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Improving Understanding of Forest Communities and Biodiversity with Multi-Dimensional Landscape Gradients

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IMPROVING UNDERSTANDING OF FOREST COMMUNITIES AND BIODIVERSITY WITH MULTI-DIMENSIONAL LANDSCAPE GRADIENTS

A Dissertation Presented

by

BENJAMIN J. PADILLA

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IMPROVING UNDERSTANDING OF FOREST COMMUNITIES AND BIODIVERSITY WITH MULTI-DIMENSIONAL LANDSCAPE GRADIENTS

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DEDICATION

This dissertation is dedicated to my family. To my Mom and Dad for letting me bring salamanders, snakes, and turtles home. And to my brothers and sister, who put up with me telling them things they didn’t care about whenever we went for a hike. And to my little nieces whose curiosity inspires me! And, in pursuit of a reunited Heaven and Earth.

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Of course, none of this would have been possible without Chris, my advisor. I would also like to thank Dave Bloniarz, whose offhand comment of a “new professor who likes salamanders” (that was you Chris) while visiting my 9th grade environmental science classroom in Springfield set me on a path to working with Chris as a doctoral student. I especially thank my committee for the time, comments, feedback, academic and emotional support! Thanks go out, as well, to those in my academic past who have spurred me on in this journey through undergrad – Greg Keller, Dorothy Boorse, Chuck Blend – and my masters work – Amanda Rodewald.

I extend the deepest and most sincere thank you to all members, current and former, of the Sutherland, Morelli, and Warren lab groups, without all of your academic and emotional support I know I would have given up long ago. I especially want to thank the following folks: Toni Lyn Morelli who has been a fantastic resource and support in all aspects of grad school and academic life; Joe Drake (and Olga and Beede) for keeping me sane; Donovan Drummey for always staying cheerful!; Alexej Siren for giving me the hope to carry on; Kadambari, Nigel, and the many more I’m forgetting who have given me feedback on work, or just a supportive smile.

Most deeply I acknowledge my family to whom this is dedicated. Mom, Dad (and Marcy!), Luke, Erin (and Nilly!), Jacob, Jose, Marta, Esteban, Abi, Ana, and Moriah. All of you are more important to me than you know.

ABSTRACT

IMPROVING UNDERSTANDING OF FOREST COMMUNITIES AND BIODIVERSITY WITH MULTI-DIMENSIONAL LANDSCAPE GRADIENTS

SEPTEMBER 2020

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This dissertation was motivated by a desire to understand the effects of habitat degradation and urbanization on a single species in a single study system in western Massachusetts, the red-backed salamander (*Plethodon cinereus*), but along the way unexpected conceptual and methodological hurdles caused the work to grow into a multi-species, multi-region, and multi-scale endeavor. As I designed my dissertation research and began considering approaches to quantifying heterogeneity and human influence in my study landscape, I recognized inconsistencies in methods used to define and quantify landscape metrics, particularly in urban systems. To investigate further, I conducted a critical review of the literature to describe the current practices of landscape quantification in urban systems and to identify any patterns or trends. The review highlighted the fact that variability among definitions of 'urban' stems from inconsistent decision making around a set of core principles in landscape ecology, and I used these to establish a standardizing framework for landscape gradient quantification. I then applied this framework to 10 ecologically distinct metro-regions across the United States and

revealed a consistent pair of gradients that offer an updated multi-dimensional perspective of landscape heterogeneity that intuitively advances the one-dimension perspective dominating exiting approaches to studying ecological responses across gradients of human influence. Having developed a framework for gradient definition, and extending the single-axis lens through which ecological enquiry is made, I applied these approaches to first investigate environmental drivers of avian community size and structure, and second, to critically evaluate the validity of the red-backed salamander as an indicator for biodiversity in human-dominated landscapes.

Inconsistencies in definitions of "urbanization" are commonly attributed to the lack of general theory describing ecosystem function in urban landscapes. In Chapter 1, I review the literature on urban landscape quantification to identify patterns and best practices that could improve the process by which urban landscape gradients are defined and quantified. This review of 250 research articles revealed striking methodological consistency that aligns with the best practices of gradient definition in landscape ecology, these are: (1) selection of features to represent the urban landscape, (2) identification of associated spatial data to characterize these features, and (3) selection of an ecologically appropriate spatial scale. However, the review also highlighted apparent inconsistencies in urban gradient definition that arise from ad-hoc and ambiguous decision making at each of these stages, and demonstrated that ecologically justified and transparent decision making can standardize gradient definition and contribute to improved understanding of ecosystem processes in human-dominated landscapes (Padilla & Sutherland, 2019).

In Chapter 2, I address the lack of standardized heterogeneity metrics that can be used to jointly measure multi-regional ecological responses that has hindered the generalization of urban stressors on ecological communities. I coupled the transparent methodological framework developed in Chapter 1 with a multivariate statistical analysis of land use data to quantify landscape structure in 10 medium sized cities representing the dominant ecoregions of the United States to determine whether consistent and biologically meaningful landscape metrics emerge across spatial domains. This work revealed two dominant axes of spatial variation that are intuitively consistent with the characteristics of human-dominated landscape mosaics but are overlooked when defining landscapes along a single axis of variation. In the context of representative landscapes in the United States, these gradients describe variation in the characteristic physical (soft to hard) and natural (brown to green) structure of landscapes influences by human activity. To develop the ecological relevance of the dual-axis landscape definition, I explored the response of American robin (*Turdus migratorius*) occupancy to these gradients across the 10 cities. This case study demonstrated that robins generally respond similarly and strongly to both landscape axes and that a multi-dimensional perspective reveals ecological nuance that may otherwise be overlooked.

In Chapter 3, I apply the concepts developed in the previous two chapters to my study system in western Massachusetts. I tested two leading theories regarding how habitat fragmentation in human-dominated landscapes impacts species communities: island biogeography theory, and spatial heterogeneity. In the case of island biogeography, I expected species diversity to linearly decline as the degree of fragmentation and human-modification to the landscape increased, whereas, spatial heterogeneity would result in a quadratic response where species diversity is greatest in moderately disturbed landscape mosaics. These hypotheses were evaluated with data on the bird communities collected at

42 sites in a 3-year field study that were analyzed using a hierarchical model that allows for estimation of site-specific abundance of each species and species richness while simultaneously accounting for imperfect detection. This analysis revealed a strong non-linear community response to both axes of the multi-dimensional landscape (soft-hard and brown-green) that suggested increased heterogeneity promotes higher species abundance as well as species richness. At the species level, there was variation that corresponded with variation in known habitat preferences and life history traits. These results suggest that variation in species richness follows expectations of the spatial heterogeneity hypothesis that predicts greatest diversity in moderately disturbed landscape mosaics. I hypothesize that this process results from a greater diversity of habitat types available in landscape mosaics, and greater structural complexity within forest fragments that are characteristic of heterogenous mosaics.

Finally, in Chapter 4 I provide a rare empirical assessment of the indicator species concept. Specifically, I evaluate the red-backed salamander (*Plethodon cinereus*) as an indicator of forest biodiversity in human-dominated landscapes. During my 3-year field study, in addition to avian community data, I collected occurrence and abundance data for trees, soil invertebrates and red-backed salamanders at each of the 42 sites. These data were analyzed using a joint-species distribution model to evaluate the salamander's indicator potential under the premise that species within a community will generally exhibit a shared response to gradients of human influence, and that an ideal indicator species represents an exemplar of the shared community response. I compared this novel approach to indicator species selection with a commonly used metric for identifying indicator species. Despite the frequency with which salamanders are promoted as

indicators of forest condition, my results provided no evidence that they are effective indicators for biodiversity based on established conceptual underpinnings of indicator species. As with the avian community, biodiversity showed a non-linear response to the dual axes of human influence where richness is highest in heterogenous landscape. Species that were identified as candidate indicators were species characteristic of edge habitat and dense forests which are common in human-dominated landscape mosaics.

In summary, my dissertation provides much needed methodological improvements to landscape gradient quantification in human-dominated systems and demonstrates the applicability of this framework both at a national scale, as demonstrated across the United States, and the local scale as demonstrated in my field system in Western Massachusetts. This framework results in a multi-dimensional perspective of landscape heterogeneity that extends does a better job of representing complex landscapes beyond single-axis measures that confound two intuitive gradients of human influence. I have demonstrated how such a multi-dimensional perspective sheds light on the processes driving the landscape scale patterns of biodiversity and can be used to build evaluate process-based conceptual models for identifying indicator species. In doing so, this work presents a standardizing framework for landscape gradient quantification in human dominated landscapes, an identification of the existence of unifying measures of human influence, and a demonstration of how coupling this approach and a multi-dimensional perspective offers an general framework for understanding spatial variation in ecological communities that exist in human dominated landscape mosaics.

