameterizations for population dynamics are available, including "constant" (shown above), "trend," "notrend," and "autoreg" (i.e., autoregressive lag-1) as well as density-dependent dynamics such as Ricker- or Gompertz-logistic growth (i.e., "ricker" and "gompertz," respectively) in the "pcountOpen" function of R's "unmarked" package version 1.0.1 (Fiske and Chandler 2011). For purposes of the candidate models, we considered each of the available parameterizations for population dynamics (i.e., "constant," "trend," "notrend," "autoreg," "ricker," and "gompertz"), and each were estimated using an intercept only structure (e.g., on apparent survival or carrying capacity as well as recruitment or maximum instantaneous population growth).

We applied a negative binomial mixture to account for varied dispersion in REVI route-level counts, assuming a carrying capacity of 200 individuals per BBS route (e.g., reasonably exceeding the maximum count recorded), as is recommended in "pcountOpen" (Fiske and Chandler 2011). We also evaluated stability in the log-likelihoods of null (intercept-only, constant dynamics) models estimated with increasing values of carrying capacity to understand

whether final abundance estimates could be considered stable and well estimated (Fiske and Chandler 2011, Dennis et al. 2015). Misspecifications of system carrying capacity are known to lead to underestimates of total population abundance (Dennis et al. 2015, Hostetler and Chandler 2015); however, model runtimes are highly protracted due to latent-state integration for broad-scale models that include multiple covariates and complex parameterizations of population dynamics (e.g., density-dependent growth)—shortcomings currently precluding sufficient performance assessments of dynamic *N*-mixture models (Dennis et al. 2015, Kéry and Royle 2016, 2021).

We estimated 13 candidate models describing range-wide REVI abundance using the "pcountOpen" function in R's "unmarked" package (Fiske and Chandler 2011). We considered one null (intercept-only, constant dynamics) model and pairs of linear and nonlinear (i.e., allometric mass-scaling) process-level models, such as: (1) linear or allometric constant dynamics, (2) linear or allometric trended dynamics, (3) linear or allometric trendless dynamics, (4) linear or allometric autoregressive lag-1 dynamics, (5) linear or allometric Ricker (logistic) density-dependent dynamics, and (6) linear or allometric Gompertz (logistic) density-dependent dynamics (Fiske and Chandler 2011). Except for the null model, all other candidate models included both linear and quadratic effects of survey effort (hrs) on the observation (detection) level. Linear (traditional) models on the process (abundance) level included linear effects of route-level temperature (ºC), precipitation (mm), temperature-precipitation interaction (ºC*mm), mean canopy cover (%), distance from range core (km), and landscape-metrics PCs 1-3 (unitless). Allometric (mass-scaling) models included the aforementioned linear effects as well as one nonlinear effect of natural-log-transformed (expected) REVI body mass (g) on the process (abundance) level. As route-level abundance (λ) is estimated on the log-link scale, the model

intercept and linearized (coefficient) effect of ln(mass) thus represent the proportionality constant and scaling exponent in a conventional allometric-scaling formula, respectively (i.e., a and b in $Y = a * M^b$; Carbone et al. 2007, White et al. 2007, Rossberg et al. 2008, Hechinger et al. 2011, Kendall et al. 2019). Therefore, as expected REVI body mass changes, the allometric-scaling effect changes nonlinearly with REVI abundance on the original (count) scale.

Model-estimation settings in the "pcountOpen" function of package "unmarked" involved 10000 total iterations and a maximum carrying capacity (K) of 200 individuals with varying population dynamics (e.g., "constant," "trend," "no trend," "autoregressive lag-1," "Ricker-logistic," and "Gompertz-logistic") as well as Nelder-Mead optimization of parameter effects to their maximum-likelihood estimates (Fiske and Chandler 2011). We assumed a negative binomial mixture and estimated apparent survival (or carrying capacity, depending on the choice of dynamics) and recruitment (or maximum instantaneous population growth, depending on the choice of dynamics) rates as intercept-only. We estimated count dispersion in the negative binomial mixture using only an intercept. To expedite model fitting, we Z-scored (i.e., standardized) all covariates in the abundance- and observation-level models, except for body mass, which was kept unstandardized for use in allometric-scaling models (i.e., estimating an effect of ln(mass) on route-level abundance, λ).

We chose to model parameters for population dynamics and dispersion as intercept-only because we lacked associated *a priori* hypotheses, and there was no supporting information in the literature regarding such aspects of REVI population ecology and count-dispersion processes. However, we predicted directions of effects for each abundance and detection covariate based on available literature. First, we expected that increased temperatures would negatively (directly and indirectly) affect, while increased precipitation would positively (directly and indirectly) affect,

REVI and its insect prey (McKellar et al. 2013, Imlay et al. 2018, Wysner et al. 2019). We expected that the interaction of temperature and precipitation would affect REVI and its insect prey (Visser et al. 2006, Schöll et al. 2016); however, we did not anticipate potential direction(s) of this effect. Second, we predicted that increased canopy cover would positively affect REVI abundance (Crawford et al. 1981), and we also expected that increased distance between BBS routes and the core of REVI range would have a negative effect on abundance (Brown 1984, 1995, Brown et al. 1995). Third, we did not anticipate the direction or magnitude of effects of landscape-metric PCs; however, we suspected that one or more PCs would associate with REVI abundance based on species affinity for large, diverse, and intact forests (Cimprich et al. 2020), and PC-axis factor loadings would enhance interpretations of contextual landscape effects. With respect to the observation-level model, we predicted that REVI detection would increase with increased survey effort, but that association would later diminish with greater amounts of effort, wherein observers surveyed along routes from dawn until closer to midday (e.g., when bird activity is typically reduced; Pardieck et al. 2014, Sauer et al. 2017, Sauer et al. 2019).

To choose among candidate models, we computed Akaike's (second-order) Information Criterion (AICc) adjusted for finite sample size and considered models < 2.0 ΔAICc of the top-ranked model as competing (Burnham and Anderson 2002). Because no goodness-of-fit tests exist for dynamic *N*-mixture models (Fiske and Chandler 2011), we evaluated multivariate (i.e., route-year) Pearson residuals and resultant population abundance estimates and uncertainty of the selected (final) model as indicators of model performance. We first checked for remaining spatial autocorrelation in the selected model by examining multivariate spline correlograms (i.e., pairwise-location [i.e., route-year residual] correlations [i.e., Moran's *I* statistic; Pebesma and Bivand 2005, Bivand et al. 2013] as a function of distance, analogous to a Mantel test) of the

Pearson residuals using R's "ncf" package version 1.2-9 (Moll et al. 2016, Moll et al. 2018, Bjornstad 2020). In addition to evaluating model residuals, we also used the "ranef" and "bup" functions of the "unmarked" package to generate Empirical Best Unbiased Predictions (EBUPs) of route-year REVI abundance, based on the posterior modes of route-level latent abundance summarized by year and estimated using empirical Bayes methods (Laird and Louis 1987, Carlin and Louis 1996, Royle and Dorazio 2008). While existing EBUP methods may underestimate variance of the posteriors for latent abundance due to lacking capacity to account for hyperparameter (e.g., route-level abundance, λ) uncertainty, basic empirical Bayes approaches estimate final parameter values from the observed data following Bayes' theorem, parameter values combined to generate estimates of latent abundance (Carlin and Louis 1996). To visualize these results, we produced boxplots of the posterior mean (route-year, total) abundances with their 95% confidence intervals.

We generated range-wide REVI population abundance estimates and extrapolated beyond the spatial limits of the filtered BBS routes to compare model estimates with those of another broad-scale monitoring program—one reliant on citizen-science surveys—*e*Bird (Sullivan et al. 2009, Fink et al. 2020). We interpolated raster surfaces across REVI range for each final model predictor, using a procedure that was identical to interpolation of REVI body mass (i.e., described above). Results of these interpolations produced continuous surfaces of predictor values projected across REVI range at a 100-km spatial resolution (i.e., identical to that of our REVI body mass raster).

Finally, we used the coefficient estimates from the final model to extrapolate (mean ± 95% CI) REVI abundance estimates range-wide using raster calculator methods in R. Because BBS data may be biased toward one or both member(s) of a REVI breeding pair at some routes

over time (Blancher et al. 2013, Will et al. 2019), we adjusted final range-wide estimates using published pair-adjustment factors (Rosenberg et al. 2017, Stanton et al. 2019) in five stages. Specifically, we multiplied final abundance estimates and their 95% confidence limits by (a) 1.0, (b) 1.25, (c) 1.5, (d) 1.75, and (e) 2.0, individually—adjustments that assume some portion of the adult population is not recorded by BBS observers (e.g., due to time of day and other sources of uncertainty; Blancher et al. 2013, Will et al. 2019). For example, a pair-adjustment factor of 1.0 assumes that both sexes are equally likely to be detected and recorded by observers, whereas a factor of 2.0 assumes that 100% of observations are biased to one sex (e.g., singing territorial males), and 25-75% of observations are biased to one sex for multipliers in between (Rosenberg et al. 2017, Stanton et al. 2019). Expecting incongruence between allometry-informed estimates and citizen-science-informed estimates (e.g., finer descriptions of continental abundance patterns in allometry-informed estimates), we report multiplier-adjusted abundance estimates in five maps and use them to compare with a REVI range-wide abundance map generated using *e*Bird citizen-science data (Sullivan et al. 2009, Fink et al. 2020).

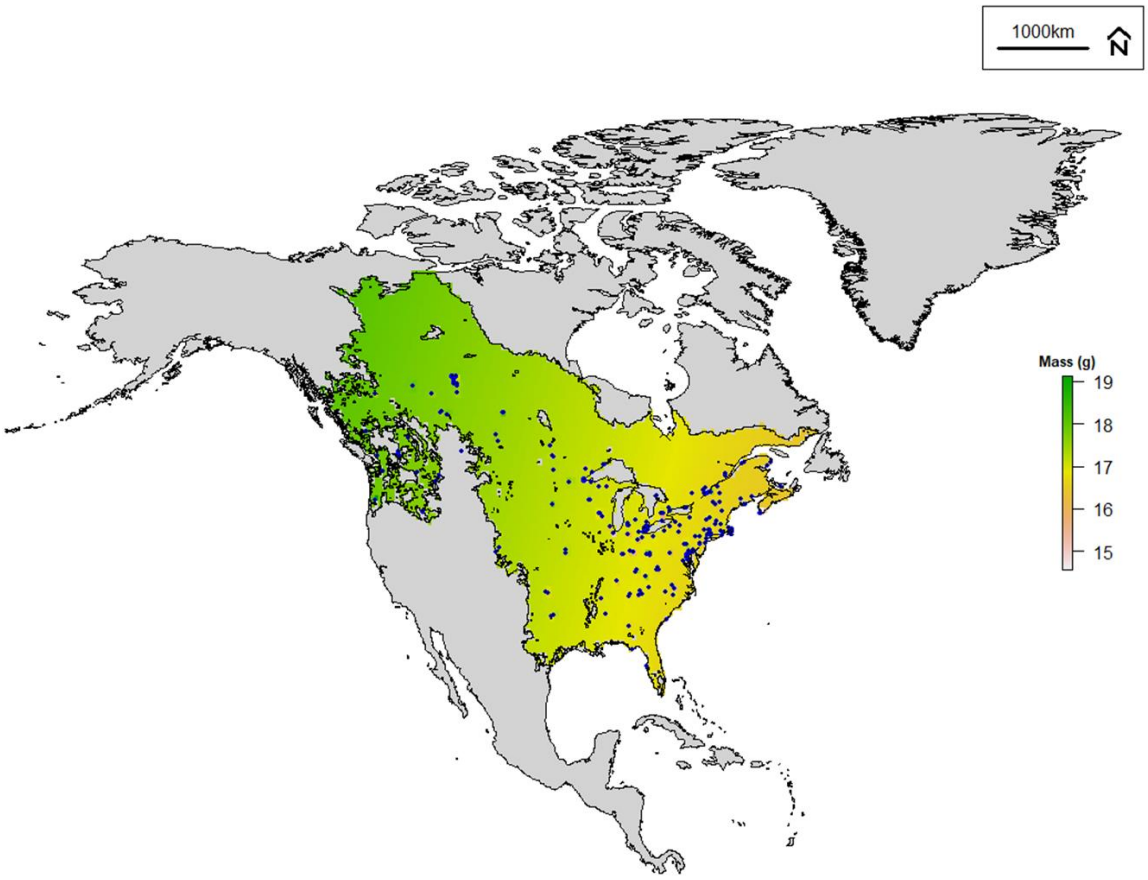
Results

Interpolation of species body mass for use in allometric-scaling models

From the U.S. Geological Survey's BBL, we received 3146 observations of REVI body mass recorded across 229 banding stations. Grand mean (± SD) mass equaled 17.08 ± 1.66 g (range: 9.2-29.4 g, n = 3146), wherein male mean (± SD) mass equaled 16.65 ± 1.70 g (range: 9.2-26.6 g, n = 447), female mean (± SD) mass equaled 17.04 ± 1.74 g (range: 11-26 g, n = 386), and unknown-sex mean (± SD) mass equaled 17.17 ± 1.63 g (range: 9.5-29.4 g, n = 2313). Aggregated (station-level) mean (± SD) mass equaled 17.03 ± 1.08 g (range: 13-23.9 g, n = 229 stations). Universal kriging of historic BBL records confirmed that REVI body mass follows an

east-west, smaller-larger gradient across North America (Figure 4.2), and this interpolation estimated a grand mean (± SE) mass of 17.27 ± 0.005 g (range: 14.57-19.13 g, *n* = 8540 grid cells).

Figure 4.2. Interpolated mean (expected) body mass (g) of red-eyed vireo universally kriged to a 100-km (spatial) resolution using records of red-eyed vireo body mass measured at bird-banding stations (i.e., *n* = 3146 total observations recorded annually May-August 2014-2018 and aggregated to site-level means at 229 sites; blue points) across continental North America. Longitudinal pattern in the kriged predictions follow expectations of an east-west, smaller-larger gradient in red-eyed vireo body size and correlated mass (Ridgway 1904). Bird-banding data were retrieved from the U.S. Geological Survey's Bird Banding Laboratory.



Allometric-scaling models, including important covariate effects and population dynamics

We filtered the BBS database from 8708 surveys that recorded REVI (i.e., collecting data based on multiple, different protocols and 1-6 visits per route over time) to 3795 surveys at 759 routes that followed official BBS sampling protocol (Pardieck et al. 2014, Sauer et al. 2019) and were

visited at least once annually during May-August 2014-2018. Of 13 candidate models, the top-ranked model carried all of the AICc weight and consisted of an allometric-scaling effect of REVI body mass plus linear effects of other covariates on route-level abundance (Table 4.3). The top-ranked model also assumed Gompertz (logistic) density-dependent growth at BBS routes over time, suggesting (1) a constant linear decrease in the maximum instantaneous growth rate, r_{max}, as the natural logarithm of population abundance increases and that (2) density dependence is strongest at small population abundances, yet its effect becomes less pronounced with abundance increases (e.g., dynamics are overcompensatory at high values of r_{max} ; Hostetler and Chandler 2015).

Table 4.3. Model selection table, including Akaike's (second-order) Information Criterion (AICc), ΔAICc, AICc weight, and number of parameters (*k*) for 13 candidate models. Candidate Model portrays the predictor(s) in each model; all observation-level (detection) models included the same covariates, both linear and quadratic effects of survey effort. Abundance covariates include allometrically scaled body mass, local weather, forest canopy cover, core-periphery distance, and principal component (PC) quantities of aggregate landscape metrics (see Tables 4.1 and 4.2).