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CHAPTER 1

A STANDARDIZED FRAMEWORK FOR TRANSPARENT QUANTIFICATION OF URBAN LANDSCAPE GRADIENTS

1.1 Introduction

The global human population has now surpassed 7.5 billion and is expected to reach 10 billion by 2050 (United Nations 2017). This growth has resulted in landscapes that are becoming increasingly dominated by sprawling urban centers. As a result, once natural landscapes are being impacted by increasing population density, impervious surface (McKinney, 2008), and environmental pollutants (McDonnell & Hahs, 2013). Urbanization is also known to directly impact ecosystems by altering species diversity (McKinney, 2008), resource availability (A. D. Rodewald & Shustack, 2008), metapopulation dynamics (Padilla & Rodewald, 2015) and increasing potential for species invasion (Rija et al., 2014). At the same time, urbanization impacts human social and economic systems, both positively (e.g. better job opportunities, Foley et al. 2005), and negatively (e.g. overpopulation, poverty, Zhou et al. 2017). As a key point of intersection between social and natural ecosystems, management of urban landscapes is vital for successful conservation of global biodiversity, and developing a thorough understanding of ecological function in urban systems will ensure future urban development is ecologically, economically, and socially sustainable (Pataki, 2015; Shochat et al., 2006).

Presently, however, a general understanding of urban ecosystem function is limited, in large part, by a lack of consensus on the conceptual definition of ‘urban’ (Fischer et al., 2015). Several authors have advocated for a systemization of terminology and methods in urban ecology, in particular the way urban landscapes are defined, to achieve a better understanding of the effects of urbanization on ecosystems and ecosystem function (Mcintyre et al. 2000, Theobald 2004, McDonnell and Hahs 2008, Caryl et al. 2014, LaPoint et al. 2015). Regardless, since its formalization in 1990 (McDonnell & Pickett, 1990), the urban gradient concept has been widely used for investigating how ecosystem function responds to human dominated landscapes. Unlike common ecological gradients (e.g., temperature or elevation), measures of urbanization are exclusively user-defined and generated using data or data products that are assumed to represent urban associated features. As a result, urban gradients are said to be highly variable, generally inconsistent, and difficult to compare or replicate (Hahs & McDonnell, 2006; McDonnell & Hahs, 2008; Short Gianotti et al., 2016; Theobald, 2004).

A number of previous reviews of the urban gradient literature report several inconsistencies and variability in urban landscape definition. McIntyre et al. (2000) first noted the vague nature of urban landscape definitions and called for *methodological* consistency. Others have since criticized the subjectivity of commonly used but poorly defined categories of urbanization (Theobald, 2004), the analytic simplicity of the gradient generation, and the large variation in spatial scales used to investigate urban influence (du Toit & Cilliers, 2011; McDonnell & Hahs, 2013; Moll et al., 2019; Muderere et al., 2018). In response a number of attempts have been made to unify the conceptual and methodological domain of urban gradient definition. These range from simple classifications based on human population density (Marzluff et al., 2001), to complex composite measures incorporating demanding remote sensing methods

(Cadenasso et al., 2007), or locally specific but difficult to source, demographic and socio-economic data (Hahs & McDonnell, 2006). Until now these approaches, each with their own merits, have failed to result in community-wide consensus, and it is important to understand why.

Notably, there appears to be no *de facto* reason that urban-rural gradients should be treated differently than any other natural gradient, and in fact, there exists a set of 'best practice' principles in landscape ecology for general gradient definition (Turner et al., 2015). Rather than revisit the inconsistencies that exist in urban-rural gradient definition, instead I ask how well urban-rural gradient definitions adhere to existing best practices in landscape gradient definition:

1) identify relevant landscape content and typology
2) select representative spatial data
3) determine appropriate spatial scale and resolution

Here I review the recent urban ecology literature to identify how well authors followed this decision framework, and in doing so, attempt to identify similarities rather than differences, in the way urban gradients are defined. What naturally emerges is an improved understanding of urban gradient ecology *as* a discipline of landscape ecology is a decision framework for quantifying landscape gradients in human dominated systems that, and a decision framework that if explicitly acknowledged, is consistent, repeatable, and transparent.

1.2 Review of the Urban Gradient Literature

I conducted a *Web of Science* [5.2.1] search for peer reviewed publications over the last decade (January 2007 through January 2017) using the topic search terms

[“*Urban Gradient*” OR “*Urban Rural Gradient*” OR “*Rural Urban Gradient*”] and the *Web of Science* categories related to [“*ecological and natural sciences*”], which yielded 1,641 articles. Based on a reading of the abstracts, only articles were retained that explicitly invoked the urban gradient concept, yielding a final sample of 250 articles representing wide taxonomic, geographic, and intellectual distribution – these are the focus of this review. This review focused specifically on characterizing and quantifying the suite of decisions being made within the three components of the best practices for gradient definition in landscape ecology: (1) *the landscape*, i.e. identifying the physical, environmental, and demographic components thought to characterize urban context ; (2) *the data*, i.e., selecting and sourcing of data used to represent the urban context; (3) *the spatial scale*, i.e., determine the spatial scale of the urban influence. A glossary and concept key in Table 1.1 provides detailed definitions of all associated terms.

First, I recorded whether and how researchers *identified the urban landscape* using the following broad classifications (*sensu* Mcintyre et al. 2000): anthropogenic (e.g. housing, roads, agriculture), natural (e.g. forest, grassland), demographic (e.g. human population), and environmental (e.g., ambient noise, soil chemistry). In addition to *which* specific landscape features were used to characterize urbanization, I also recorded whether a single or multiple landscape metrics were used to characterize the urban gradient (e.g., *only* percent impervious surface or impervious surface *and* road proximity). Author-defined definitions of urban were also recorded when they were reported in the text, e.g., ‘≥50% impervious surface’ (Judith et al., 2013), and when such a definition was not reported, I derived a definition based on the features used.

Second, I recorded the *type and source of data* selected to quantify urbanization. Data types were assigned to one of four categories: open-sourced remote sensed, user generated remote sensed, data collected *in situ*, and other/unknown. I also recorded whether researchers used a subjective (e.g. qualitative assessment of ortho-imagery) or objective (quantitatively defined) classification, whether the resulting gradient was continuous or categorical, and whether the gradient was defined by compound multivariate metrics, or single univariate metrics.

Finally, I recorded several metrics associated with *the spatial scale* of the gradient definition and analysis. I recorded the landscape model as one of six categories (Table 1.1): *landscape level, grid cell, patch level, site level, site/patch with buffer,* and *point and radius*; the spatial extent defined by the total area encompassed by study system, and the scale of landscape analysis (e.g., grid size, buffer width, radius, see *spatial grain* in Table 1.1). Lastly, I recorded whether decisions of spatial scale were biologically justified by the authors.

In addition to reviewing gradient-specific components, I also recorded a number of general features of the research, including the location (state and country), the focal taxa, and whether the primary inference objective focused on ‘pattern’ (e.g., patterns of diversity along urban gradient), or on ‘process’ (e.g., identifying mechanisms driving patterns along gradient). The Concept Key (Table 1.1) provides expanded definitions for all of the themes, key words, and classifications used to conduct the review.

Table 1.1: The key to and definition of terms used in the review to code and quantify concepts.

CONCEPT KEY

The Landscape: features selected to describe change in urbanizing landscapes

(i) Physical, demographic, and environmental aspects of urbanizing landscapes

- Anthropogenic Land Cover ~ physical feature of the landscape that has been modified by human influence such as agriculture, pasture, housing, or industry
- Natural Land Cover ~ physical feature of the landscape that is not a result of direct human modification such as forest cover or waterways
- Demographic / Social ~ direct human component that is not structural, such as population or political boundaries
- Ecological / Environmental ~ local environmental characteristics, such as temperature or soil chemistry

(ii) Definition of urbanization

- Conceptual, or material definition of ‘urban’ used in establishing landscape gradient. Recorded as a brief description of urban context either explicitly or implicitly defined by the authors

The Data: quantitative and qualitative metrics used to analyze features of the urbanizing landscape

(i) Data type

- Remote-sensed / GIS data ~ collected using remote techniques such as satellites, typically geo-spatial; often freely available and open-source, may be generated by the user
- Field data ~ collected on site by researchers; may represent features of the ecological, demographic, or physical landscape
- Demographic / other ~ census data, topographic maps, or historical records

(ii) Objective / subjective

- Objective: urbanization value determined via analysis of quantifiable data
- Subjective: urbanization value assigned without use of data, or, data applied after establishing urban gradient