Candidate Model	**Dynamics**[†]	**AICc**	**ΔAICc**	**AICc Weight**	***k***
Allometric	Gompertz-logistic	27914.66	0.00	1.00	16
Allometric	Ricker-logistic	27928.73	14.07	0.00	16
Linear	Gompertz-logistic	27930.23	15.57	0.00	15
Linear	Ricker-logistic	27944.40	29.74	0.00	15
Allometric	Trend	27976.01	61.34	0.00	15
Allometric	AR1	27978.21	63.54	0.00	16
Linear	Trend	27991.70	77.04	0.00	14
Linear	AR1	27993.94	79.27	0.00	15
Allometric	Constant	31123.76	3209.10	0.00	16
Linear	Constant	31138.10	3223.44	0.00	15
Allometric	No Trend	31143.60	3228.94	0.00	15
Linear	No Trend	31156.56	3241.90	0.00	14
Intercept-only (null)	Constant	31617.91	3703.25	0.00	5

[†]Population dynamics' settings as described in the "pcountOpen" function of R's "unmarked" package (Fiske and Chandler 2011).

Increases in body mass significantly scaled 0.45, or negatively (i.e., coefficient < 1.0; Hilbe 2011), with REVI abundance on the event-rate ratio scale (i.e., -0.801 on the log scale; Tabel 4.4). Increases in temperature also significantly and negatively associated with abundance (Table 4.4). Precipitation, and the interaction between temperature and precipitation were not significantly related to REVI abundance (Table 4.4). Increases in forest canopy cover associated both significantly and positively (i.e., coefficient > 1.0) with REVI abundance, whereas increasing distance from the range core to BBS routes associated significantly and negatively with abundance (Table 4.4).

The first three principal component (PC) axes explained 86% of the variation in landscape composition and configuration metrics across REVI range. Based on the factor loadings of individual axes (Table 4.5), PC1 represented a gradient of increasingly homogeneous, connected, and neighboring patches, whereas PC2 represented a gradient of increasingly small, dense, and neighboring patches. PC3 represented a gradient of increasingly dense and diverse patches (Table 4.5). While landscape metric PC1 did not relate to REVI abundance, increases in landscape-metrics PC2 and PC3 significantly and negatively related to REVI abundance (Table 4.4). Increases in PC2 correlated positively with total edge density, Euclidean (mean) nearest-neighbor distance between patches, and patch density and correlated negatively with patch (mean) area, contagion, total number of patches, patch richness, and Shannon diversity index (Table 4.5). Increases in PC3 correlated positively with Euclidean (mean) nearest-neighbor distance between patches, patch density, patch richness, and Shannon diversity index as well as correlated negatively with patch (mean) area, contagion, total edge density, and total number of patches (Table 4.5).

Table 4.4. Abundance- and observation-level effect estimates of the top-ranked dynamic *N*-mixture model reported on the event-rate ratio (i.e., inverse-log or exponentiated) and inverse-logit scales, respectively. Exponential-scale intercept estimates for maximum instantaneous population growth rate (r_{max}), carrying capacity (ω, also known as K), and dispersion (θ), including their associated point estimates, standard errors, 95% confidence intervals, *z* scores, and *p*-values are reported. Covariates, including allometrically-scaled (i.e., natural-logarithm transformed) body mass, *Z*-scored (i.e., standardized) local weather, forest canopy cover, core-periphery distance, and principal component (PC) quantities of aggregate landscape metrics, are described in Tables 4.1 and 4.2. Bolded *p*-values indicate statistically significant effects (i.e., α = 0.05).

Parameter	**Estimate (± SE)**	**95% CI**
Abundance (λ)		
Intercept	2389.884 (± 2.692)	**(343.132, 16649.481)**
ln(Body Mass)	-0.801 (± 0.190)	**(-1.173, -0.428)**
Temperature	0.656 (± 1.037)	**(0.611, 0.704)**
Precipitation	1.045 (± 1.041)	(0.966, 1.130)
Temperature*Precipitation	0.955 (± 1.027)	(0.906, 1.007)
Canopy Cover at 39-km	1.550 (± 1.039)	**(1.437, 1.673)**
Distance to Core of Range	0.917 (± 1.041)	**(0.848, 0.992)**
LSM PC1 at 39-km	0.949 (± 1.036)	(0.884, 1.018)
LSM PC2 at 39-km	0.873 (± 1.035)	**0.817, 0.934**
LSM PC3 at 39-km	0.913 (± 1.033)	**(0.853, 0.973)**
Population Growth Rate (r_{max})		
Intercept	0.144 (± 1.134)	**(0.113, 0.185)**
Carrying Capacity (ω)		
Intercept	66.686 (± 1.097)	**(55.583, 80.030)**
Detection (p)		
Intercept	0.561 (± 0.507)	**(0.548, 0.575)**
Effort	0.499 (± 0.504)	(0.492, 0.507)
Effort^2	0.494 (± 0.502)	**(0.491, 0.498)**
Dispersion (θ)		
Intercept	2.104 (± 0.055)	**(0.636, 0.852)**

Table 4.5. Factor loadings of each principal component (PC) with landscape metrics (see Table 4.2). "Factor Loading" indicates the correlation coefficient per landscape metric linearly associated with the direction of each PC. Absolute-valued loadings > 0.25 are highlighted in bold and used to characterize gradients of variation in associated landscape metrics.

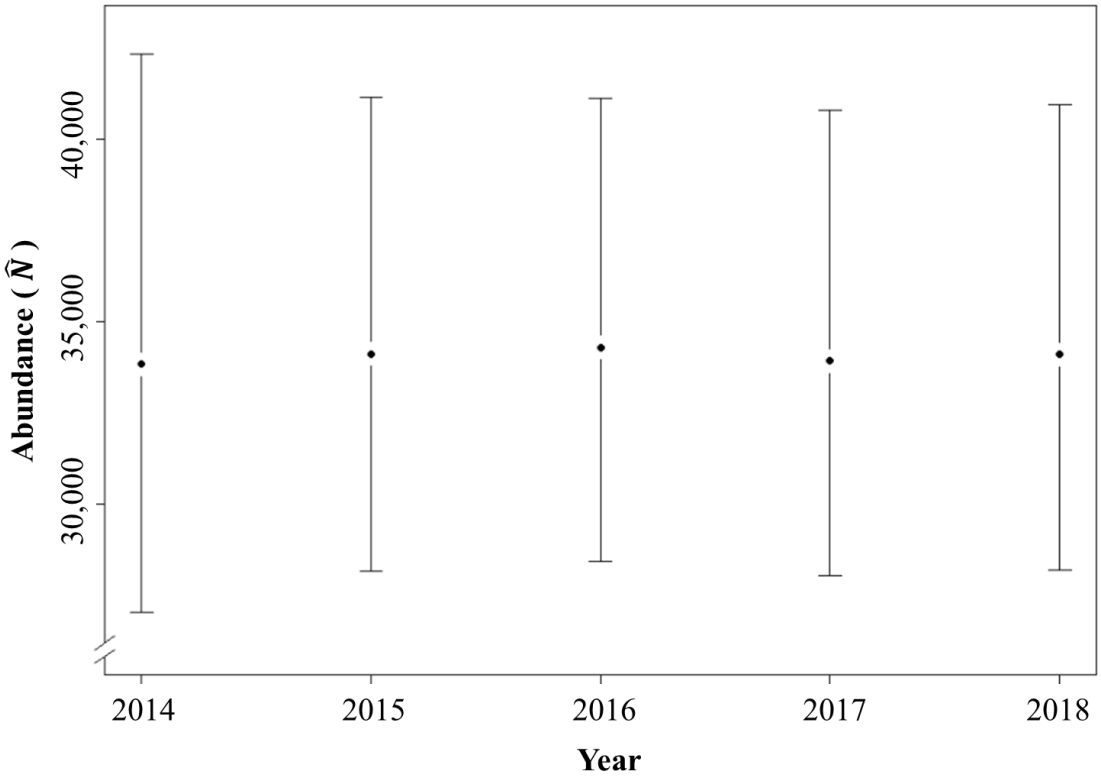
PC	Variance Explained	Landscape Metric	Factor Loading
1	48%	AREA_MN	0.195
		CONTAG	**0.492**
		ED	**-0.480**
		ENN_MN	**0.286**
		NP	**-0.449**
		PD	-0.056
		PR	-0.003
		SHDI	**-0.451**
2	25%	AREA_MN	**-0.549**
		CONTAG	-0.064
		ED	0.026
		ENN_MN	**0.460**
		NP	-0.085
		PD	**0.626**
		PR	**-0.286**
		SHDI	-0.035
3	13%	AREA_MN	-0.106
		CONTAG	-0.011
		ED	-0.214
		ENN_MN	0.051
		NP	-0.178
		PD	**0.261**
		PR	**0.851**
		SHDI	**0.341**

In the observation (detection) level model, increases in hours of survey effort did not significantly associate with REVI detection on the log-odds scale however, the quadratic effect of effort both significantly and positively related to detection on the log-odds scale, indicating that REVI detection waned as survey effort increased (e.g., likely beyond the time of peak bird activity). Finally, both maximum instantaneous population growth and dispersion rate varied significantly and positively over time (e.g., suggesting limited REVI population growth [i.e., $r_{max} < 1.0$] and overdispersion [i.e., $\theta > 1.0$] in REVI counts over time, respectively), and route-level carrying capacity was statistically significant and numbered ~67 (95% CI: 56-80) individuals (Table 4.4).

Extrapolated species abundance estimates contrasting other monitoring programs

The top-ranked (i.e., allometric with Gompertz-logistic growth; Table 4.3) model predicted, within sample (i.e., across filtered BBS routes), a posterior mean abundance of 33,835 (95% CI: 27,022-42,338) individuals in 2014, 34,119 (95% CI: 28,148-41,177) individuals in 2015, 34,290 (95% CI: 28,424-41,124) individuals in 2016, 33,933 (95% CI: 28,030-40,814) individuals in 2017, and 34,100 (95% CI: 28,195-40,955) individuals in 2018 (Figure 4.3). Additionally, grand mean (± SE) detection probabilities were 0.56 ± 0.01 (range: 0.44-0.56 and 95% CI: 0.54-0.57). Estimated REVI abundances by year illustrates population stability at filtered BBS routes over time, following a mean (± SE) maximum instantaneous population growth rate of 0.144 (± 1.134; i.e., suggesting little growth over time) on the exponential scale (Table 4.4).

Figure 4.3. Interpolated mean abundance (± 95% confidence intervals) of red-eyed vireos recorded at 759 Breeding Bird Survey routes across continental North America. These estimates are derived from a single-species multi-season *N*-mixture model, assuming a negative binomial mixture and Gompertz-logistic (recruitment) dynamics as well as open population states between sampling seasons, respectively (Dail and Madsen 2011, Fiske and Chandler 2011).



REVI population estimates based on the top-ranked model and extrapolated range-wide suggest a mean abundance of 7.526 million (95% CI: 1.160-49.843 million) individuals, following a pair-adjustment factor of 1.0 (Figure 4.4A). Assuming a pair-adjustment factor of 1.25, estimated mean abundance is 9.408 million (95% CI: 1.450-62.304 million) individuals (Figure 4.4B). Estimated mean abundance totals 11.289 million (95% CI: 1.740-74.765 million) individuals, with a pair-adjustment factor of 1.5 (Figure 4.4C). Assuming a pair-adjustment factor of 1.75, estimated mean abundance equals 13.171 million (95% CI: 2.030-87.226 million) individuals (Figure 4.4D). Finally, estimated mean abundance totals 15.052 million (95% CI: 2.320-99.686 million) individuals, following a pair-adjustment factor of 2.0 (Figure 4.4E).

Figure 4.4. Extrapolated mean abundance of red-eyed vireo across North America, based on data from the Breeding Bird Survey during 2014-2018. We generated these predictions using universally kriged (raster) datasets of the input predictor variables at a 100-km (spatial) resolution and their associated coefficient (effect and SE) estimates from a single-species multi-season *N*-mixture model, assuming a negative binomial mixture and Gompertz-logistic (recruitment) dynamics as well as open population states between sampling seasons, respectively (Dail and Madsen 2011, Fiske and Chandler 2011). Estimates based on an assumed (A) pair-adjustment factor of 1.0 (i.e., both sexes are equally likely to be detected and recorded by observers), (B) pair-adjustment factor of 1.25 (i.e., 25% of observations are biased to one sex), (C) pair-adjustment factor of 1.5 (i.e., 50% of observations are biased to one sex), (D) pair-adjustment factor of 1.75 (i.e., 75% of observations are biased to one sex), and (E) pair-adjustment factor of 2.0 (i.e., 100% of observations are biased to one sex; Stanton et al. 2019).

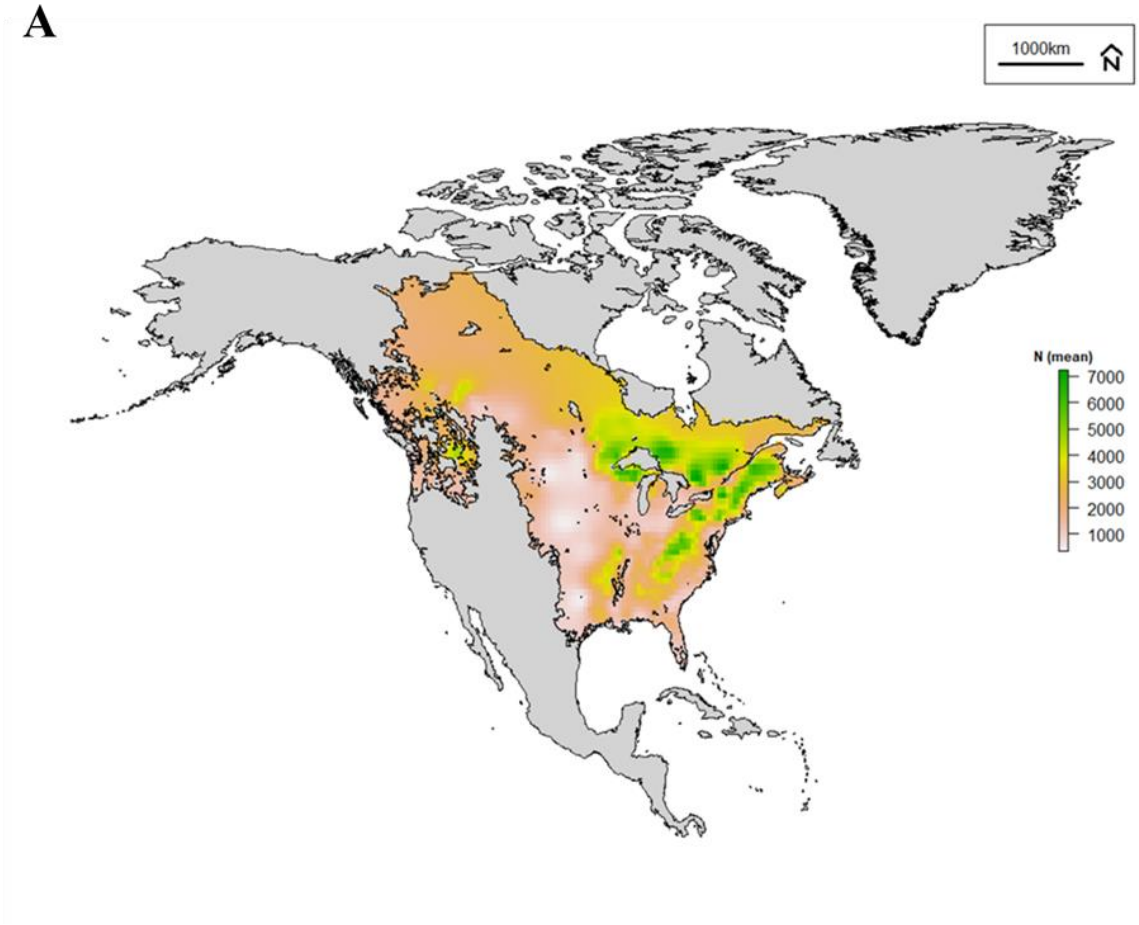
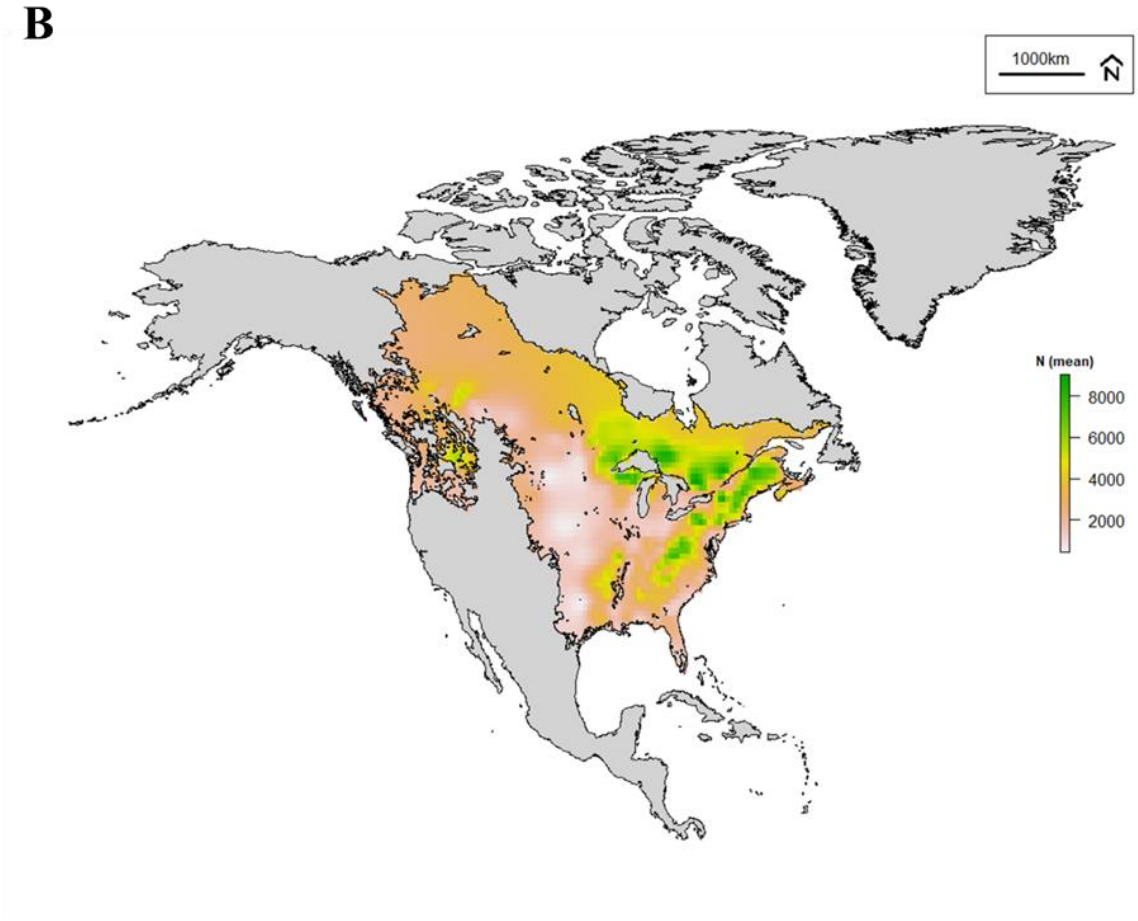


Figure 4.4 (cont'd)



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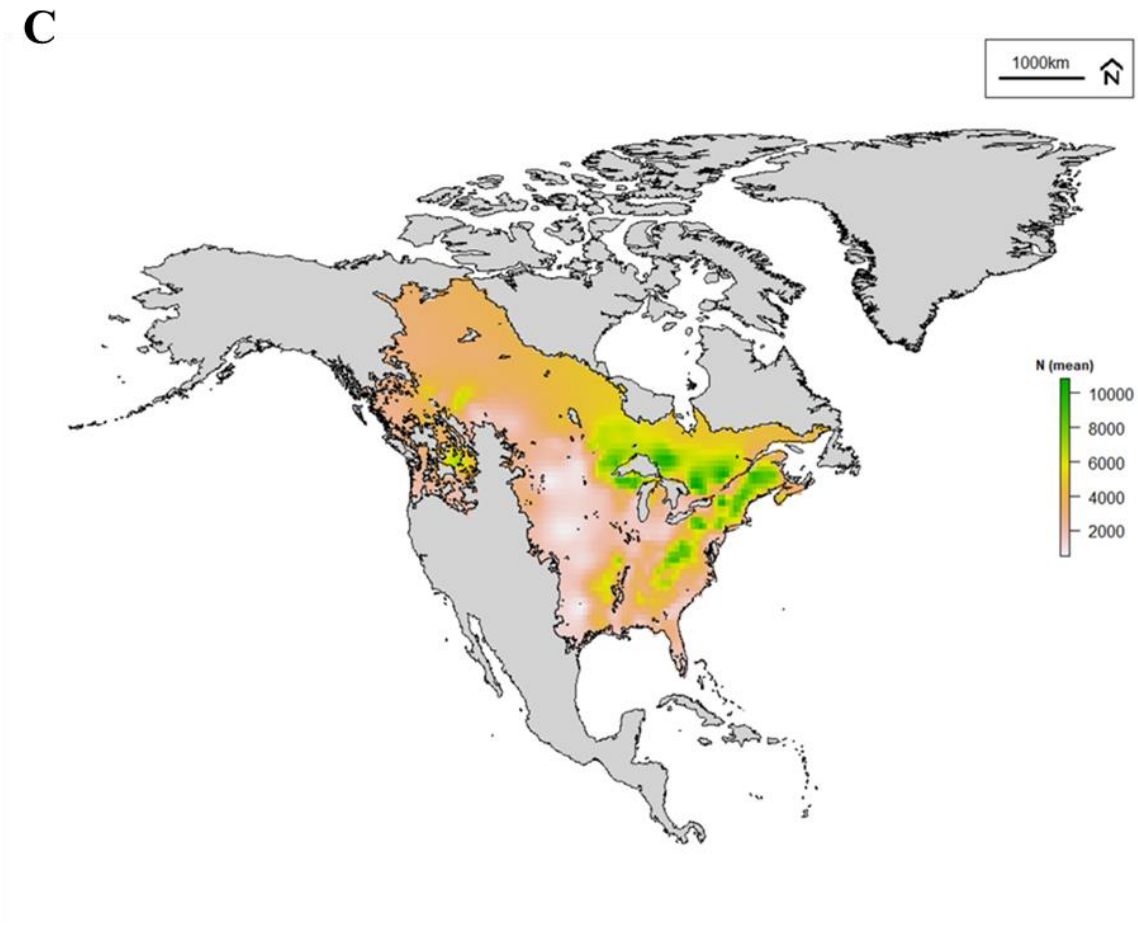

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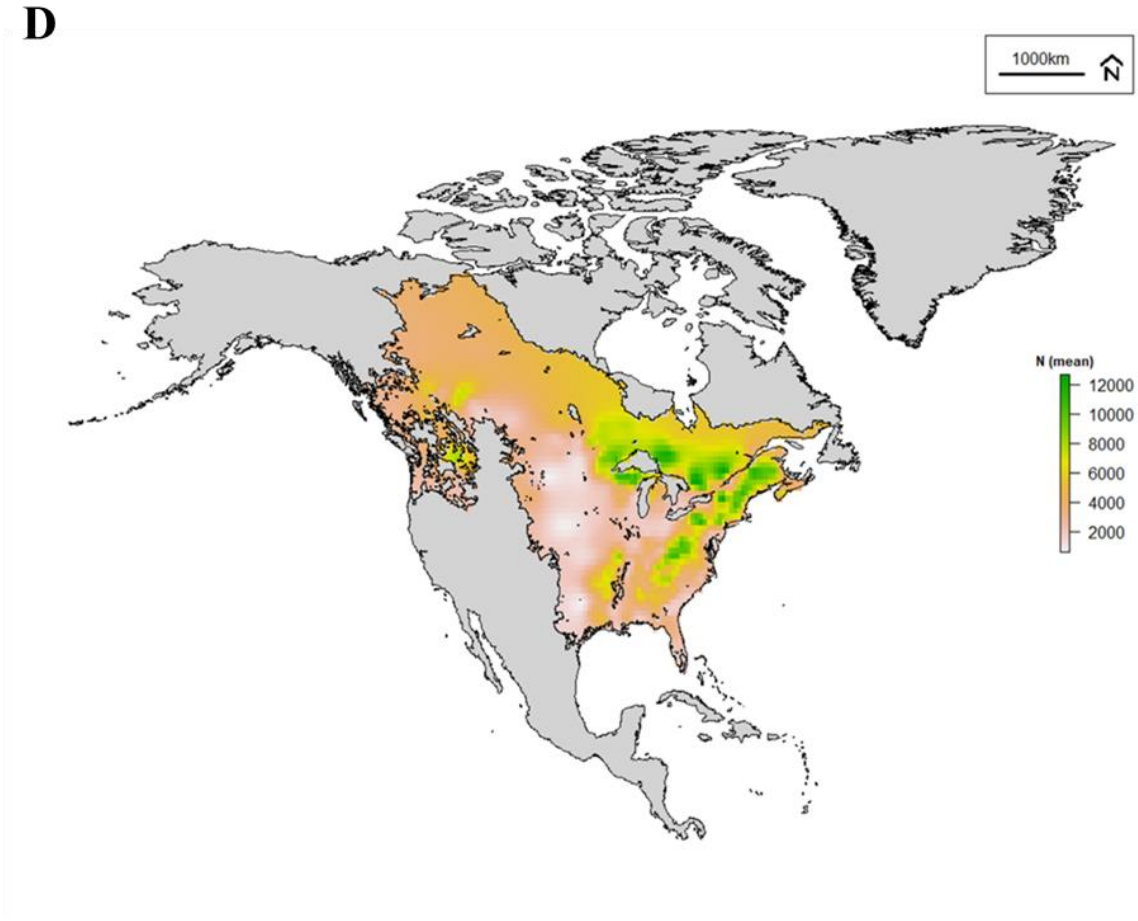

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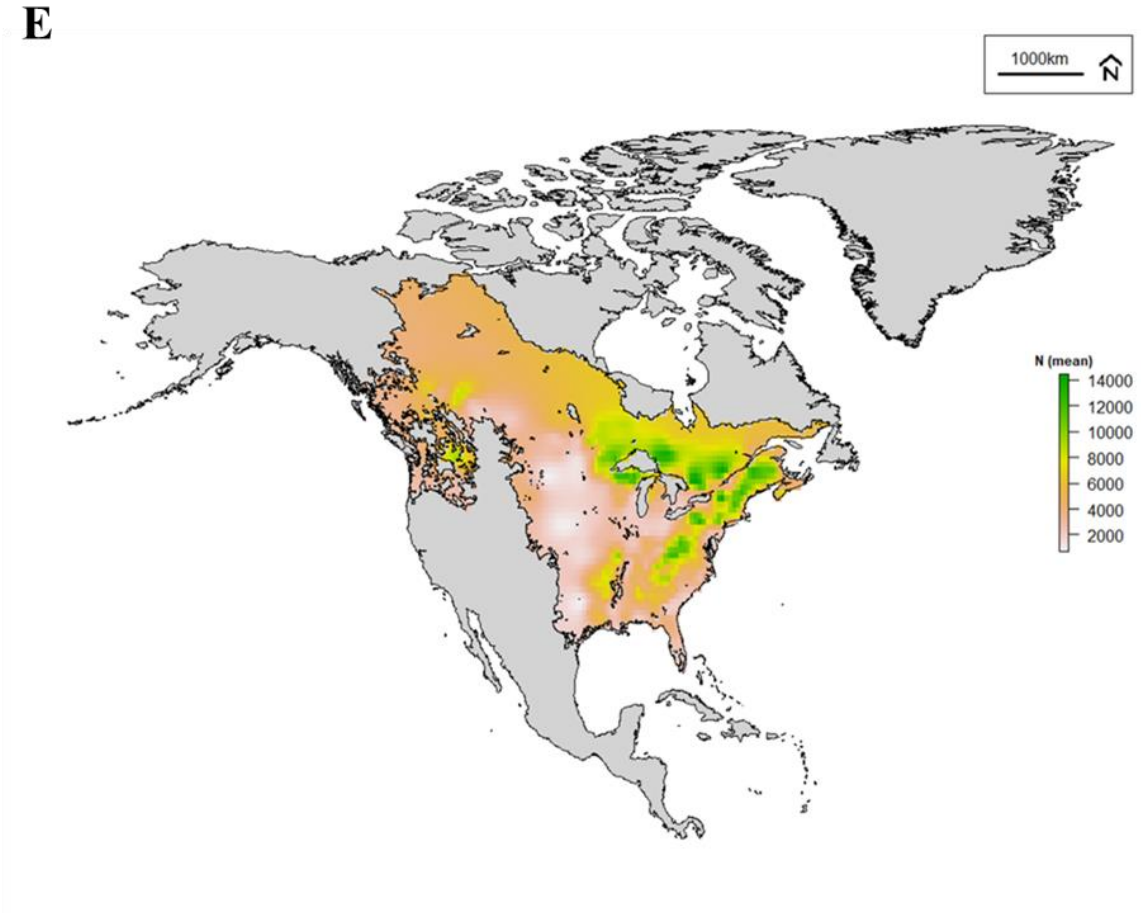


When viewing resultant estimates compared to patterns generated using historic citizen-science *e*Bird data (Figure 4.5), estimates derived from our top-ranked model (i.e., regardless of pair-adjustment factors) consistently highlight the following areas as locations that support the greatest numbers of REVI in North America, the (a) northern Rocky Mountains in British Columbia and Alberta, CAN, (b) central-southern Manitoba, Ontario, and Quebec, CAN, (c) northern Minnesota, Wisconsin, and Michigan, USA, (d) eastern Missouri and Arkansas, USA, and (e) Appalachian Mountain corridor throughout the eastern USA and southeastern CAN. In comparison, modeled estimates based on citizen-science *e*Bird data suggest similar range-wide abundance patterns from east to west, albeit on much smaller count scales (i.e., 0-4 individuals detected by an observer at the optimal time of day; Fink et al. 2020). Despite contrasts between

our model's range-wide abundance estimates and those of *e*Bird, our top-ranked model sufficiently accounts for spatial autocorrelation in REVI counts at filtered BBS routes (Figure 4.6).

Figure 4.5. Predicted abundance of red-eyed vireo across North and South America as generated using *e*Bird records collected during 2005-2019 (Fink et al. 2020) for comparison with estimates displayed in Figures 4.4-4.8. The original (unmodified) figure is reprinted here with reproduction permission of the Cornell Lab of Ornithology.