(iii) Analytical approach

- Univariate ~ gradient developed using a single landscape feature or data variable, typically represented as percent cover, or population
- Multivariate ~ gradient developed using more than one landscape feature or data metrics; analytical approaches may include: relative proportions of land-uses, or statistical ordination techniques
- Categorical ~ discrete binning of study locations into ‘urban’ categories based on data analysis or subjective assignment (e.g., urban, sub-urban, rural)
- Continuous ~ non-discrete numeric representation of landscape such as percent cover of landscape feature or derived from analytical output

The Spatial Scale: landscape conceptual model, spatial extent, and spatial

(i) Landscape conceptual model

- Landscape ~ urbanization is analyzed and quantified continuously across the entire spatial extent
- Gridded landscape ~ landscape extent divided into grid cells each of which is analyzed individually
- Patch level ~ urbanization analyzed for individual focal patches containing one or more study location, the landscape beyond patch boundary is not considered
- Site level ~ urbanization analyzed for each study location individually, landscape beyond site boundary is not considered
- Patch and buffer ~ patch, or site level, incorporating landscape features beyond patch/site boundary at a predetermined buffer distance
- Point and radius ~ study site or observation point, incorporating landscape features within a predetermined radius distance from each point

(ii) Spatial extent ~ the full extent of the study landscape for which the urban landscape gradient is analyzed

(iii) Spatial grain ~ the specific scale or scales (i.e. Meters, etc.) At which the gradient is analyzed

1.3 Results

I reviewed a total of 250 urban gradient articles from 121 peer-reviewed journals, with the most common being *Urban Ecosystems* (*n*=28) and *Landscape and Urban Planning* (*n*=21, Appendix A.1). The number of relevant publications was four times greater in 2016 than a decade previous (51 in 2016 vs. 12 in 2007). Our analysis included research conducted on all continents excluding Antarctica (Figure 1.1.A), however the geographic distribution of research was highly skewed towards North America (*n=104*) and Europe (*n=71*), with Asia (*n=26*), Latin America (*n=20*), and Africa (*n=7*) being underrepresented. Most studies took place in the United States (*n*=96), followed by Australia (*n*=18), France (*n*=13), and Hungary (*n*=10). Our sample included large cities, e.g. New York, NY, USA, as well as much smaller towns and villages such as Phalaborwa, South Africa (Coetzee & Chown, 2016). All major taxa were represented (Figure 1.1.B), although birds comprised more than a third of all studies (*n=87*), followed by invertebrates (*n=53*), and plants (*n=35*). Far fewer studies examined the effects of urbanization on herpetofauna (*n=20*), fish (*n=8*), or multiple taxa simultaneously (*n=* 13).

The *urban landscape* was universally defined using one or more anthropogenic, natural, demographic, or environmental features, including instances where landscape features were not explicitly identified by researchers. The majority used physical landscape features to inform definition of urbanization (*>80%*), with the most frequent being types of human dominated land-use or physical structures (e.g. residential housing, agriculture, or number of buildings; *n=195*), while natural landscape features (e.g. forest types, waterways) were less common (*n=124*). Demographic or environmental variables were used far less frequently, and when they were used, it was in addition to anthropogenic or natural landscape features. Based on classification into 4 broad classes of urban-defining features, very rarely were multiple feature classifications used to define urbanization (only 22.4% used > 1 feature type), and all four feature types were used in only 6 studies (2.4%, Figure 1.3.A).

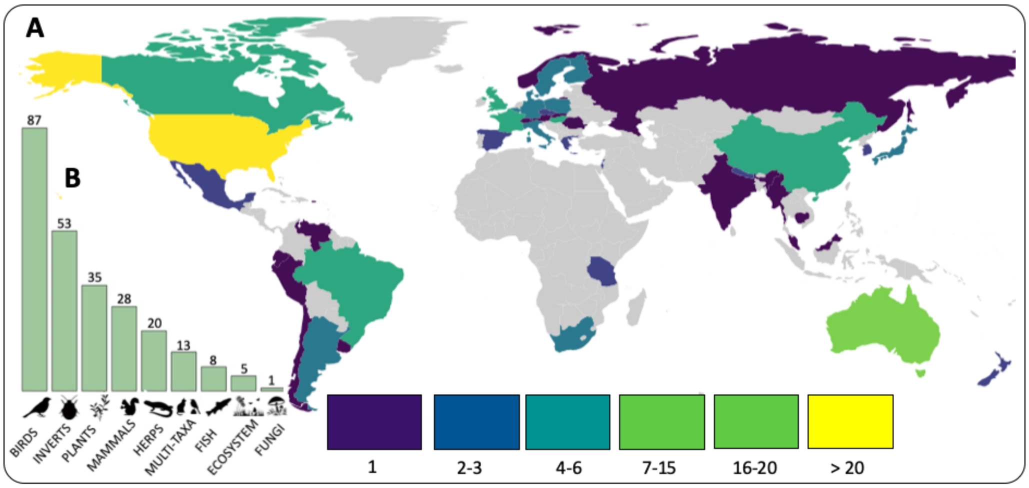

Figure 1.1: (A) The global distribution of urban gradient research from 2007 to 2017. The majority (n = 96) were conducted in the United States. Ten or more studies were conducted in only four countries: United States (96), Australia (18), France (13), and Hungary (10). This map highlights the lack of urban gradient research in regions such as sub-Saharan Africa, Central America, and Southeast Asia, where rates of urbanization are highest. (B) The number of studies by taxa. 'Herps' includes both reptiles (n = 8) and amphibians (n = 12). 'Multi-taxa' studies are those that included more than one species of different taxa, while 'Ecosystem' studies analyzed a suite of data to capture ecosystem level response.

Landscape data was used to quantify the urban gradient in the majority of the studies reviewed (*79.6%*); the remaining (*n=51*) studies generally selected study locations along an assumed gradient of urbanization informed by subjective assessments such as a pond's proximity to the nearest building (Villasenor et al., 2017) or presence/absence of housing subdivisions (Botch & Houseman, 2016). Remote-sensed data, GIS data, and ortho-imagery, either open-source or user-generated, were unsurprisingly the most frequently used data types. Data recorded *in situ* (e.g., environmental variables collected at the study sites) and other assorted data types (e.g. census records, topological maps) were less common. In some cases (*9.2%*) authors were not explicit, or were otherwise unclear, about the type or source of the data used to define the urban gradient.

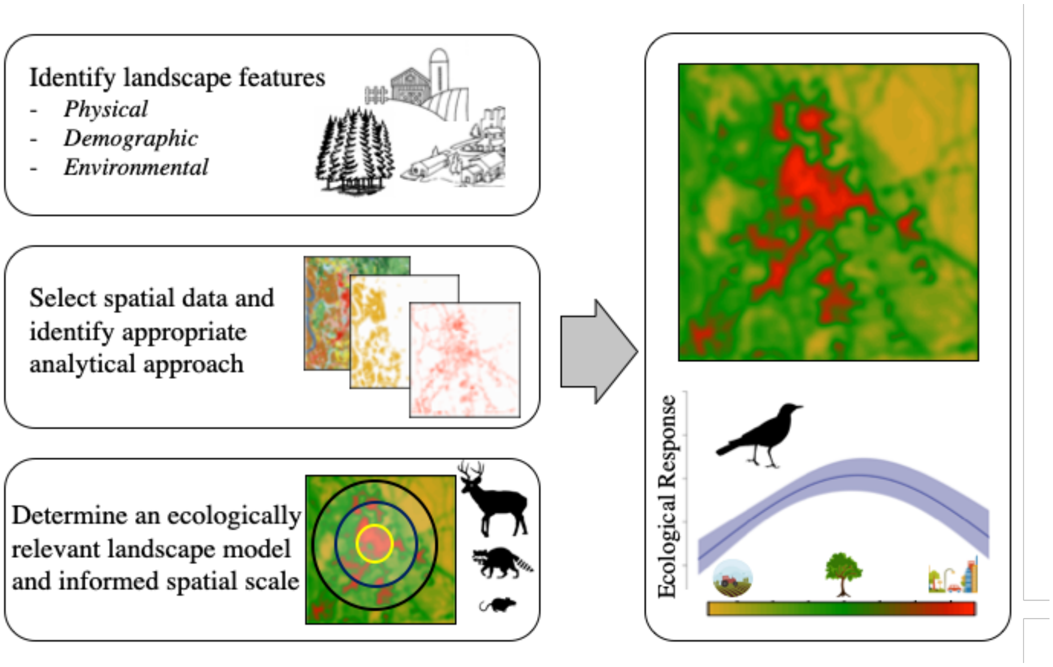

Figure 1.2: The three-step framework for urban gradient definition, incorporating landscape conceptualization, data characterization, and scale selection in adherence to accepted methods in landscape ecology. To the right of the framework diagram is a visualization of urbanization output, interpretation, and ecological analysis once the landscape gradient framework has been implemented.