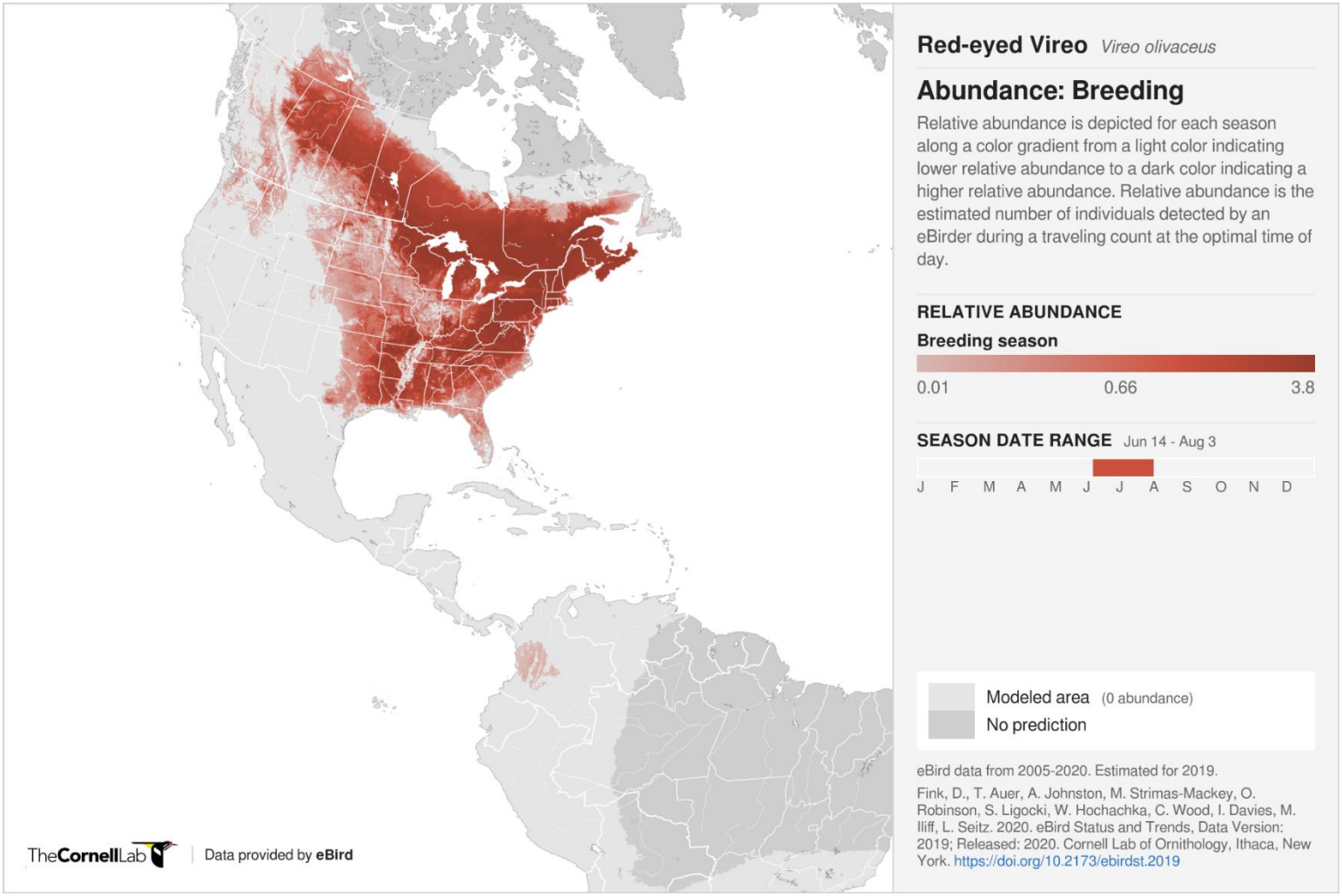
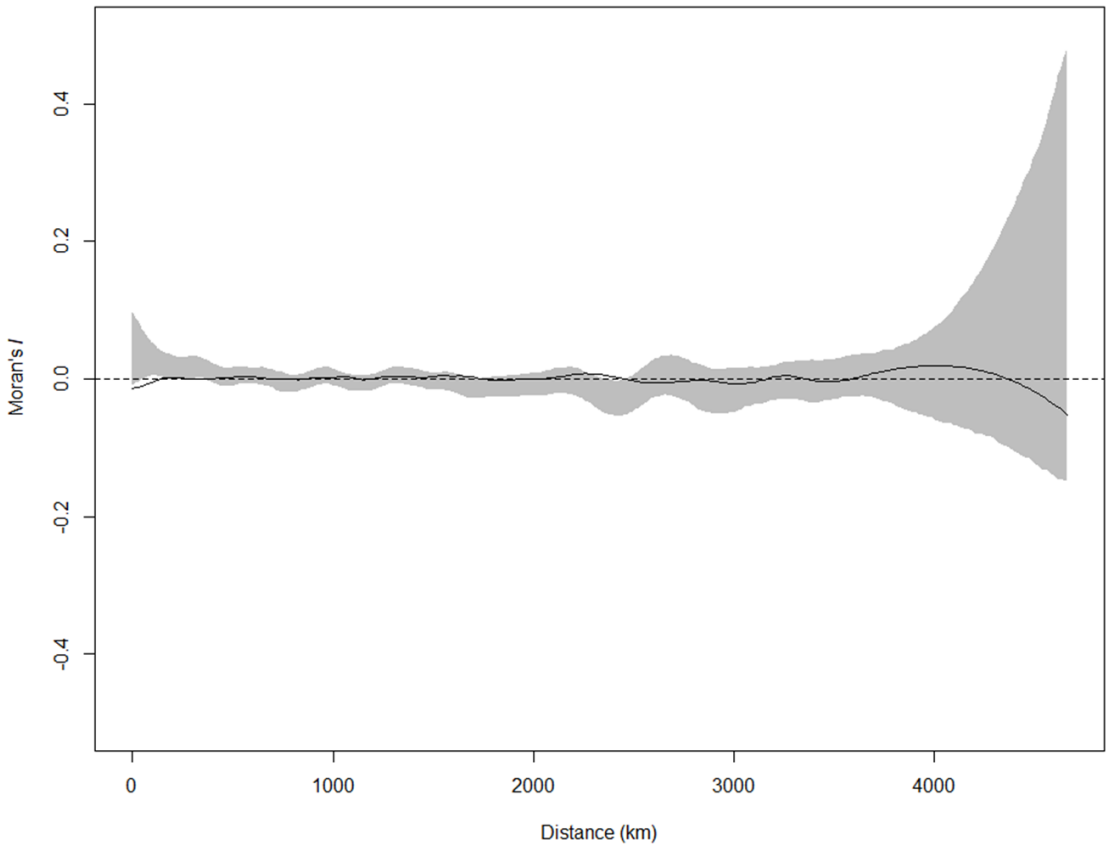


Figure 4.6. Spline correlograms of multivariate (i.e., multi-season) Pearson residuals estimated per BBS route per year during 2014-2018. Moran's *I* indicates the pairwise-location correlation coefficient as it changes with increasing distance of separation between survey routes, where the mean (solid line) and 95% confidence bands (gray) are displayed. Confidence bands consistently overlapping with Moran's *I* = 0 indicates that spatial autocorrelation in abundance (i.e., across years and among survey routes) is sufficiently accounted for by the top-ranked model, which is summarized in Table 4.3.



Discussion

We demonstrated utility of dynamic *N*-mixture models that incorporate both linear (covariate) and nonlinear (allometric-scaling) effects for estimating range-wide abundance of birds sampled by broad-scale monitoring programs such as the BBS in North America. The top-ranked model included allometric-scaling and linear covariate effects on REVI abundance, while controlling for some aspects of imperfect species detection as well as density dependence in recruitment at BBS routes over time. This result answers our main research question (i.e., "do allometric

relationships and traditional ecological covariates better inform models of abundance range-wide than models excluding mass-abundance scaling?”) in the affirmative.

Allometric-scaling models outrank traditional linear models and generate unique patterns

Derived estimates of REVI abundance from the top-ranked, allometry-inclusive model indicated stability in the population across BBS routes over time; however, range-wide (extrapolated) abundance estimates were underestimated by 30-80 million individuals when compared to the Partners in Flight’s Population Estimates database (i.e., which also uses BBS data, but from 2006 to 2015; Will et al. 2019). Such discrepancies were based on the upper bounds of the top-ranked model’s 95% confidence intervals and range of pair-adjustment factors we considered. Broad-scale patterns in REVI range-wide estimates reflected those of another continental monitoring program (i.e., *e*Bird; Sullivan et al. 2009); however, our work presented range-wide (total) abundance patterns at a broader spatial resolution; for instance, at 100-km in the current study compared to 2.96-km in Fink et al. (2020).

Our abundance estimates revealed highest total REVI numbers in the Rocky Mountains of CAN and Great Lakes Region near southern CAN as well as the Appalachian and Ozark Mountain areas of the USA. Additionally, *e*Bird-based estimates suggest that northern areas of Alberta, Saskatchewan, Manitoba, and Ontario, CAN as well as areas of the southeastern, eastern-coastal, and upper-midwestern USA comprise REVI abundance hotspots (Fink et al. 2020). Representing a novel approach for the state-space analysis toolbox, allometric (mass-abundance) scaling relationships estimated alongside effects of traditional ecological covariates (i.e., while accounting for imperfect observer detection) produce range-wide abundance maps that identify broad-scale species strongholds beyond (relative) abundance estimates based on citizen-science counts of species (Sullivan et al. 2009, Fink et al. 2020).

Allometric-scaling model effects, interpretations, and a priori expectations

Universally kriged interpolations of BBL body mass records successfully corroborated a known smaller to larger body size gradient in REVI body mass that runs east to west across North America. We predicted that route-level (expected) mass would scale nonlinearly with abundance to the -0.75 power, as is commonly reported in vertebrate studies of mass-abundance allometry (Hechinger et al. 2011). After accounting for variation in other (linear) covariate effects, REVI body mass scaled -0.801 (± 0.190, mean ± SE; 95% CI: -1.173, -0.428) with route-level abundance on the log scale (i.e., scaling 0.45 on the event-rate ratio scale), which was significantly different from zero on the log scale (i.e., from 1.0 on the event-rate ratio scale; e.g., event-rate ratios comprise multiplicative effects on mean abundance, and ratios < 1.0 indicate decreases in the dependent variable; Hilbe 2011). Despite some slight imprecision in this allometric-scaling effect, resulting in a lower confidence bound < −1.0, the 95% confidence interval included -0.75, suggesting that measurement error in REVI body mass and other (linear) model covariates may be reducing the precision of this effect (Lovegrove 2000, Bokma 2004, Carroll et al. 2006). Regardless of this imprecision, it is noteworthy that our top-ranked model retrieved theoretically valid values for mass-abundance scaling, especially considering inputs on a continental scale and associated with other model covariates subject to observation uncertainties of their own (e.g., we universally kriged historic body mass and downloaded weather variables at a 100-km and 1-km spatial resolution, respectively).

We expected that increased temperatures and route-to-core distances would each have a negative effect on REVI abundance, and results of our top-ranked model confirmed these expectations. Corroborating expectations under the core-periphery hypothesis (Brown 1984, 1995), as distance from range core increased, REVI abundance decreased accordingly.

Specifically, expected REVI abundance significantly (i.e., $p < 0.05$), though slightly, decreased by -0.086 on the log scale or 0.917 on the event-rate ratio scale, which suggests an ~8.3% decrease in mean abundance for every unit increase in route-start distance from range core. Regarding temperature, many bird species and other wildlife respond negatively to global climate warming (Jetz et al. 2007, Pörtner et al. 2021), and bird communities may experience increased turnover due to changing species-patch colonization and extinction rates related to higher maximum and minimum temperatures and decreased precipitation (i.e., dry conditions; Jarzyna et al. 2015). We also predicted that increased precipitation and canopy cover (e.g., influencing fine-scale temperatures and food resources; Marshall and Cooper 2004, Visser et al. 2006, Schöll et al. 2016) would positively affect REVI abundance (Crawford et al. 1981), and model results confirmed these predictions; however, only canopy cover (and not precipitation) significantly associated with route-level abundance. Additionally, we anticipated that the temperature-precipitation interaction would have a noteworthy effect on abundance, and although the estimated association was negative, it was not statistically different from zero on the log scale.

Only landscape-metric PC2 and PC3 significantly associated with route-level abundance, and factor loadings suggested that PC2 and PC3 represented gradients of (a) landscapes with smaller, fewer, less connected, and less diverse REVI-habitat patches to larger, more connected and homogenous patches, and (b) landscapes with smaller, less connected, and more isolated, but more diverse, REVI-habitat patches with reduced edge to larger, more connected, and less diverse patches with high amounts of edge, respectively. In other words, as REVI habitat patches were smaller and less connected, route-level REVI abundance significantly decreased. Thus,

larger, more connected, and densely configured patches positively related to REVI abundance on broad scales (Cimprich et al. 2020).

Allometric-scaling model dynamics, comparisons with other estimates, and analysis limitations

The top-ranked model indicated that: (1) allometric (mass-abundance) relationships paired with other (linear) covariates and population dynamics can, in fact, be used to estimate spatially-explicit abundance, and (2) patterns in our extrapolated (range-wide) abundance estimates for REVI resembled, though differed in total abundance and scale-defined patterns from, existing abundance products for REVI informed by citizen-science *e*Bird (Sullivan et al. 2009, Fink et al. 2020). With respect to uncertainty in our extrapolated abundance results, the top-ranked model underestimated range-wide abundance by 30-80 million individuals for pair-adjustments of 1.0 and 2.0, respectively, and contrasted with range-wide estimates retrieved from Partners in Flight's Population Estimates database (i.e., based on BBS data from 2006 to 2015), which reports (annual mean) abundance totals of 130 million (95% CI: 120-140 million) individuals across North America (e.g., based on subtracting upper 95% confidence bounds for 1.0 and 2.0 pair-adjusted estimates from 130 million individuals; Will et al. 2019). Unlike important sources of uncertainty addressed by Partners in Flight's species assessments (Blancher et al. 2013, Stanton et al. 2019, Will et al. 2019), our models did not account for the following BBS-biasing conditions: (a) regional (i.e., Bird Conservation Region; BSC and NABCI 2014) variation in BBS counts not captured by model covariates (e.g., degree of urbanization and interspecies dynamics), (b) proportion of the species range covered by BBS routes, (c) detectability variation among BBS observers, especially novices, or (d) amount of (route) area surveyed and distance-to-subject effects on detection probabilities.

We suspect that sizable uncertainty in extrapolated estimates from our top-ranked model manifested for several reasons. First, we modeled aggregated (summed) REVI counts at the route-level (Hostetler and Chandler 2015), and we did this because BBS does not provide geographic coordinates for individual route stops, only route starting locations (Robbins et al. 1986, Pardieck et al. 2014). Therefore, using route-level sums (i.e., rather than [raw] route-stop counts) introduced considerable dispersion in the dependent variable of our candidate models (e.g., mean and variance in annual route-sums equaled 25.02 and 580.85 individuals, respectively), necessitating that we fit models assuming (notoriously sluggish) negative binomial mixtures (Dail and Madsen 2011, Fiske and Chandler 2011, Dennis et al. 2015). We suspect that being able to analyze route-stop counts (i.e., while also extracting context-relevant covariates at such stops) would decrease the total amount of dispersion in the dependent variable and possibly reduce uncertainty in derived estimates *post hoc* (e.g., dispersion affects the estimated variance of expected counts, not the expected counts themselves; Hilbe 2011). Second, to address overdispersion in the input route-level data, we applied a negative binomial mixture in each candidate model, rather than conventional (i.e., equidispersion-assuming) or zero-inflated (i.e., varied-dispersion-assuming) Poisson mixtures. Not only were route-level sums not equidispersed, but none of the routes we filtered included a total of zero REVI (e.g., BBS does not associate species identification codes with routes overlapping estimated species ranges, whether observers record individuals or not; Pardieck et al. 2014). Consequently, such limitations of our analysis design likely contributed estimation uncertainties downstream procedurally.