Based on definitions of objectivity (Table 1.1), the majority of researchers (*65.2%*) were objective in their gradient definition. Surprisingly, around 20% of the studies reviewed used a subjective definition of an urban gradient, instead relying on a qualitative determination (e.g., qualitative assessment of study locations), or qualitative categorization of the landscape. Multiple data variables (e.g. % impervious *and* % forest cover; *70.8%*) were used to characterize the urban gradient more often than a single feature. Authors used categorical gradients more often than continuous (*50.0% vs, 36.0%*, respectively, Figure 1.3.C). The number of categorical classes ranged from 2 to 10 (median = 4).

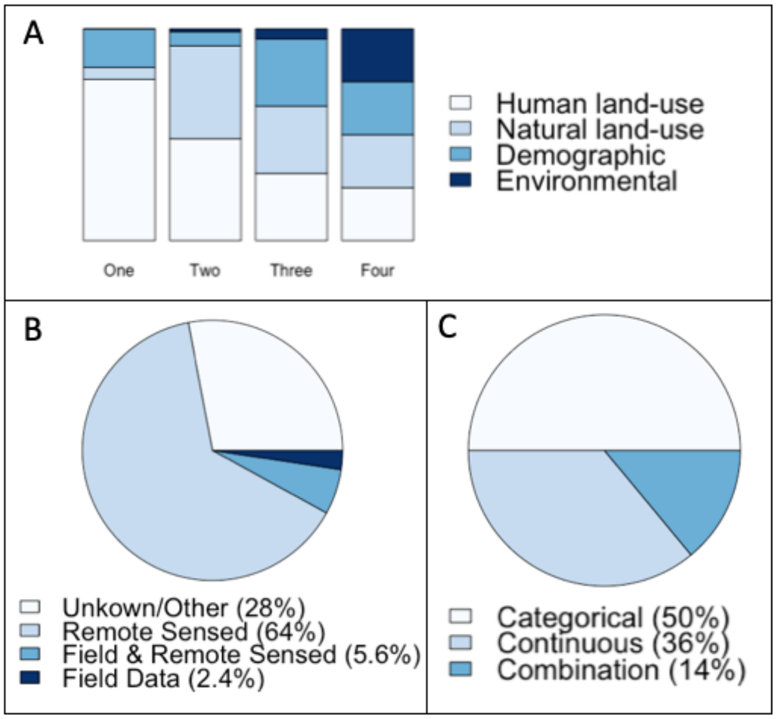

Figure 1.3: (A) The number of landscape features used in gradient definition. Proportions on each bar represent the percentage of studies using a given landscape feature type. (B) pie chart showing the distribution of data types used by studies reviewed. (C) pie chart showing categorical vs. continuous gradients. 'Combination' refers to studies where urbanization was considered as both a continuous and categorical predictor variable.

Spatial context of reviewed articles showed a great deal of variation both in how the urban context of a site was quantified and in the spatial scale used to define that urban influence. The two most common extent definition categories were point and radius (*27.2%*) and site level (*26.4%*) studies. These approaches vary significantly in their treatment of the landscape, the former incorporating features of the surrounding landscape matrix (ecology *of* cities), while the latter solely considers characteristics of the site itself (ecology *in* cities). The spatial scale used to define the area over which the urban influence is quantified varied drastically, ranging from a minimum of 20 *m* to a maximum of 100 *km* (mean=2655 *m*). More surprisingly, over two-thirds of all studies (*68.8%*) did not offer any ecological, environmental, or analytical justification for the spatial scale used. In testing whether the choice was implicit based on species ecology (e.g., resource use or home range), I found no relationship between spatial scale used and mean taxonomic body size which I used as a proxy for home range size (Appendix A.4).

1.4 Discussion

Urban-exurban regions, characterized by a high degree of physical, ecological, and social heterogeneity are complex landscapes expected to exert strong influence on biological communities. However, a lack of consistency in defining urban heterogeneity has limited the generality of ecological inference in human dominated landscapes (Li & Wu, 2004; McDonnell & Hahs, 2008; Theobald, 2004). Although often considered to be “novel ecosystems”, it is important to recognize that, in truth, they represent spatially heterogeneous spatial patterns like any traditional landscape. My review highlighted the fact that researchers consistently follow this general framework for landscape quantification, however, transparency, forethought, and ecological justification in the decision making was regularly lacking. The apparent differences in urban gradient definition that has been the focus of much criticism in previous reviews, therefore arise from when and how the same decisions are made, and can be attributed to specifics of the study system, species, or research objectives. I argue that apparent inconsistencies can in fact can be attributed to a lack of transparency in reporting and ecological justification in specific decisions. I advocate for the continued development of urban gradients following the established best practices in landscape ecology, but that these decisions be part of a transparent reporting process: (*1*) define of the characteristics of the landscape of interest, (*2*) select data that appropriately represent that definition, and (*3*) select the spatial scale that best matches underlying ecology. Doing so will encourage the consistency and clarity required for reproducible and relatable urban gradients, while maintaining flexibility for diverse taxonomic or geographic focus.

1.4.1 Defining the Landscape

Step 1 in the decision framework is a formal identification of the landscape features that that define areas as being more or less urban. Even when urbanization is based on ones' assumptions (i.e. is subjective), researchers implicitly use landscape features to classify the urban gradient. Changes to the physical landscape are among the most obvious impacts of urbanization and are almost universally used when quantifying urban landscapes. Therefore, it is unsurprising that variation in the extent of human-altered land-uses (e.g., agriculture, Verboven et al. 2012) or measures of human presence (e.g., impervious surface, Buxton and Benson 2016) are used to define it. When anthropogenic features weren't used, their inverse, the extent of natural land-cover, was used such as forest cover (Gortat et al. 2015, Haggerty and Crisman 2015), or fragment age (Magle et al., 2010). Some commonly used demographic variables such as city population depend upon socially constructed delineations or political boundaries with little ecological relevance. While such socio-political boundaries should certainly be considered in management of urban landscapes, they rarely overlap with meaningful ecosystem boundaries and should be avoided when evaluating ecosystem processes (Dallimer & Strange, 2015). Site-specific ecological or environmental data are valuable in that they often represent the most proximate drivers of ecological pattern, however because they are site-specific, cannot easily be extended to other systems (McDonnell &

Hahs, 2008). To reduce some of the variation in urban gradients local environmental features should be included in addition to a more generalizable suite of physical landscape variables (see example in Appendix A.5).

1.4.2 The Data

The majority of studies (*80.4%)* used landscape data in their quantification of the urban gradient, although there was variability in the types of data selected, and how those data were analyzed. In recent decades, the availability of high quality remote-sensed geospatial data has increased and offers a reliable data source for research in spatial ecology; unsurprisingly more than 70% of studies used some form of remote sensed data. Though some researchers used raw ortho-imagery to calculate customized geospatial statistics, in most cases, researchers relied on freely available land-use and land-cover databases developed at either the national (e.g. National Land Cover Database Homer et al. 2015, South African National Land Cover, Luck et al. 2010), or regional scale (e.g. Puerto Rico GAP Analysis Project, Gould et al. 2008) to generate quantitative measures of variation in urbanization. Creating personalized metrics directly from raw ortho-imagery may offer more control over thematic and spatial resolution, but these methods are neither intuitive nor accessible for most ecologists, and are often location or context-specific (Pettorelli et al., 2014). On the other hand, standardized national or regional datasets (e.g. Anderson Classification System for NLCD, Homer et al. 2015), while potentially coarse and imperfect, are highly reproducible. The ability to conduct spatial analysis using published data products that are freely available and have associated data processing procedures have obvious benefits, including reproducibility, transferability, and standardization, all of which should be considered when producing a landscape gradient (McDonnell & Hahs, 2013).

The majority of studies reviewed (more than *70%*) used multiple spatial data variables in landscape quantification, thereby increasing the likelihood that it will represent the true heterogeneity of the landscape (Hahs & McDonnell, 2006). Multiple variables were used in gradient quantification both as simple additive combinations of land cover classes (Lee et al. 2015), and more complex multivariate analyses like principle components analysis (Paukert & Makinster, 2009; Shustack & Rodewald, 2008; Smallbone et al., 2011), factor analysis (van der Walt et al., 2015), or cluster analyses (McLaughlin et al., 2014; Schmiedel et al., 2015). Multivariate approaches are preferred for quantifying spatially heterogeneous landscapes (Frazier & Kedron, 2017b; McGarigal et al., 2009); they are regularly used in landscape ecology to generate statistically meaningful landscapes (Li & Wu, 2004),or to reduce multiple highly correlated data into few, multivariate indices that describe variability in a landscape (Frazier & Kedron, 2017b; Hahs & McDonnell, 2006). It was unsurprising to find that studies using a multivariate approach were moderately more likely to observe a significant effect of urbanization on ecological process than those using a single variable ($p = 0.076$, Appendix A.4). National land-use and land-cover datasets (e.g., NLCD), in spite of potential downsides, offer a number of key benefits such as ease of access and quality control. Furthermore, landscape metrics such as this type of land-use and land -cover data, are naturally multi-colinear yet are important drivers of ecological process. Though they have been criticized for creating potentially misleading indices (Frazier & Kedron, 2017b) multivariate approaches are extremely valuable for consolidating the complex reality of heterogeneous landscapes into a meaningful metric (Wu & Hobbs, 2002). For these reasons, using accessible land-use and land-cover data with a multivariate analytical approach is ideal for urban gradient quantification.