Third, and relatedly, it is well known that negative binomial mixtures used with dynamic *N*-mixture models can underestimate population abundance due to carrying-capacity (*K*)

misestimation (Fiske and Chandler 2011, Dennis et al. 2015); however, protracted runtimes (e.g., weeks of fitting models in parallel on a high-powered computing cluster) precluded identifying the tuning value of *K* at which model log-likelihoods stabilized. Regardless, each candidate model converged and thus retrieved valid maximum-likelihood estimates (Kéry and Royle 2016, 2021). Fourth, we only analyzed filtered BBS routes that followed standard sampling protocols, which limited our analysis to routes visited only once between survey seasons (Pardieck et al. 2014, Sauer et al. 2019). Consequently, our negatively biased estimates of (extrapolated) range-wide and (interpolated) survey-wide abundance may also be associated with potential bias of population-dynamic parameters (e.g., maximum instantaneous population growth) as well as potential bias of imperfect species detection by BBS observers, model parameters which were estimated based on data from single-visit surveys (Lele et al. 2012, Peach et al. 2017). The top-ranked model estimated mean (± SE) detection probabilities at 0.56 ± 0.01, and REVI are not only common in North America, but also relatively easy to detect by sight or sound at point-count locations, which often conveys estimated detection probabilities of 0.85-0.98 within 5-20 minutes of survey start (Dawson et al. 1995). The top-ranked model likely underestimated REVI detection due to our implementation of single-visit observation models (Knape and Korner-Nievergelt 2015, 2016, Dennis et al. 2015); however, BBS routes are inconsistently visited more than once, especially while also following established protocols, over time (Pardieck et al. 2014, Sauer et al. 2019). Negatively biased detection probabilities can lead to overestimation of species abundance spatially (Fewster et al. 2008, Marques et al. 2010, Kéry and Royle 2016, 2021), but we also acknowledge that our abundance estimates may be negatively biased when compared to products of other broad-scale analyses (Will et al. 2019, Fink et al. 2020).

Research-management implications of trait-based ecological models

To our knowledge, this is the first study testing how allometric-scaling models perform compared to models with only traditional (linear) covariates (i.e., both model types that include population dynamics) toward estimating species abundance via state-space (hierarchical) models at a continental scale. Specifically, our approach comprises a trait-based model estimated on broad spatiotemporal scales—an approach that attempts to functionally link species body size to its population structure and an emergent property thereof (e.g., range-wide abundance; Messier et al. 2010, Laughlin 2014, Meunier et al. 2017, Blonder 2018, Zakharova et al. 2019). While our top-ranked model converged on valid maximum-likelihood estimates, and several expected effects were confirmed (e.g., including a reasonable mass-abundance scaling effect), lingering broad-scale measurement error in covariates and unaccounted for sources of uncertainty likely limited estimation accuracy and precision of the model. We judged performance of the top-ranked model based on estimation of its effects, its uncorrelated residuals, and its extrapolated estimates of species abundance, and we compared our results to abundance estimates derived from similar broad-scale monitoring datasets.

We discovered evidence to suggest that state-space (hierarchical) models evaluating effects of allometric-scaling (i.e., trait-based model) relationships outrank (e.g., our top-ranked allometric-scaling model carried all of the AICc weight) models that evaluate traditional (ecological) covariates alone—particularly when both approaches account for imperfect detection and population dynamics over time. However, likely due to limitations of (a) BBS filtering (i.e., non-zero REVI records based on single [BBS-protocol compliant] visits to routes), (b) input data (i.e., at the route-level rather than at each route stop), (c) associated covariate summaries (i.e., route-start location and surrounding area), and (d) software (e.g., inefficient

estimation of carrying capacity, *K*; Fiske and Chandler 2011, Dennis et al. 2015), range-wide abundance estimates extrapolated from our top-ranked model were biased low compared to results of similar broad-scale monitoring and analysis efforts (Stanton et al. 2019, Will et al. 2019, Fink et al. 2020). Such limitations underscore that, while trait-based models are powerful tools for inference to ecological population and community structure on broad scales, sufficient data (e.g., georeferenced at fine scales and species-range inclusive), computational capabilities (e.g., estimation speed and efficiency), and established theoretical foundations (e.g., allometric-scaling laws) are necessary for more comprehensive explanation (Messier et al. 2010, Laughlin 2014, Meunier et al. 2017, Blonder 2018, Zakharova et al. 2019).

Therefore, future development of trait-based approaches that use georeferenced species attributes, BBS indices of species abundance and occupancy, and state-space (hierarchical) models should likely focus on (1) expanding input data (e.g., including geolocated route-stops and associated covariates to model fine-scale abundance dynamics and limit dispersion impacts to model uncertainty), (2) enhancing statistical software in terms of model estimator efficiency (i.e., processes such as latent-state integration or marginalization to better estimate *K*; Fiske and Chandler 2011, Dennis et al. 2015, Yackulic et al. 2020), (3) evaluating surveys containing > 1 replicate visit to BBS routes between years, (4) incorporating additional sources of abundance- and observation-process uncertainty (e.g., route-range coverage, observer proficiencies, and more; Thogmartin et al. 2006, Runge et al. 2009, Thogmartin 2010, Machtans and Thogmartin 2014, Thogmartin et al. 2014), and (5) leveraging traits beyond species body mass toward generating more comprehensive explanations of ecological patterns and processes, especially in today's data-rich period (Luo et al. 2011, Wilman et al. 2014, Myhrvold et al. 2015, Elliott et al. 2016, Klug et al. 2017). Finally, this work demonstrates corroborative and comparative utility of

estimates derived from dynamic trait-based (e.g., allometric-scaling) models to conduct continental investigations of species (range-wide) abundance distributions using state-space frameworks that also account for uncertainty associated with observation processes—especially toward generating information necessary to set and achieve broad-scale conservation goals in an era of accelerated global change.

Acknowledgments

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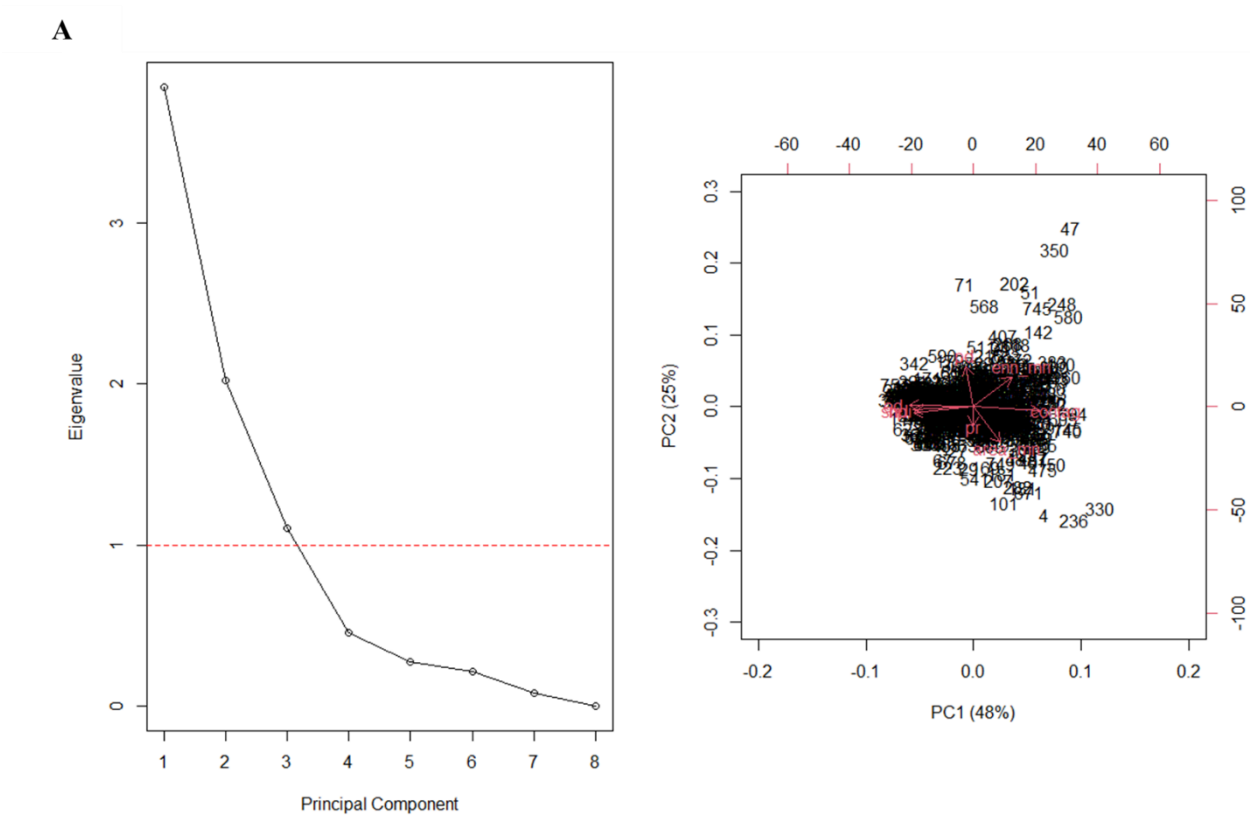
APPENDIX

APPENDIX

Table C4.1. Reclassification of level-2 cover types from the from the 2015 North American Land Change Monitoring System (CEC 2015, Homer et al. 2017) to "REVI habitat" and "inhospitable matrix" classes. The second and third columns note class codes from the NALCMS Land Cover Classification System (LCCS; i.e., codes in parentheses) to the current study.

Class	LCCS Definition and Code	Reclassification
REVI Habitat	Temperate or sub-polar needleleaf forest (20134)	1
	Sub-polar taiga needleleaf forest (20229)	2
	Tropical or sub-tropical broadleaf evergreen forest (20090)	3
	Tropical or sub-tropical broadleaf deciduous forest (20132)	4
	Temperate or sub-polar broadleaf deciduous forest (20227)	5
	Mixed forest (20092, 20090, 20134, 20132, 20229, and 20227)	6
	Tropical or sub-tropical shrubland (21450-13476)	7
	Temperate or sub-polar shrubland (21450-12050)	8
Inhospitable Matrix	Tropical or sub-tropical grassland (21669)	NA
	Temperate or sub-polar grassland (21537-12212)	NA
	Sub-polar or polar shrubland-lichen-moss (20022-12050, 21454-12212, and 21439-3012)	NA
	Sub-polar or polar barren-lichen-moss (21468, 21454-12212, and 20022-12050)	NA
	Wetland (42349 and 41809)	NA
	Cropland (10037, 10025, 21441, and 21453)	NA
	Barren lands (6001 and 6004)	NA
	Urban and built-up lands (5003)	NA
	Open water (7001 and 8001)	NA
	Snow and ice (8005 and 8008)	NA

Figure C4.1. Pairs of scree and bivariate (axis) plots derived from Principal Component Analyses, which we used to determine the number of principal component (PC) axes describing the most variation in multivariate gradients of eight (aggregate) landscape metrics summarized at 39-km surrounding Breeding Bird Survey routes. We estimated metrics using the "landscapemetrics" package version 1.5.0 (Hesselbarth et al. 2019) and FRAGSTATS version 4.2.1 in R version 4.0.2 (McGarigal et al. 2014, R Core Development Team 2020). Mean eigenvalue (red dotted line) is noted in the scree plot, and vectors of factor loadings (red arrows) are noted in the three bivariate plots (i.e., displaying PC1:PC2, PC1:PC3, and PC2:PC3), one vector per landscape metric and displayed alongside survey route ID numbers (i.e., 1-759 locations). Landscape metrics, including their names and identifying codes, are described in Tables 4.1 and 4.2.



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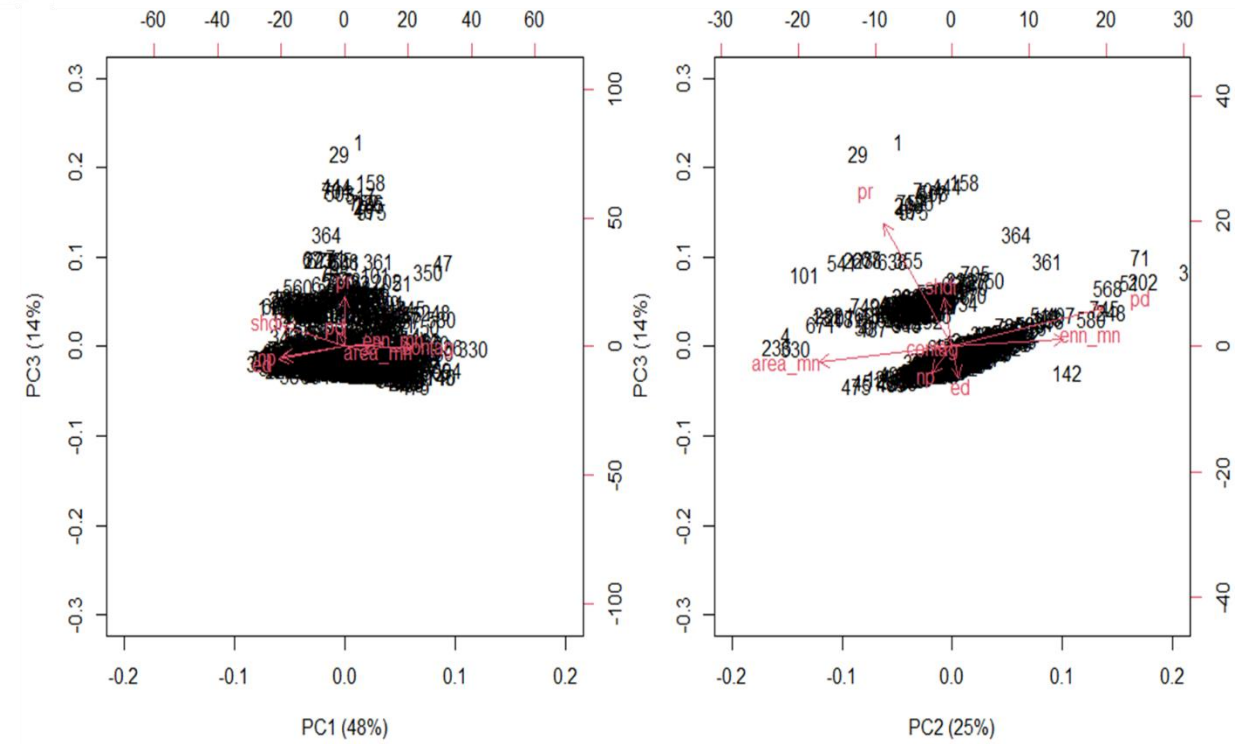

REFERENCES

REFERENCES

Bagchi, R., R. E. Gallery, S. Gripenberg, S. J. Gurr, L. Narayan, C. E. Addis, R. P. Freckleton, et al. 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* 506:85-88.

Bahn, V., W. B. Krohn, and R. J. O'Connor. 2008. Dispersal leads to spatial autocorrelation in species distributions: a simulation model. *Ecological Modelling* 213:285-292.