1.4.3 The Spatial Scale

Any spatial analysis of landscape data should consider both the spatial extent (area of analysis) and spatial grain (resolution of analysis). We recorded five possible approaches used to define the spatial extent that differ conceptually in how area is defined (see Table 1 for details). The *patch mosaic paradigm* (site or patch level) views habitat as islands a sea of unsuitable landscape matrix ignoring conditions outside of the focal patch, whereas the gradient approach (*landscape level*) considers an entire heterogeneous landscape as a continuum of variously suitable habitat. In the context of urban landscapes, the former has been criticized for viewing patches of urban green space as set apart from the surrounding urbanization without integrating the complex social and physical characteristics of the landscape (Cadenasso et al., 2007). This ‘ecology *in* cities’ approach differs from the ‘ecology *of* cities’ gradient view in which ecological processes are viewed as interacting parts of an urban ecosystem (Boone et al., 2014; Zhou et al., 2017). While more than a quarter adopted the patch mosaic approach, the majority of studies in my review adopted the continuous gradient definition, an approach I see as better aligning with our current understanding of how ecological communities are adapting to urban settings (i.e., the ecology *of* cities, McPhearson et al. 2016).

Given that the choice of spatial scale is known to influence ecological response (Guisan et al., 2007; Martin, 2018), the dramatic variability in the spatial scales used in studies reviewed was surprising, a finding that has been corroborated by recent reviews

(Moll et al., 2019). Perhaps more alarming, however, was the nearly ubiquitous lack of justification for spatial scale used, more than two thirds of articles in this review (*68.8%*) offered no clear ecological justification for the spatial scale selected in analysis. When defining a gradient of influence, such as how urban a specific location is based on the surrounding area (e.g., grid cell size or buffer radius), the gradient itself is sensitive to data resolution and spatial scale, and these should be chosen to reflect that scale that matches the ecological processes of interest. For instance, more mobile species with large home ranges require a larger spatial scale than less mobile organisms, and a global land-cover database at a 1-km resolution should not be used to create an urbanization gradient at a 500-m scale. As an example, two studies investigating response of gray squirrel (*Sciurus carolinensis*) to urbanization used drastically different scales to assess urbanization (2-km surrounding focal urban parks, vs, the town in which focal park is located; Parker and Nilon 2012; Sarno et al. 2015); in this case, a more thoughtful consideration of the ecology of the species may have resulted in more similar urbanization analysis, and hence increases comparability. Scale of gradient analysis is one of the most significant drivers of variation and strength of ecological response both in conventional (i.e. natural) (McGarigal et al., 2016; Turner et al., 1989; Zeller et al., 2017) and urban systems (Cunningham & Lindenmayer, 2017; Locke et al., 2016) making it the most consequential decision involved. With this in mind, lack of consideration and ecological justification of spatial scale in urban gradient definition is especially concerning.

1.4.4 Towards a Global Understanding of Urban Ecology

My review of the contemporary urban ecology literature highlights the fact that analysis of urban landscapes is conceptually similar to that of any landscape pattern, and that any observed differences likely arise as a function of the ecological context within which the decisions are made. Rather than advocate for a novel and unique definition of ‘urban’, instead I advocate for increased candor and transparency in the shared decisions made in each step of the process. This clarity will serve to improve replicability and reproducibility of research in urban ecology, moving the community closer to a general understanding of ecological and ecosystem function in urban-exurban landscapes.

In an attempt to improve standardization in urban ecology, several authors have worked to develop a single unifying metric to define ‘urban’, yet widespread adoption has not occurred (Cadenasso et al., 2007; Hahs & McDonnell, 2006; Short Gianotti et al., 2016; Theobald, 2004). Each of these proposed methods have a number of valuable components, and yet fall short for several reasons. They lack ecological intuition and accessibility due to their computational or methodological complexity, for example, the reliance on detailed census and economic data that may not be available in all areas, and requires reclassification of Landsat imagery (Hahs & McDonnell, 2006). While valuable in many respects, these approaches do not offer flexibility in the process, nor do they encourage transparency for efficient repeatability. Adhering to the recommended standardized landscape gradient framework that emerges from this review ensures best practices from landscape ecology will be applied in urban gradient quantification. Additionally, it enforces critical consideration and justification when making heretofore implicit decisions, and will facilitate a progression toward increased transferability and reproducibility between definitions of urban landscapes.

Urbanization is a global issue that is most accelerated in south Asia and sub-Saharan Africa, yet, only *13.3%* of studies reviewed were conducted in Africa or Asia, revealing a striking geographic mismatch in where the effects of urbanization is investigated and where it has its greatest impact. It is vital to better understand ecosystem function on the front lines of urbanization in order to inform sustainable development practices. This mismatch exists taxonomically as well: the literature is replete with research describing distribution and abundance of urban birds and some groups of insects (*34.8%* and *21.2%* respectively), yet other groups, including reptiles and amphibians (*0.8%*) that are declining globally in response to anthropogenic influences, are vastly underrepresented (Figure 1.B). To fully understand ecosystem function in urbanizing landscapes it is vital to take a community-based approach and understand response of all taxa exposed to urban influences.

Human dominance of the global ecosystem has ushered in a new geological epoch defined by the human species – The Anthropocene (Zalasiewicz et al., 2010). Urbanization and human development continue to transform and degrade ecosystems, while species extinction rates have reached new highs. In the face of such rapid global change, it is increasingly clear that our future, and the future of global biodiversity, is tied to our ability to design and implement ecologically and socially sustainable cities. This endeavor requires a thorough understanding the complex interactions playing out in social-ecological systems, the ecology *of* cities. An overarching theory of urban ecology is hampered in part by inconsistencies in research methods and terminology surrounding definitions of ‘urban’. By reducing the variance in urban landscape quantification through intentional thought and transparency, we can move toward improved reproducibility and comparability of urban landscape metrics, move closer to a sustainable urban future.

CHAPTER 2

MULTI-DIMENSIONAL LANDSCAPE GRADIENT DEFINITIONS FOR HUMAN DOMINATED LANDSCAPES

2.1 Introduction

As the human population and associated ecological footprint expands, the effect of high rates of landscape transformation on resource and habitat availability, habitat quality, and species distributions is of increasing concern (Scheiner & Willig, 2008). In order to predict how natural systems are likely to respond to continued change, informed conservation and ecosystem management requires an understanding of how ecological processes respond to the underlying structure of heterogeneous landscapes (Turner, 1989). That is, landscape pattern must be understood and quantified in such a way to be explicitly linked to the ecological process. Nevertheless, well documented variability in the quality, complexity, and ecological relevance of conceptual descriptions and quantitative measurements of landscape structure contribute to a lack of general and scalable understanding of how ecology responds to landscape heterogeneity, particularly along gradients of human modification (Li & Wu, 2004; Wu & Hobbs, 2002).

The need for ecologically relevant measures of landscape heterogeneity prior to understanding drivers of ecosystem response has been recognized for decades (Watt, 1947), and over time numerous theoretical and applied solutions have been posited (du Toit & Cilliers, 2011; Gustafson, 2018; Li & Wu, 2004; Wu & Hobbs, 2002). The patch mosaic, or fragmentation paradigm defines landscape heterogeneity as a mosaic of suitable habitat patches of different quality situated within an un-suitable matrix (Zhou et al., 2014). This binary (habitat vs. not-habitat) representation of the landscape has proven valuable in many contexts, especially in regions of high spatial heterogeneity (Frazier & Kedron, 2017b). However, because the complex landscape mosaic to coarse binary categories has been criticized as an oversimplification that fails to consider the importance of inherent complexity and of the surrounding matrix (Frazier & Kedron, 2017b; Gustafson, 1998; Uuemaa et al., 2013).

Efforts to improve ecological relevance and realism of landscape characterizations has led to the development of models thought to better represent the continuous nature of landscape heterogeneity and ecological processes (Eigenbrod et al., 2011), including the variegation model (A. S. McIntyre & Barrett, 1992), continuum model (Fischer's 2006), and surface metrics (McGarigal et al. 2009). These, among others, extend a patch-centered perspective to incorporate the composition of the entire landscape, thereby extending ecological realism. Regardless of the metrics used, Costanza *et al.* (2019) argue that successful integration of ideas in spatial ecology across systems and scales requires an improved appreciation for what landscape descriptors are measuring, and how they relate to ecosystem processes.