Barlow, J. C. and D. M. Power. 1970. An analysis of character variation in red-eyed and Philadelphia vireos (Aves: Vireonidae) in Canada. *Canadian Journal of Zoology* 48:673-694.

Barlow, J. C. and J. C. Rice. 1977. Aspects of the comparative behavior of red-eyed and Philadelphia vireos. *Canadian Journal of Zoology* 55:528-541.

Bellier, E., M. Kéry, and M. Schaub. 2016. Simulation-based assessment of dynamic *N*-mixture models in the presence of density dependence and environmental stochasticity. *Methods in Ecology and Evolution* 7:1029-1040.

Bevers, M. and C. H. Flather. 1999. The distribution and abundance of populations limited at multiple spatial scales. *Journal of Animal Ecology* 68:976-987.

Bird Studies Canada (BSC) and North American Bird Conservation Initiative (NABCI). 2014. Bird Conservation Regions. Bird Studies Canada on behalf of the North American Bird Conservation Initiative. <http://www.birdscanada.org/research/gislab/index.jsp?targetpg=bcr>. Accessed Jan 2020.

Bivand, R. S., E. Pebesma, and V. Gomez-Rubio. 2013. Applied Spatial Data Analysis with R, Second Edition. Springer-Verlag, New York, NY, USA.

Bjornstad, O. N. 2020. ncf: Spatial Covariance Functions. R package version 1.2-9. <https://CRAN.R-project.org/package=ncf>. Accessed Aug 2020.

Blancher, P. J., K. V. Rosenberg, A. O. Panjabi, B. Altman, A. R. Couturier, and W. E. Thogmartin. 2013. Handbook to the Partners in Flight population estimates database, version 2.0. Partners in Flight Technical Series Number 6. Partners in Flight and Bird Conservancy of the Rockies, Denver, CO, USA.

Blonder, B. 2018. Hypervolume concepts in niche-and trait-based ecology. *Ecography* 41:1441-1455.

Bokma, F. 2004. Evidence against universal metabolic allometry. *Functional Ecology* 18:184-187.

Bolen, E. G. 1998. Ecology of North America. John Wiley and Sons, Inc., New York, NY, USA.

Bowers, M. A. and J. L. Dooley Jr. 1999. A controlled, hierarchical study of habitat fragmentation: responses at the individual, patch, and landscape scale. *Landscape Ecology* 14:381-389.

Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago, IL, USA.

Brown, J. H. and B. A. Maurer. 1986. Body size, ecological dominance and Cope's rule. *Nature* 324:248-250.

Brown, J. H. and B. A. Maurer. 1987. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. *American Naturalist* 130:1-17.

Brown, J. H. and B. A. Maurer. 1989. Macroecology: the division of food and space among species on continents. *Science* 243:1145-1150.

Brown, J. H., D. W. Mehlman, and G. C. Stevens. 1995. Spatial variation in abundance. *Ecology* 76:2028-2043.

Brown, J. 1984. On the relationship between abundance and distribution of species. *The American Naturalist* 124:255-279.

Burnham, K.P. and D. R. Anderson. 2002. Model Selection and Multi-Model Inference: A Practical Information-theoretic Approach, Second Edition. Springer-Verlag, New York, NY, USA.

Carbone, C., J. M. Rowcliffe, G. Cowlishaw, and N. J. B. Isaac. 2007. The scaling of abundance in consumers and their resources: implications for the energy equivalence rule. *American Naturalist* 170:479-484.

Carlin, B. P. and T. A. Louis. 1996. Bayes and Empirical Bayes Methods for Data Analysis. Chapman and Hall, CRC Press, London, UK.

Carroll, R. J., D. Ruppert, L. A. Stefanski, and C. M. Crainiceanu. 2006. Measurement Error in Nonlinear Models: a Modern Perspective, Second Edition. Chapman and Hall, CRC Press, London, UK.

Chapman, B. R. and E. G. Bolen. 2015. Ecology of North America. John Wiley and Sons, Inc., New York, NY, USA.

Cimprich, D. A., F. R. Moore, and M. P. Guilfoyle. 2020. Red-eyed vireo (*Vireo olivaceus*) (online). *In* Birds of the World, version 1.0, P. G. Rodewald (Ed.). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi-org.proxy1.cl.msu.edu/10.2173/bow.reevir1.01>. Accessed May 2020.

Commission for Environmental Cooperation (CEC). 2015. Land Cover Change 30m, 2010-2015 (Landsat). North American Land Change Monitoring System, version 2.0. <http://www.cec.org/north-american-environmental-atlas/land-cover-change-30m-2010-2015-landsat/>. Accessed Jan 2020.

Crawford, H. S., R. G. Hooper, and R. W. Titterington. 1981. Songbird population response to silvicultural practices in central Appalachian hardwoods. *Journal of Wildlife Management* 45:680-692.

Cressie, N. A. C. 1993. Statistics for Spatial Data. John Wiley and Sons, Inc., New York, NY, USA.

Cressie, N. and C. Wikle. 2011. Statistics for Spatio-temporal Data. John Wiley and Sons, Inc., New York, NY, USA.

Dail, D. and L. Madsen. 2011. Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics* 67:577-587.

Dawson, D. K., D. R. Smith, and C. S. Robbins. 1995. Point count length and detection of forest neotropical migrant birds. Pages 35-44 *in* Monitoring Bird Populations by Point Counts, C. J. Ralph, J. R. Sauer, and S. Droege (Eds.). General Technical Report PSW-GTR-149, U.S. Forest Service, Albany, CA, USA.

Dennis, E. B., B. J. T. Morgan, and M. S. Ridout. 2015. Computational aspects of *N*-mixture models. *Biometrics* 71:237-246.

Dunning, J. B., Jr. 1993. CRC Handbook of Avian Body Masses. CRC Press, Boca Raton, FL, USA.

Elliott, K. C., K. S. Cheruvelil, G. M. Montgomery, and P. A. Soranno. 2016. Conceptions of good science in our data-rich world. *BioScience* 66:880-889.

Fewster, R. M., C. Southwell, D. L. Borchers, S. T. Buckland, and A. R. Pople. 2008. The influence of animal mobility on the assumption of uniform distances in aerial line-transect surveys. *Wildlife Research* 35:275-288.

Ficken, R. W., M. S. Ficken, and J. P. Hailman. 1974. Temporal pattern shifts to avoid acoustic interference in singing birds. *Science* 183:762-763.

Fink, D., T. Auer, A. Johnston, M. Strimas-Mackey, O. Robinson, S. Ligocki, W. Hochachka, et al. 2020. eBird Status and Trends, version 2019, released 2020. Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/ebirdst.2019>. Accessed Jan 2021.

Fiske, I. J. and R. B. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43:1-23.

González-Megías, A., J. M. Gómez, and F. Sánchez-Piñero. 2005. Consequences of spatial autocorrelation for the analysis of metapopulation dynamics. *Ecology* 86:3264-3271.

Graber, J. W., R. R. Graber, and E. L. Kirk. 1985. Illinois birds: vireos. Illinois Natural History Survey, Champaign, IL, USA.

Gräler, B., E. Pebesma, and G. Heuvelink. 2016. Spatio-temporal interpolation using gstat. *The R Journal* 8:204-218.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* 1:e1500052.

Haddad, N. M., R. D. Holt, R. J. Fletcher Jr., M. Loreau, and J. Clobert. 2017. Connecting models, data, and concepts to understand fragmentation's ecosystem-wide effects. *Ecography* 40:1-8.

Hamel, P. B. 1992. Land Manager's Guide to the Birds of the South. The Nature Conservancy, Chapel Hill, NC, and U.S. Forest Service, Southeastern Forest Experiment Station, Atlanta, GA, USA.

Hansen, M. C., P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, et al. 2013. High-resolution global maps of 21st-Century forest cover change. *Science* 342:850-853. Data available at: <http://earthenginepartners.appspot.com/science-2013-global-forest>. Accessed Jan 2020.

Hanski, I. 1998a. Connecting the parameters of local extinction and metapopulation dynamics. *Oikos* 83:390-396.

Hanski, I. 1998b. Metapopulation dynamics. *Nature* 396:41-49.

Hartfelder, J., C. Reynolds, R. A. Stanton, M. Sibiya, A. Monadjem, R. A. McCleery, and R. Fletcher Jr. 2020. The allometry of movement predicts the connectivity of communities. *Proceedings of the National Academy of Sciences of the United States of America* 117: 22274-22280.

Hechinger, R. F., K. D. Lafferty, A. P. Dobson, J. H. Brown, and A. M. Kuris. 2011. A common scaling rule for abundance, energetics, and production of parasitic and free-living species. *Science* 333:445-448.

Heffernan, J. B., P. A. Soranno, M. J. Angilletta Jr., L. B. Buckley, D. S. Gruner, T. H. Keitt, J. R. Kellner, et al. 2014. Macrosystems ecology: understanding ecological patterns and processes at continental scales. *Frontiers in Ecology and the Environment* 12:5-14.

Hendriks, A. J. 2007. The power of size: a meta-analysis reveals consistency of allometric regressions. *Ecological Modelling* 205:196-208.

Hesselbarth, M. H. K., M. Sciaini,, K. A. With, K. Wiegand, and J. Nowosad. 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. R package version 1.5.0. *Ecography* 42:1648-1657.

Hiemstra, P. H., E. J. Pebesma, C. J. W. Twenhöfel, and G. B. M. Heuvelink. 2009. Real-time automatic interpolation of ambient gamma dose rates from the Dutch radioactivity monitoring network. *Computers and Geosciences* 35:1711-1721.

Hijmans, R. J. 2020. raster: Geographic data analysis and modeling. R package version 3.3-7. <https://CRAN.R-project.org/package=raster>.

Hilbe, J. M. 2011. Negative Binomial Regression, Second Edition. Cambridge University Press, Cambridge, MA, USA.

Homer, C., R. R. Colditz, R. Latifovic, R. M. Llamas, D. Pouliot, P. Danielson, C. Meneses, et al. 2017. Developing a new North American land cover product at 30m resolution: methods, results, and future plans. *Proceedings of the American Geophysical Union* Abstract #GC52C-01.

Hostetler, J. A. and R. B. Chandler. 2015. Improved state-space models for inference about spatial and temporal variation in abundance from count data. *Ecology* 96:1713-1723.

Imlay, T. L., J. M. Flemming, S. Saldanha, N. T. Wheelwright, and M. L. Leonard. 2018. Breeding phenology and performance for four swallows over 57 years: relationships with temperature and precipitation. *Ecosphere* 9:e02166.

James, R. D. 1976. Foraging behavior and habitat selection of three species of vireos in southern Ontario. *Wilson Society Bulletin* 88:62-75.

Jarzyna, M. A., W. F. Porter, B. A. Maurer, B. Zuckerberg, and A. O. Finley. 2015. Landscape fragmentation affects responses of avian communities to climate change. *Global Change Biology* 21:2942-2953.

Jetz, W., D. S. Wilcove, and A. P. Dobson. 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology* 5:1211-1219.

Kaiser, H. F. 1960. The application of electronic computers to factor analysis. *Educational and Psychological Measurement* 20:141-151.

Kelemen, E. P. and S. M. Rehan. 2020. Opposing pressures of climate and land-use change on a native bee. *Global Change Biology* 27:1017-1026.

Kendall, L. K., R. Rader, V. Gagic, D. P. Cariveau, M. Albrecht, K. C. R. Baldock, B. M. Freitas, et al. 2019. Pollinator size and its consequences: robust estimates of body size in pollinating insects. *Ecology and Evolution* 9:1702-1714.

Kéry, M. and J. A. Royle. 2016. Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance, and Species Richness in R and BUGS, Volume 1: Prelude and Static Models. Academic Press, Cambridge, MA, USA.

Kéry, M. and J. A. Royle. 2021. Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance, and Species Richness in R and BUGS, Volume 2: Dynamic and Advanced Models. Academic Press, Cambridge, MA, USA.

Kilmer, J. T. and R. L. Rodríguez. 2017. Ordinary least squares regression is indicated for studies of allometry. *Journal of Evolutionary Biology* 30:4-12.

Klug, J. L., C. C. Carey, D. C. Richardson, and R. Darner Gougis. 2017. Analysis of high-frequency and long-term data in undergraduate ecology classes improves quantitative literacy. *Ecosphere* 8:e01733.

Knape, J. and F. Korner-Nievergelt. 2015. Estimates from non-replicated population surveys rely on critical assumptions. *Methods in Ecology and Evolution* 6:298-306.

Knape, J. and F. Korner-Nievergelt. 2016. On assumptions behind estimates of abundance from counts at multiple sites. *Methods in Ecology and Evolution* 7:206-209.

Laird, N. M. and T. A. Louis. 1987. Empirical Bayes confidence intervals based on bootstrap samples. *Journal of the American Statistical Association* 82:739-750.

Laughlin, D. C. 2014. Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters* 17:771-784.

Lawrence, L. K. 1953. Nesting life and behaviour of the red-eyed vireo. *Canadian Field Naturalist* 67:47-77.

Lele, S. R., M. Moreno, and E. Bayne. 2012. Dealing with detection error in site occupancy surveys: what can we do with a single survey? *Journal of Plant Ecology* 5:22-31.

Loria, D. E. and F. R. Moore. 1990. Energy demands of migration on red-eyed vireos (*Vireo olivaceus*). *Behavioral Ecology* 1:24-35.

Lovegrove, B. G. 2000. The zoogeography of mammalian basal metabolic rate. *American Naturalist* 156:201-219.

Luo, Y., K. Ogle, C. Tucker, S. Fei, C. Gao, S. LaDeau, J. S. Clark, et al. 2011. Ecological forecasting and data assimilation in a data-rich era. *Ecological Applications* 21:1429-1442.

Machtans, C. S. and W. E. Thogmartin. 2014. Understanding the value of imperfect science from national estimates of bird mortality from window collisions. *The Condor: Ornithological Applications* 116:3-8.

Marques, T. A., S. T. Buckland, D. L. Borchers, D. Tosh, and R. A. McDonald. 2010. Point transect sampling along linear features. *Biometrics* 66:1247-1255.

Marquet, P. A., F. A. Labra, and B. A. Maurer. 2004. Metabolic ecology: linking individuals to ecosystems. *Ecology* 85:1794-1796.

Marshall, M. R and R. J. Cooper. 2004. Territory size of a migratory songbird in response to caterpillar density and foliage structure. *Ecology* 85:432-445.

Marshall, M. R. 2000. The effects of naturally occurring and experimentally reduced prey abundance on the breeding ecology and territory dynamics of the red-eyed vireo. Ph.D. dissertation, University of Georgia, Athens, GA, USA.

Marshall, M. R., R. J. Cooper, J. A. DeCecco, J. Strazanac, and L. Butler. 2002. Effects of experimentally reduced prey abundance on the breeding ecology of the red-eyed vireo. *Ecological Applications* 12:261-280.

Maurer, B. A. and M. L. Taper. 2002. Connecting geographic distributions with population processes. *Ecology Letters* 5:223-231.

McGarigal, K., S.A. Cushman, and E. Ene. 2014. FRAGSTATS: Spatial pattern analysis program for categorical and continuous maps, version 4.2.1. <http://www.umass.edu/landeco/research/fragstats/fragstats.html/>. Accessed Oct 2016.

McKellar, A. E., P. P. Marra, S. J. Hannon, C. E. Studds, and L. M. Ratcliffe. 2013. Winter rainfall predicts phenololgy in widely separated populations of a migrant songbird. *Oecologia* 172:595-605.

Messier, J., B. J. McGill, and M. J. Lechowicz. 2010. How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* 13:838-848.

Meunier, C. L., M. Boersma, R. El-Sabaawi, H. M. Halvorson, E. M., Herstoff, D. B. Van de Waal, R. J. Vogt, et al. 2017. From elements to function: toward unifying ecological stoichiometry and trait-based ecology. *Frontiers in Environmental Science* 5:1-10.

Mokany, K., T. D. Harwood, K. J. Williams, and S. Ferrier. 2012. Dynamic macroecology and the future for biodiversity. *Global Change Biology* 18:3149-3159.

Moll, R. J., J. D. Cepek, P. D. Lorch, P. Dennis, T. Robison, J. Millspaugh, and R. Montgomery. 2018. Humans and urban development mediate the sympatry of competing carnivores. *Urban Ecosystems* 21:765-778.

Moll, R. J., K. Kilshaw, R. A. Montgomery, L. Abade, R. D. Campbell, L. A. Harrington, J. J. Millspaugh, et al. 2016. Clarifying habitat niche width using broad-scale, hierarchical occupancy models: a case study with a recovering mesocarnivore. *Journal of Zoology* 300:177-185.

Mortelliti, A,, G. Sozio, D. A. Driscoll, L. Bani, L. Boitani, and D. Lindenmayer. 2014. Population and individual-scale responses to patch size, isolation and quality in the hazel dormouse. *Ecosphere* 5:1-21.

Myhrvold, N. P., E. Baldridge, B. Chan, D. Sivam, D. L. Freeman, and S. M. Ernest. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles: Ecological Archives E096-269. *Ecology* 96:3109-3109.

Newbold, T., L. N. Hudson, S. L. L. Hill, S. Contu, I. Lysenko, R. A. Senior, L. Börger, et al. 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520:45-50.

Newman, K. B., S. T. Buckland, B. J. T. Morgan, R. King, D. L. Borchers, D. J. Cole, P. Besbeas, et al. 2014. Integrated population modelling. Pages 169-195 *in* Modelling Population Dynamics, Methods in Statistical Ecology Series. Springer-Verlag, New York, NY, USA.

Oliveira, M. O., B. M. Freitas, J. Scheper, and D. Kleijn. 2016. Size and sex-dependent shrinkage of Dutch bees during one-and-a-half centuries of land-use change. *PLoS One* 11:e0148983.

Padoa-Schioppa, E., M. Baietto, R. Massa, and L. Bottoni. 2005. Bird communities as bioindicators: the focal species concept in agricultural landscapes. *Ecological Indicators* 170:11.

Pagel, J. and F. M. Schurr. 2012. Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Global Ecology and Biogeography* 21:293-304.

Pardieck, K. L., D. J. Ziolkowski Jr., and M.-A. R. Hudson. 2014. North American Breeding Bird Survey Dataset 1966-2013, version 2013.0. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD, USA. <http://www.pwrc.usgs.gov/BBS/RawData/>. Accessed May 2016.

Peach, M. A., J. B. Cohen, and J. L. Frair. 2017. Single-visit dynamic occupancy models: an approach to account for imperfect detection with Atlas data. *Journal of Applied Ecology* 54:2033-2042.

Pebesma, E. J. 2004. Multivariable geostatistics in S: the gstat package. *Computers and Geosciences* 30:683-691.

Pebesma, E. J. 2018. Simple features for R: standardized support for spatial vector data. *The R Journal* 10:439-446.

Pebesma, E. J. and R. S. Bivand. 2005. Classes and methods for spatial data in R. *R News* 5:9-13.

Pianka, E. R. 1970. On r-and K-selection. *American Naturalist* 104:592-597.

Pianka, E. R. 1972. r and K selection or b and d selection? *American Naturalist* 106:581-588.

Pörtner, H. O., R. J. Scholes, J. Agard, E. Archer, A. Arneth, X. Bai, D. Barnes, et al. 2021. Scientific outcome of the IPBES-IPCC co-sponsored workshop on biodiversity and climate change. IPBES Secretariat, Bonn, Germany. <doi:10.5281/zenodo.4659158>. Accessed Jun 2021.

Price, J. 2002. Climate change, birds and ecosystems—why should we care. Pages 465-469 *in* Managing for Healthy Ecosystems, D. J. Rapport, B. L. Lasley, D. E. Rolston, N. O. Nielsen, C. O. Qualset, and A. B. Damania (Eds.). Lewis Publishers, Boca Raton, FL, USA.

R Core Development Team. 2020. R Statistical Software v. 4.0.2. R Foundation for Statistical Computing, Vienna, Austria.

Ralph, C. J., J. R. Sauer, and S. Droege (Eds.). 1995. Monitoring Bird Populations by Point Counts, General Technical Report PSW-GTR-149, U.S. Forest Service, Albany, CA, USA.

Rice, J. C. 1978. Ecological relationships of two interspecifically territorial vireos. *Ecology* 59:526-538.

Ridgway, R. 1904. The birds of North and Middle America, Part III. *United States National Museum Bulletin* 50:1-801.

Robbins, C. S., D. Bystrak, and P. H. Geissler. 1986. The Breeding Bird Survey: its first fifteen years, 1965-1979. Resource Publication 157, U.S. Fish and Wildlife Service, Washington, DC, USA.

Roberts, R. N. and D. Muir. 1998. Data from a constant-effort mist net station. *North American Bird Bander* 23:33-35.

Robinson, S. K. and R. T. Holmes. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. *Ecology* 63:1918-1931.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, et al. 2019. Decline of the North American avifauna. *Science* 366:120-124.

Rosenberg, K. V., P. J. Blancher, J. C. Stanton, and A. O. Panjabi. 2017. Use of North American Breeding Bird Survey data in avian conservation assessments. *The Condor: Ornithological Applications* 119:594-606.

Rossberg, A. G., R. Ishii, and T. Amemiya, and K. Itoh. 2008. The top-down mechanism for body-mass-abundance scaling. *Ecology* 89:567-580.

Royle, J. A. 2004. *N*-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60:108-115.

Royle, J. A. and R. M. Dorazio. 2008. Hiearchical Modeling and Inference in Ecology. Academic Press, Cambridge, MA, USA.

Runge, M. C., J. R. Sauer, M. L. Avery, B. F. Blackwell, and M. D. Koneff. 2009. Assessing allowable take of migratory birds. *Journal of Wildlife Management* 73:556-566.

Sandberg, R. and F. R. Moore. 1996. Migratory orientation of red-eyed vireos, *Vireo olivaceus*, in relation to energetic condition and ecological context. *Behavioral Ecology and Sociobiology* 39:1-10.

Sauer, J. R., J. E. Hines, G. Gough, I. Thomas, and B. G. Peterjohn. 1997. The North American Breeding Bird Survey Results and Analysis, version 96.4. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD, USA.

Sauer, J. R., K. L. Pardieck, D. J. Ziolkowski, Jr., A. C. Smith, M.-A. R. Hudson, V. Rodriguez, H. Berlanga, et al. 2017. The first 50 years of the North American Breeding Bird Survey. *The Condor: Ornithological Applications* 119:576-593.

Sauer, J. R., W. A. Link, D. J. Ziolkowski, K. L. Pardieck, and D. J. Twedt. 2019. Consistency counts: modeling the effects of a change in protocol on Breeding Bird Survey counts. *The Condor: Ornithological Applications* 121:1-12.

Scheffers, B. R., L. D. Meester, T. C. L. Bridge, A. A. Hoffmann, J. M. Pandolfi, R. T. Corlett, S. H. M. Butchart, et al. 2016. The broad footprint of climate change from genes to biomes to people. *Science* 354:aaf7671.

Schöll, E. M., J. Ohn, K. F. Hoffmann, and S. M. Hille. 2016. Caterpillar biomass depends on temperature and precipitation, but does not affect bird reproduction. *Acta Oecologica* 74:28-36.

Schurr, F. M., J. Pagel, J. Sarmento Cabral, J. Groeneveld, O. Bykova, R. B. O'Hara, F. Hartig, et al. 2012. How to understand species' niches and range dynamics: a demographic research agenda for biogeography. *Journal of Biogeography* 39:2146-2162.

Septon, G., J. B. Marks, and T. Ellestad. 1995. A preliminary assessment of peregrine falcon (*Falco peregrinus*) recovery in midwestern North America. *Acta Ornithologica* 30:65-69.

Sergio, F., I. Newton, L. Marchesi, and P. Pedrini. 2006. Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology* 43:1049-1055.

Sheridan, J. A. and D. Bickford. 2011. Shrinking body size as an ecological response to climate change. *Nature Climate Change* 1:401-406.

Smith, A. C. and B. P. M. Edwards. 2021. North American Breeding Bird Survey status and trend estimates to inform a wide range of conservation needs, using a flexible Bayesian hierarchical generalized additive model. *The Condor: Ornithological Applications* 123:1-16.

Smith, A. C., L. Fahrig, and C. M. Francis. 2011. Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. *Ecography* 34:103-113.

Smith, G. J. 2013. The U.S. Geological Survey Bird Banding Laboratory: an integrated scientific program supporting research and conservation of North American birds. Open-File Report (OFR) 2013-1328, U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD, USA.

Snäll, T., R. B. O'Hara, C. Ray, and S. K. Collinge. 2008. Climate-driven spatial dynamics of plague among prairie dog colonies. *American Naturalist* 171:238-248.

Solomou, A. D. and A. I. Sfougaris. 2015. Bird community characteristics as indicators of sustainable management of olive grove ecosystems of central Greece. *Journal of Natural History* 49:301-325.

Sólymos, P. and S. R. Lele. 2016. Revisiting resource selection probability functions and single-visit methods: clarification and extensions. *Methods in Ecology and Evolution* 7:196-205.

Sólymos, P., S. Lele, and E. Bayne. 2012. Conditional likelihood approach for analyzing single visit abundance survey data in the presence of zero inflation and detection error. *Environmetrics* 23:197-205.

Southern, W. E. 1958. Nesting of the red-eyed vireo in the Douglas Lake region, Michigan. *Jack Pine Warbler* 36:105-130.

Stanton, J. C., P. Blancher, K. V. Rosenberg, A. O. Panjabi, and W. E. Thogmartin. 2019. Estimating uncertainty of North American landbird population sizes. *Avian Conservation and Ecology* 14:4.

Stewart, R. E. and J. W. Aldrich. 1952. Ecological studies of breeding bird populations in northern Maine. *Ecology* 33:226-238.

Sullivan, B. L., C. L. Wood, M. J. Iliff, R. E. Bonney, D. Fink, and S. Kelling. 2009. *e*Bird: a citizen-based bird observation network in the biological sciences. *Biological Conservation* 142:2282-2292.

Sutton, G. M. 1949. Studies of the Nesting Birds of the Edwin S. George Reserve, Part I: The Vireos. Miscellaneous Publications of the Museum of Zoology 74. University of Michigan, Ann Arbor, MI, USA.

Thogmartin, W. E. 2010. Sensitivity analysis of North American bird population estimates. *Ecological Modelling* 221:173-177.

Thogmartin, W. E., F. P. Howe, F. C. James, D. H. Johnson, E. T. Reed, J. R. Sauer, and F. R. Thompson. 2006. A review of the population estimation approach of the North American landbird conservation plan. *The Auk: Ornithological Advances* 123:892-905.

Thogmartin, W. E., S. M. Crimmins, and J. Pearce. 2014. Prioritizing bird conservation actions in the Prairie Hardwood transition of the Midwestern United States. *Biological Conservation* 176:212-223.

Thornton, M. M., R. Shrestha, Y. Wei, P. E. Thornton, S. Kao, and B. E. Wilson. 2020. Daymet: monthly climate summaries on a 1-km grid for North America, version 4. Oak Ridge National Laboratory, Distributed Active Archive Center, Oak Ridge, TN, USA. <https://doi.org/10.3334/ORNLDAAC/1855>. Accessed Dec 2020.

Tyler, W. M. 1950. *Vireo olivaceus* (Linnaeus) red-eyed vireo. Pages 335-348 *in* Life Histories of North American Wagtails, Shrikes, Vireos, and their Allies, A. C. Bent (Ed.). *United States National Museum Bulletin* 197.

Urban, M. C. 2015. Accelerating extinction risk from climate change. *Science* 348:571-573.

U.S. Geological Survey (USGS) Bird Banding Laboratory. 2020. North American bird banding and band encounter data set. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD, USA. 26 August 2020.

Visser, M., L. Holleman, and P. Gienapp. 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* 147:164-172.

Whelan, C. J., Ç. H. Şekercioğlu, and D. G. Wenny. 2015. Why birds matter: from economic ornithology to ecosystem services. *Journal of Ornithology* 156:227-238.

Whelan, C. J., D. G. Wenny, and R. J. Marquis. 2008. Ecosystem services provided by birds. *Annals of the New York Academy of Sciences* 1134:25-60.

White, E. P., S. K. M. Ernest, A. J. Kerkoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution* 22:323-330.

Will, T., J. C. Stanton, K. V. Rosenberg, A. O. Panjabi, A. Camfield, A. Shaw, W. E. Thogmartin, et al. 2019. Handbook to the Partners in Flight population estimates database, version 3.0. Partners in Flight Technical Series Number 7. Partners in Flight and Bird Conservancy of the Rockies, Denver, CO, USA.

Williamson, P. 1971. Feeding ecology of the red-eyed vireo (*Vireo olivaceus*) and associated foliage-gleaning birds. *Ecological Monographs* 41:129-152.

Wilman, H., J. Belmaker, J. Simpson, C. de la Rosa, M. M. Rivadeneira, and W. Jetz. 2014. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals: Ecological Archives E095-178. *Ecology* 95:2027-2027.

Wysner, T. E., A. W. Bartlow, C. D. Hathcock, and J. M. Fair. 2019. Long-term phenology of two North American secondary cavity-nesters in response to changing climate conditions. *The Science of Nature* 106:1-10.

Yackulic, C. B., M. Dodrill, M. Dzul, J. S. Sanderlin, and J. A. Reid. 2020. A need for speed in Bayesian population models: a practical guide to marginalizing and recovering discrete latent states. *Ecological Applications* 30:e02112.

Zakharova, L., K. M. Meyer, and M. Seifan. 2019. Trait-based modelling in ecology: a review of two decades of research. *Ecological Modelling* 407:108703.

Zipkin, E. F., E. R. Zylstra, A. D. Wright, S. P. Saunders, A. O. Finley, M. C. Dietze, M. S. Itter, et al. 2021. Addressing data integration challenges to link ecological processes across scales. *Frontiers in Ecology and the Environment* 19:30-38.

Zipkin, E. F., J. T. Thorson, K. See, H. J. Lynch, E. H. Campbell Grant, Y. Kanno, R. B. Chandler, et al. 2014. Modeling structured population dynamics using data from unmarked individuals. *Ecology* 95:22-29.

CONCLUSION

In this dissertation, I used literature review and synthesis and conducted three empirical studies to examine challenges associated with modeling spatiotemporal dynamics of single- and multi-species vertebrate systems—particularly from fine (e.g., local) to broad (e.g., regional and continental) spatial extents. Such modeling challenges included: (1) describing ecological patterns and processes at singular or multiple dimensions and scales, (2) evaluating intra- and inter-species' dynamics at the levels of populations and communities in space, time, or both, (3) accounting for imperfect observer detection of surveyed species, (4) choosing study levels and scales, constrained by data acquisition, resource limitations, and theoretical foundations, to collect sufficient amounts of data, and (5) describing patterns and processes quantitatively manifested as observed indicators of hidden ecological states (e.g., occupancy and abundance; Kéry and Schaub 2011, Royle and Dorazio 2008, Kéry and Royle 2016, 2021).