In spite of recognized shortcomings in landscape metrics, there is support for the role of spatial heterogeneity in human dominated landscapes shaping ecological responses. In particular, species richness has been shown to decrease with increasing human-mediated disturbance in birds (Chace & Walsh, 2006; Sacco et al., 2015), invertebrates (Bennett & Gratton, 2012; Smith & Schmitz, 2016), plants (Adhikari et al., 2012; McMullin et al., 2016), and more (Cavia et al., 2009; Shu et al., 2016), often with a peak in areas of intermediate disturbance (Ackley et al., 2009; Clucas & Marzluff, 2015). Species specific responses, however, are variable and depend on the ecology of the species in question (Banaszak-Cibicka & Zmihorski, 2012; Lizée et al., 2011; Marzluff, 2017). Fragmentation and human population density have also been linked to decreases in movements and home range size in many species (Burdett et al., 2010; Marsh et al., 2004; Munshi-South et al., 2016; Patrick & Gibbs, 2010). Much of the literature, however, has shown very little support for relationship between various ecological processes and changes in the landscape (e.g., Aida et al., 2016; Cameron, Culley, Kolbe, Miller, & Matter, 2015; Dahirel, Seguret, Ansart, & Madec, 2016), or uncertain results (e.g., Hedblom & Soderstrom, 2010; Lee & Carroll, 2015), suggesting that observed responses to gradients of human influences may be context- or locale-specific and lack the generality that is required to advance ecological understanding in urbanizing systems.

Attempts to bolster the applicability and scalability of spatial metrics has led to landscape metrics that are almost exclusively represented as one-dimensional axes of variation despite the fact that landscape heterogeneity is highly dimensional (Cunningham & Lindenmayer, 2017; Hobbs, 1997), and as such, ecological processes are likely to respond to that underlying complexity. Thus, collapsing highly dimensional spatially structured landscapes into a relatively simple one-dimensional axis of variation is likely to fall short in terms of ecological realism, thus limiting the ability to infer links between landscape pattern and ecological process. Overlooking the underlying complexity of ecosystem function in heterogeneous landscapes is likely to have important consequences regarding how ecological processes are understood and managed in the Anthropocene. We propose an extension of the typical one-dimensional approach to landscape characterization in favor of the development of landscape measures that explicitly acknowledge the multiple dimensions of landscape heterogeneity.

In this paper, I evaluate the utility and ecological interpretability of a multi-dimensional approach to defining landscape heterogeneity for making inferences about species distributions in human dominated landscapes. The generality of multi-dimensional gradients is then demonstrated by jointly analyzing a set of urban-exurban landscapes in ten demographically similar but ecologically distinct cities in the United States and identify two significant and biologically intuitive axes of variation. We then demonstrate the ecological relevance of these axes by evaluating distribution patterns of the American robin (*Turdus migratorious*), a widespread generalist species commonly associated with areas of human activity, and highlighting the importance of quality landscape metrics in species management and ecosystem conservation.

2.2 Methods

I selected ten geographically distributed medium sized cities across the United States (population between 200,000 and 500,000), representing distinct Level I ecoregions as defined by the U.S. EPA (Omernik, 1995). These were Worcester, Massachusetts, Lexington, Kentucky; Jackson, Mississippi; Lincoln, Nebraska; Lubbock, Texas; Salt Lake City, Utah; Albuquerque, New Mexico; Bakersfield, California; Portland, Oregon; and Spokane, Washington (Fig. 1). For each city, I extracted 30-m resolution 2016 National Land Cover Database (Yang et al., 2018) for a 50-by-50 kilometer window surrounding the city center. This spatial extent was selected because it extended well into exurban regions, and thus represented the full extent of landscape heterogeneity for each city. I used freely available NLCD data to facilitate reproducibility of the approach, and to reflect dominant landcover types from ‘natural’ (e.g., forests, wetlands) to human ‘modified’ (e.g., industrial, pastures). Details for each city are provided in Table 2.1.

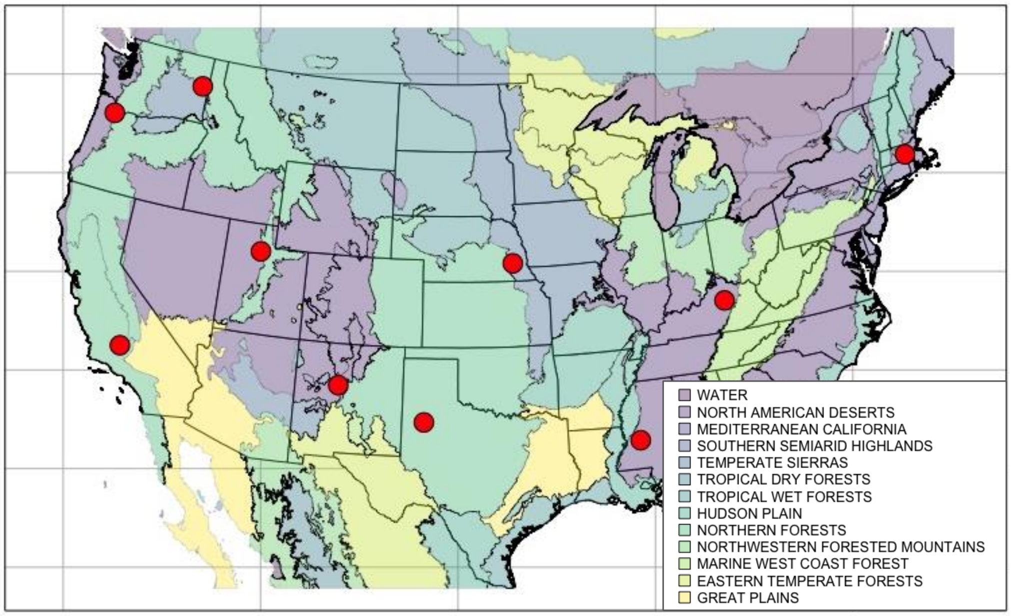

Figure 2.1:Map of entire study extent with locations of all study cities for landscape quantification and ecological case study. Background colors represent unique Level 1 EPA Eco-Regions. Study cities are represented by red points.

Landscape analyses followed the landscape quantification framework of Padilla and Sutherland (2019). In accordance with this framework, Table 2.2 provides definitions of, and justification for decisions made regarding landscape features, data, and spatial scales. Landscapes of study cities were characterized by a mosaic of natural (forests and wetlands) and un-natural (crop and developed) land-cover, as such, I selected NLCD data because it captures natural and human modified land cover and land use.

Table 2.1: List of ten urban-exurban regions used for landscape comparisons, including population size (2010 census) and US-EPA Ecoregion.

City, State	***Population***	***Level I Ecoregion***	***Open Water***	***Devel.***	***Forests***	***Scrub Grass***	***Crop Pasture***
Worcester, MA	185,877	ER5 – Northern Forests	3.33%	23.15%	65.51%	2.54%	6.11%
Spokane, WA	208,916	ER6 – NW Forested Mountains	1.23%	14.46%	31.31%	31.91%	20.62%
Salt Lake City, UT	200,591	ER6 – NW Forested Mountains	11.02%	23.00%	36.37%	23.34%	5.29%
Portland, OR	583,776	ER7 – Marine West Coast Forest	3.12%	37.06%	23.43%	7.85%	28.54%
Lexington, KY	323,780	ER8 – Eastern Temperate Forests	0.56%	15.31%	16.65%	1.03%	66.44%
Jackson, MS	164,422	ER8 – Eastern Temperate Forests	4.85%	30.11%	43.29%	12.16%	18.87%
Lubbock, TX	255,885	ER9 – Great Plains	0.15%	12.58%	0.23%	14.89%	72.15%
Lincoln, NE	287,401	ER9 – Great Plains	1.54%	13.02%	5.86%	29.4%	50.82%
Albuquerque, NM	560,218	ER10 – North American Deserts	0.23%	17.66%	15.96%	67.71%	3.37%
Bakersfield, CA	383,679	ER11 – Mediterranean	0.51%	13.96%	1.19%	37.93%	46.41%

Each pixel in the 30-m resolution NLCD raster is classified as a single cover type. We extracted binary surfaces of each class (1 if focal class, 0 if otherwise) and, to account also for the landscape surrounding a given location, i.e., to quantify the landscape context. A spatially weighted average for each pixel was computed using a Gaussian kernel, resulting in a continuous surface ranging from 0 (no focal class within smoothing kernel) to 1 (smoothing neighborhood entirely focal class). This was done for each NLCD category, resulting in a smoothed surface for each. The width of the kernel is set by a bandwidth parameter, σ, and should be determined by the ecological process in question (Boyce et al., 2017). A 500-m spatial scale was selected for this analysis based on the typical breeding home range size of the case study focal species, the American robin, established in the literature (Knupp et al., 1977). I tested sensitivity of landscape quantification to smoothing scale by replicating the analysis at 1,500-m (Appendix B).

All analysis was done in R Version 3.5.3 (R Core Team, 2019) and Gaussian smoothing used the 'smoothie' package (Gilleland, 2013).

To identify dominant patterns of variation in these data, we used Principal Components Analysis (PCA). PCA synthesizes multivariate datasets, such as the category-specific smoothed NLCD surfaces described above, into concise measures that describe dominate sources of variation and are well suited to large and potentially correlated datasets. Prior to PCA analysis, a single data matrix was produced from the spatially weighted smoothed raster surfaces of each land-cover class where each column consisted of smoothed pixel values for a single NLCD class. I conducted PCA on landscape data for each city individually and also for all cities combined such that variation across all cities was captured and values directly comparable. Dominant principal components (i.e., ≥10% variance explained) were identified and closely examined for ecological relevance. Finally, for the dominant components explaining ≥10% of the total variance, I produced a spatially explicit gradient of habitat heterogeneity where the value for each pixel in the resulting raster surface is PCA weighted average calculated as the sum of that pixel's smoothed NLCD values multiplied by the corresponding PC weight.

I tested the hypothesis that multi-dimensional measures of landscape heterogeneity have the potential to offer improved inference about ecological processes using observational data for the American robin (*Turdus migratorious*), a widespread generalist species widely considered to be human-adaptive. Robin detection histories were analyzed using a single season hierarchical occupancy model which simultaneously makes inference on occupancy while accounting for imperfect detection (Mackenzie et al., 2002). Stationary, complete checklists (non-reporting of a species assumed to be nondetection) from April 1st through September 30th 2018 were extracted from the Cornell Lab of Ornithology's *eBird* database (Sullivan et al., 2009) using the R package 'auk' (Strimas-Mackey & Hochachka, 2018), and detection data from all cities were pooled. Because there was substantial variation in the number of sampling locations in each city, the data were randomly thinned to a maximum of 250 locations to improve balance and reduce regional bias (Appendix B.1).

Hierarchical occupancy models consist of two sub-models, a logit-linear model describing detection probability (p) by location and sampling event, and a site-specific logit-linear model for occupancy (Ψ). I considered the following potential effects on detection probability: city (a categorical factor for a given city), sampling date, and sampling date squared (i.e., a quadratic effect to allow for moderate nonlinearity), and each of the two dominant landscape gradients (unique to each sampling location). Date was scaled (0 – 18) such that a one unit increase in date reflected 10 calendar days to improve parameter interpretation and aid model convergence. For the occupancy component, a city effect, each of the dominant landscape gradients, and all combinations of city-gradient interactions were considered (Table 2.3).

I adopted a two-stage modeling approach whereby I fit and compared all possible combinations of detection covariates, each with the most complex model for the occupancy component. Using Akaike's Information Criterion (AIC) to rank models, the best supported model for detection was carried over to the second stage where I compared models for occupancy. Finally, the model selected for inference was evaluated by examining model residuals and performing goodness of fit tests. Occupancy analysis was conducted in the package 'unmarked' (Fiske & Chandler, 2011), while AIC model selection and goodness of fit tests were done using the 'AICcmodavg' package (Mazerolle, 2019). All analyses, were conducted in R Version 3.5.3 (R Core Team, 2019).

Table 2.2: Decisions made within landscape gradient framework for analyzing urban landscapes in jointly across study cities and in the city-specific analysis. This follows the framework outlined in Padilla & Sutherland 2019. Justification provided here is in light of my dual analytical goals.

	Decision	***Justification***
1) Landscape Features	Physical land-cover and demographic land-use	'Land-cover' categories (i.e. forest, shrub) track changes in 'natural' landscapes, while 'land-use' (devel., crop) tracks the human footprint and approximate population density
2) Spatial Data	Remote-sensed, National Land Cover Data (2016)	NLCD land-cover data is readily available and is a consistent data-source to represent landscape features in all 10 study cities
3) Spatial Scale	500-m and 1,500-m Gaussian kernel	Spatial extent (50 *x* 50-km) chosen to capture sufficient spatial and ecological heterogeneity. Primary spatial grain (500-m kernel) selected to represent breeding home range of American robin. 1,500-m as a common scale in ecological research selected to compare effects of scale.

2.3 Results

Aggregate landscape composition across all cities was fairly balanced between the three dominant land cover categories – developed, forests, and agriculture (Table 2.1) and contained fifteen of the nineteen Anderson Land-Cover classes used by the NLCD, the remaining four ('Perennial Ice-Snow', 'Dwarf Scrub', 'Sedge-Herbaceous', 'Lichen') are restricted to Alaska or high elevation locations. City specific landscape composition, however, was variable; forested classes dominated Worcester and Spokane (39.08%, 30.22%), Albuquerque was largely scrubland (46.81%), Lexington dominated by pasture (62.31%), and agriculture in Lincoln, Bakersfield, and Lubbock (47.61%, 42.2%, and 72.15%, respectively).

Table 2.3: Model selection tables for both detection and occupancy components of the American robin analysis. Detection was assessed with the global occupancy model and the best model for detection was used in all models for occupancy.

	Detection Model Structure		K	AIC_c	ΔAIC_c	Wt	- LogLik
1	~ city*date+date^2+HS+BG	~ Ψ	63	6544.02	0.0	1	-3206.45
2	~ city*date+HS+BG	~ Ψ	62	6611.83	67.81	0	-3241.44
3	~ city*HS	~ Ψ	60	6998.33	454.31	0	-3436.84
4	~ city	~ Ψ	43	7001.75	457.73	0	-3456.69
5	~ date	~ Ψ	42	7038.66	494.64	0	-3476.20
6	~ BG	~ Ψ	42	7450.53	906.51	0	-3682.13
7	~ 1	~ Ψ	41	7450.69	906.67	0	-3683.27
8	~ HS	~ Ψ	42	7452.32	908.30	0	-3683.03

	Occupancy Model Structure		K	AIC_c	ΔAIC_c	Wt	- LogLik
1	~ ρ	~ city*HS+BG	44	6530.44	0	0.91	-3219.98
2	~ ρ	~ city*(HS+BG)	53	6535.21	4.77	0.09	-3212.80
3	~ ρ	~ city*HS	43	6542.84	12.40	0	-3227.23
4	~ ρ	~ city*(HS*BG)	63	6544.02	13.58	0	-3206.45
5	~ ρ	~ city+HS*BG	36	6567.86	37.42	0	-3247.10
6	~ ρ	~ city+HS+BG	35	6572.90	42.46	0	-3250.67
7	~ ρ	~ city+HS	34	6578.90	48.46	0	-3254.71
8	~ ρ	~ city*BG+HS	44	6580.24	49.80	0	-3244.88
9	~ ρ	~ HS*BG	27	6580.55	50.11	0	-3262.81
10	~ ρ	~ city*BG	43	6581.49	51.05	0	-3246.56
11	~ ρ	~ city+BG	34	6582.03	51.59	0	-3256.27
12	~ ρ	~ city	33	6587.86	57.42	0	-3260.23
13	~ ρ	~ BG	25	6490.33	59.89	0	-3269.76
14	~ ρ	~ HS+BG	26	6591.46	61.02	0	-3269.29
15	~ ρ	~ HS	25	6600.95	70.51	0	-3275.07
16	~ ρ	~ 1	24	6601.16	70.72	0	-3276.21

Principal components analysis of combined smoothed NLCD data yielded three important axes of variation explaining 37.1% of the variation in the combined landscape (Table 2.3), and between 42.60% and 54.89% in the individual city analysis (Appendix B.1). The first principal component explaining the largest proportion of data variation for the combined data (16.7%) was strongly negative for developed land-cover classes (impervious surfaces), with neutral or positive loadings for natural classes (forested, open, and agricultural, Table 2.4). Thus, this first descriptor of landscape pattern can be interpreted as a transition from hard (characterized by impervious surfaces) to soft (unpaved natural or agricultural) landscapes; which we refer to as the hard-soft gradient.

The second principal component explained 11.2% of the variation and showed a strong differentiation between types of non-impervious (soft) landscape types. Specifically, this axis distinguishes between human modified but un-developed areas (cultivated croplands) from more natural areas (forests or wetlands). This axis is intuitively interpretable as a shift from modified agricultural landscapes, to un-developed natural regions, a brown-green gradient. While the hard-soft axis does not distinguish between dominant types of soft landscapes, the second accounts for this variation between brown and green areas and represents an important second axis of variation.