Multiple important lessons resulted from the literature synthesis and statistical analyses presented in this dissertation. The first is that there is a clear need to formally recognize how ecological restoration efforts may be enhanced by expanded application of new and old macroecological tools (Brown and Maurer 1987, 1989, Dennhardt et al. 2016), particularly informed by foundations of island biogeography theory (MacArthur and Wilson 1963, 1967). In Chapter 1, I showed that many multi-scale tools exist, undergoing continued development toward incorporating multiple species as well as their traits, interactions with other species, and population vital rates. My work in this chapter advances fundamental and applied wildlife ecology by emphasizing continued development, application, and utility of (a) macro-scale perspectives (e.g., broad spatiotemporal inquiries), (b) multi-level (e.g., populations and

communities) and -scale (e.g., local and regional) ecological theories (e.g., metapopulation and metacommunity dynamics), and (c) hierarchical statistical models toward improved ecological restoration efforts in an era of accelerated global change. This work underscores that multi-scale (hierarchical) versions of species distribution models (Hampe 2004, Araújo and Peterson 2012, Falk and Millar 2016), species-area models (Arrhenius 1921, Preston 1962, MacArthur and Wilson 1963, 1967, Rosenzweig 1995), metapopulation models (Levins 1970, Hanski 1998a, b, 1999), and neutral-assembly (Hubbell 2001, 2005, 2006) and metacommunity (Leibold et al. 2004, Holyoak et al. 2005) models most effectively describe underlying data correlations and natural complexities of ecological systems. Therefore, such approaches will likely enhance performance of ecological restoration efforts on broad spatiotemporal scales (Dennhardt et al. 2016).

The second lesson learned is that multi-species community studies conducted on broad scales are crucial for accurately evaluating the conservation status of international multi-species wildlife resources. In Chapter 2, I showed that most freshwater fish communities declined in the CAN jurisdictional waters in Lake Huron, and such declines were associated with invasive-species driven or climate-induced changes in the freshwater environment, despite strong similarities among communities in terms of diversity. My work in this chapter advances fundamental and applied wildlife ecology by (a) demonstrating the utility of hierarchical (state-space) models of multi-species abundance patterns, (b) identifying common broad- and fine-scale correlates of species population declines to target and manage in large freshwater systems, and (c) offering novel ideas for lake management and potential ecosystem-level governance of international wildlife resources. This work highlights that, to better conserve multi-species communities, research and management should focus finite resources on implementing

ecosystem-level governance and expanding collaborative data networks. Additionally, this work suggests that increasing invasive-species control and promoting structural-climatic conditions (e.g., manipulated lake depth, available vegetation, and wind or water diversion structures) may help manage water temperatures and nutrient cycling in freshwater environments, especially while under threat of continued climate change (Arthington et al. 2016).

The third lesson learned is that multi-species community studies investigating effects of land management prescriptions necessitate extensive surveying on broad spatiotemporal scales. In Chapter 3, I showed that most grassland-obligate bird species did not collectively respond to land-management practices (i.e., Conservation Practice [CP]), existing vegetation levels, or contextual (landscape-level) variables in a consistent manner, despite considerable literary support for such considerations (Bakker et al. 2002, Cunningham and Johnson 2006, Scholtz et al. 2017, Shahan et al. 2017). My work in this chapter advances fundamental and applied wildlife ecology by (a) illustrating the usefulness of hierarchical (state-space) models of multi-species occupancy patterns, (b) garnering useful conservation information from sparse multi-species datasets, and (c) cautioning against broad inference to rare system-obligate species that require more extensive study and careful evaluation in restored grasslands. Despite inconsistent responses to predictors of interest, of seven species whose occupancy-detection patterns I studied, occupancy probability for three species responded significantly and positively to non-native (CP1; i.e., bobolink, *Dolichonyx oryzivorous*) or native (CP23; i.e., eastern meadowlark, *Sturnella magna*, and grasshopper sparrow, *Ammodramus savannarum*) planting types. Furthermore, grassland-obligate bird diversity were comparable between grassland set-aside (i.e., Conservation Reserve Enhancement Program [CREP]) lands and citizen-science survey locations, indicating that CREP surveys reflect grassland bird occupancy across the region. This

work highlights the (a) importance of comprehensive experimental and survey design for multi-species communities and (b) conservation hazards associated with grouping rare species for broad inference, particularly when system-obligate species are known to be considerably rare compared to system-facultative species (Vickery et al. 1999, Riffell et al. 2015).

The fourth lesson learned is that species allometric-scaling models outrank traditional (ecological) linear models toward estimating species abundance on broad spatiotemporal scales, particularly when plentiful data are available from governmental and citizen-science monitoring programs (Robbins et al. 1986, Sullivan et al. 2009, Pardieck et al. 2014). In Chapter 4, I showed that hierarchical models estimating species mass-abundance scaling consistently outranked models considering only traditional linear effects of ecological covariates. My work in this chapter advances fundamental and applied wildlife ecology by (a) showing that trait-based (e.g., allometric-scaling) models outrank traditional models of single-species (range-wide) abundance patterns, (b) developing a novel approach to modeling an emergent property of species populations as a function of traits and traditional (ecological) covariates, and (c) highlighting important data and analytical considerations necessary to improve such broad-scale (continental) investigations and to expand the relevance of associated findings to global conservation. That said, however, model derived estimates and extrapolations underestimated similar quantities based on citizen-science monitoring programs and their statistical tools (i.e., information useful for corroborative or comparative purposes, but not necessarily treated as truth due to various data-quality concerns; Sullivan et al. 2009, Fink et al. 2020). Therefore, negatively biased estimates and extrapolations likely manifested due to the shortcomings of existing analytical software—causing protracted model runtimes, even operating in parallel on a high-powered computing cluster (e.g., analyses of *N*-mixture model sensitivity to the choice of equilibrium

abundance, *K*, necessitate many evaluations; Royle 2004, Dail and Madsen 2011, Fiske and Chandler 2011, Dennis et al. 2015). This work highlights the need for enhanced tools capable of integrating over or marginalizing discrete latent states in hierarchical species abundance models (e.g., as in Bayesian applications; Ponisio et al. 2020, Yackulic et al. 2020), especially considering multi-decadal datasets collected on macroecological (continental) scales.

Challenges associated with hierarchical descriptions of biological organization across ecological systems (i.e., the "economy of nature") have been well documented in ecology for centuries (Linnaeus 1751, Lyell 1853, Egerton 2007, Wells 2020), yet conclusions about how to best address system hierarchies are now becoming more apparent, particularly concerning single- and multi-species systems investigated on broad spatiotemporal scales (Brown and Maurer 1987, 1989, Hanski 1998a, b, 1999, Leibold et al. 2004, Holyoak et al. 2005). Ecology is increasingly data rich thanks to novel technologies that help researchers and students connect extensive wildlife monitoring with near real-time and historical datasets describing essential variabilities within and between diverse landscapes and aquascapes (Luo et al. 2011, Elliott et al. 2016, Klug et al. 2017). Future studies leveraging multi-scaled data to evaluate ecological phenomena across spatiotemporal dimensions will be most effective in increasing model accuracy and precision as well as elucidating scales at which phenomena manifest. Such research will help improve the breadth and depth of basic and applied theories, and novel inquiries will likely facilitate enhanced conservation through revealing clearer linkages between ecological patterns and processes, including how linkages can be modified and influenced. With respect to conservation of global biodiversity, data-rich and multi-scaled ecological research comprises a critical effort of scientific inquiry and wildlife management during a geological epoch of significant human impacts to Earth's geology, ecosystems, and climate—the Anthropocene.

REFERENCES

REFERENCES

Araújo, M. B. and A. T. Peterson. 2012. Uses and misuses of bioclimatic envelope modeling. *Ecology* 93:1527-1539.

Arrhenius, O. 1921. Species and area. *Journal of Ecology* 9:95-99.

Arthington, A. H., N. K. Dulvy, W. Gladstone, and I. J. Winfield. 2016. Fish conservation in freshwater and marine realms: status, threats and management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 26:838-857.

Bakker, K. K., D. E. Naugle, and K. F. Higgins. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. *Conservation Biology* 16:1638-1646.

Brown, J. H. and B. A. Maurer. 1987. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. *American Naturalist* 130:1-17.

Brown, J. H. and B. A. Maurer. 1989. Macroecology: the division of food and space among species on continents. *Science* 243:1145-1150.

Cunningham, M. A. and D. H. Johnson. 2006. Proximate and landscape factors influence grassland bird distributions. *Ecological Applications* 16:1062-1075.

Dail, D. and L. Madsen. 2011. Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics* 67:577-587.

Dennhardt, A. J., M. E. K. Evans, A. Dechner, L. E. F. Hunt, and B. A. Maurer. 2016. Macroecology and the theory of island biogeography: abundant utility for applications in restoration ecology. Pages 455-483 *in* Foundations of Restoration Ecology, Second Edition, M. A. Palmer, J. B. Zedler, and D. A. Falk (Eds.). Island Press, Washington, DC, USA.

Dennis, E. B., B. J. T. Morgan, and M. S. Ridout. 2015. Computational aspects of *N*-mixture models. *Biometrics* 71:237-246.

Egerton, F. N. 2007. A history of the ecological sciences, Part 23: Linnaeus and the economy of nature. *The Bulletin of the Ecological Society of America* 88:72-88.

Elliott, K. C., K. S. Cheruvelil, G. M. Montgomery, and P. A. Soranno. 2016. Conceptions of good science in our data-rich world. *BioScience* 66:880-889.

Falk, D. A. and C. I. Millar. 2016. The influence of climate variability and change on the science and practice of restoration ecology. Pages 484-513 *in* Foundations of Restoration Ecology, Second Edition. Palmer, M. A., J. B. Zedler, and D. A. Falk (Eds.). Island Press, Washington, DC, USA.

Fink, D., T. Auer, A. Johnston, M. Strimas-Mackey, O. Robinson, S. Ligocki, W. Hochachka, et al. 2020. eBird Status and Trends. Copyright © 2020 Cornell Lab of Ornithology.

Reproduced by permission of Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/ebirdst.2019>. Accessed Jan 2021.

Fiske, I. J. and R. B. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43:1-23.

Hampe, A. 2004. Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography* 13:469-476.

Hanski, I. 1998a. Connecting the parameters of local extinction and metapopulation dynamics. *Oikos* 83:390-396.

Hanski, I. 1998b. Metapopulation dynamics. *Nature* 396:41-49.

Hanski, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. *Oikos* 87:209-219.

Holyoak, M., M. A. Leibold, N. M. Mouquet, R. D. Holt, and M. F. Hoopes. 2005. Metacommuninites: a framework for large-scale community ecology. Pages 1-31 *in* Metacommunities: Spatial Dynamics and Ecological Communities, M. Holyoak, M. A. Leibold, and R. D. Holt (Eds.). University of Chicago Press, Chicago, IL, USA.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Monographs in Population Biology, Volume 32. Princeton University Press, Princeton, NJ, USA.

Hubbell, S. P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology* 19:166-172.

Hubbell, S. P. 2006. Neutral theory and the evolution of ecological equivalence. *Ecology* 87:1387-1398.

Kéry, M. and J. A. Royle. 2016. Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance, and Species Richness in R and BUGS, Volume 1: Prelude and Static Models. Academic Press, Cambridge, MA, USA.

Kéry, M. and J. A. Royle. 2021. Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance, and Species Richness in R and BUGS, Volume 2: Dynamic and Advanced Models. Academic Press, Cambridge, MA, USA.

Kéry, M. and M. Schaub. 2011. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Cambridge, MA, USA.

Klug, J. L., C. C. Carey, D. C. Richardson, and R. Darner Gougis. 2017. Analysis of high-frequency and long-term data in undergraduate ecology classes improves quantitative literacy. *Ecosphere* 8:e01733.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601-613.

Levins, R. 1970. Extinction. *In* Some Mathematical Questions in Biology, M. Gerstenhaber (Ed.). American Mathematical Society, Providence, RI, USA.

Linnaeus, C. 1751. Specimen Academicum de Oeconomia Naturae. *Amoenitas Academicae* 2:1-58.

Luo, Y., K. Ogle, C. Tucker, S. Fei, C. Gao, S. LaDeau, J. S. Clark, et al. 2011. Ecological forecasting and data assimilation in a data-rich era. *Ecological Applications* 21:1429-1442.

Lyell, C. 1853. Principles of Geology or, The Modern Changes of the Earth and its Inhabitants Considered as Illustrative of Geology. J. Murray, London, UK.

MacArthur, R. H. and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373-387.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Monographs in Population Biology, Volume 1. Princeton University Press, Princeton, NJ, USA.

Pardieck, K. L., D. J. Ziolkowski, Jr., and M.-A. R.Hudson. 2014. North American Breeding Bird Survey Dataset 1966–2013, version 2013.0. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD, USA. <http://www.pwrc.usgs.gov/BBS/>. Accessed Apr 2015.

Ponisio, L. C., P. de Valpine, N. Michaud, and D. Turek. 2020. One size does not fit all: customizing MCMC methods for hierarchical models using NIMBLE. *Ecology and Evolution* 10:2385-2416.

Preston, F. W. 1962. The canonical distribution of commonness and rarity: Part I. *Ecology* 43:185-215.

Riffell, S. K., A. P. Monroe, J. A. Martin, K. O. Evans, L. W. Burger, Jr., and M. D. Smith. 2015. Response of non-grassland avian guilds to adjacent herbaceous field buffers: testing the configuration of targeted conservation practices in agricultural landscapes. *Journal of Applied Ecology* 52:300-309.

Robbins, C. S., D. Bystrak, and P. H. Geissler. 1986. The Breeding Bird Survey: its first fifteen years, 1965-1979. Resource Publication 157, U.S. Fish and Wildlife Service, Washington, DC, USA.

Rosenzweig, M. L. 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge, MA, USA.

Royle, J. A. 2004. *N*-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60:108-115.

Royle, J. A. and R. M. Dorazio. 2008. Hiearchical Modeling and Inference in Ecology. Academic Press, Cambridge, MA, USA.

Scholtz, R., J. A. Polo, S. D. Fuhlendorf, and G. D. Duckworth. 2017. Land cover dynamics influence distribution of breeding birds in the Great Plains, USA. *Biological Conservation* 209:323-331.

Shahan, J. L., B. J. Goodwin, and B. C. Rundquist. 2017. Grassland songbird occurrence on remnant prairie patches is primarily described by landscape characteristics. *Landscape Ecology* 32:971-988.

Sullivan, B. L., C. L. Wood, M. J. Iliff, R. E. Bonney, D. Fink, and S. Kelling. 2009. *e*Bird: a citizen-based bird observation network in the biological sciences. *Biological Conservation* 142:2282-2292.

Vickery, P. D., P. L. Tubaro, J. M. Cardoso da Silva, B. G. Peterjohn, J. R. Herkert, and R. B. Cavalcanti. 1999 Conservation of grassland birds in the Western Hemisphere. *Studies in Avian Biology* 19:2-26.

Wells, A. 2020. Kant, Linnaeus, and the economy of nature. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences* 83:101294.

Yackulic, C. B., M. Dodrill, M. Dzul, J. S. Sanderlin, and J. A. Reid. 2020. A need for speed in Bayesian population models: a practical guide to marginalizing and recovering discrete latent states. *Ecological Applications* 30:e02112.