The third principal component explained 9.3% of the total variation and was not used to produce a gradient surface as I only produced spatial metrics for principal components explaining greater than 10% of the total variance. Like the second axis, PC3 reflected a divergence between modified and un-modified undeveloped areas. While PC2 differentiated natural deciduous and mixed forests from modified croplands, the third axis is a gradient from evergreen forests and scrub, to pastures (Table 2.4). Both PC2 and PC3, therefore, can be interpreted as brown-green in different habitat and land-use types.

Due to the inherent complementarity of the two dominant components, this approach considers these axes together, however, it is worth considering these in the context of existing approaches. Hard-soft is consistent with traditional urban gradients focusing on the built environment (e.g., impervious surface or housing density) (McDonnell & Hahs, 2008; Moll et al., 2019; Padilla & Sutherland, 2019). Brown-green, on the other hand, is a less common measure of human modification and is typical only in research in agricultural landscapes.

Table 2.4: Dominant Principal Component axes. Variables with significant weight are in boldened. The first two axes were selected based on the a minimum 10% of total variation explained.

NLCD Layer		***Obs. Freq.***	***PC1***	***PC2***	***PC3***
Std.Dev.			1.581	1.295	1.182
Variance Explained (%)			16.7	11.1	9.3
Water	11 - OpenWater	2.70%	0.042	0.030	-0.04
Developed	21 - DevelOpen	6.49%	**-0.360**	0.055	0.017
	22 - DevelLow	6.72%	**-0.545**	0.047	-0.040
	23 - DevelMid	4.78%	**-0.553**	0.015	-0.125
	24 - DevelHigh	1.61%	**-0.392**	-0.007	-0.148
Barren	31 – Barren	0.79%	0.039	-0.017	-0.116
Forest	41 - ForestDeciduous	10.17%	*0.119*	**0.469**	0.171
	42 - ForestEvergreen	8.96%	*0.154*	0.269	**-0.349**
	43 - ForestMixed	2.14%	0.087	**0.433**	0.001
Shrubland	52 - Scrub/Shrub	10.56%	*0.151*	-0.012	**-0.554**
Herbaceous	71 -Grass/Herb	10.85%	*0.140*	**-0.339**	-0.282
Cultivated	81 - Pasture/Hay	11.25%	0.053	0.082	**0.446**
	82 - Crop/Cultivated	19.41%	*0.119*	**-0.491**	**0.387**
Wetlands	90 - WoodyWetl.	2.81%	0.043	**0.378**	0.157
	95 - HerbaceousWetl.	0.77%	0.032	0.075	-0.039

As a test of whether these axes are consistent at more local scales, the same analysis of NLCD data was conducted for each city independently as well. City specific analyses revealed the same dominant axes of variation as the combined analysis (Appendix B.2). As expected, the component weights of NLCD classes and absolute values of axes differed, nevertheless, interpretation of these axes remained consistent.

These landscape gradients, hard-soft and brown-green were applied in a case study with the American robin. This analysis included data from 1,703 sampling locations (sites) in all cities (range: 31 in Bakersfield to 250 in Worcester, Albuquerque, Portland, and Salt Lake City). There were a total of 5,779 sampling visits in all cities across all sites, with a mean number of visits per site of 1.95 (range: 1–172, Appendix

B.1). The overall proportion of sites with a minimum of one observation was 43.05%, which varied by city from 38.7% in Spokane, to 48.2% in Bakersfield (Appendix B.1).

Site-specific landscape gradient outputs (hard-soft and brown-green) were included as covariates in the occupancy models, resulting in a total of 27 candidate models for detection probability noting that date^2 was only included in models with date. These were fitted with the global occupancy model (Table 2.3). Of the 27 detection models considered, eight fully converged, of those the top model (AIC$_c$ weight=1.0) included additive effects of both landscape gradients, a quadratic effect of date and a city by date interaction (Table 2.3). In the second step, the best supported detection model was used to evaluate 16 candidate occupancy models. Here, a single model held the majority of support (AIC$_c$wt=0.91, Table 2.3) and included the effects of both landscape gradients, city, and an interaction city and hard-soft. The two best supported models showed consistent patterns in robin detectability and occupancy, however, standard errors were much larger in the second ranked model. Model evaluation and model-based predictions were carried out on the top ranked full model for detection and occupancy:

$$logit(\rho_{ij}) = city_i * date_{ij} + date_{ij}^2 + HS_i + BG_i$$

$$logit(\psi_i) \ = \ city_i * HS_i + BG_i$$

Where HS_i, BG_i, *and* $city_i$ are the site-specific covariates for each sampling location, *i*, and $date_{ij}$ is the survey date for sampling location, *i*, in survey, *j*.

There was a significant quadratic effect of survey date, such that detection probability increased, reached a peak, and declined (Figure 2.2; Appendix B.2). Robin detection varied significantly along the brown-green axis, with robins more likely to be observed in more ‘green’ landscapes (0.14 ± 0.05), and showed a negative relationship with hard-soft, though confidence intervals overlapped zero (-0.38 ± 0.04). Date of peak detectability ranged from April 1st in Bakersfield (*date* = 0.0) to July 23rd in Portland (*date*=11.3), while peak detection probability ranged from 0.330 in Worcester, to 0.871 in Jackson.

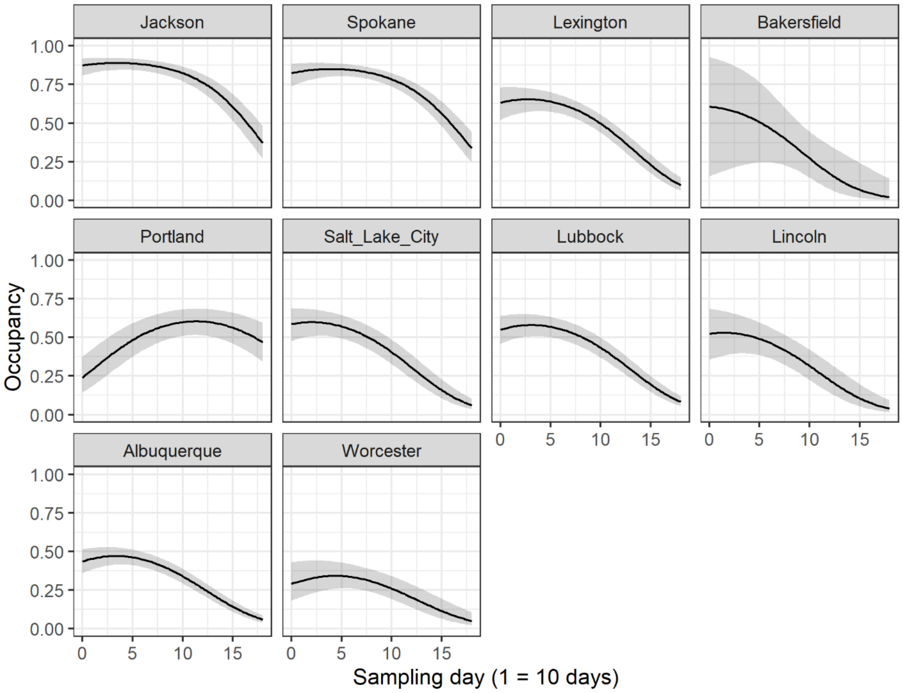

Figure 2.2: Robin Detection probability as a function of survey date for each city predicted from the top model. Grey shaded area represents 95% confidence intervals and solid is the expected value.

Mean robin occupancy varied slightly by study city, increasing significantly along the brown-green axis (0.52 ± 0.01). Regions characterized by less impervious surface, according to the hard-soft axis, had slightly higher occupancy probability (0.032 ± 0.57), however the direction and magnitude of this response varied regionally (Figure 2.2). Examination of model residuals and a Chi-Square goodness of fit test showed adequate model fit.

2.4 Discussion

Analysis of spatially heterogeneous landscapes surrounding ten metropolitan regions revealed two statistically important and ecologically intuitive axes of variation which challenges the conventional one-dimensional approach to investigating ecological responses in human-dominated landscapes. Despite regional variation in landscape composition and configuration (Table 2.1, Appendix B.1) the dual-gradient approach I present here consistently distinguished between two distinct types of anthropogenic influences: a hard-soft gradient capturing a continuum of the built human environment, and a brown-green gradient capturing the human agricultural footprint (Figure 2.3). This analysis of the robin data demonstrates that in addition to being fundamental properties of the landscape, these axes provide insight about species distribution across the landscape that would have been overlooked if viewed through a single-axis lens. This multi-dimensional perspective highlights the importance of considering the complexity of human-dominated landscapes and identifies a triangular distribution of human influence that presents an intuitive and generalizable framework for understanding patterns of ecological function and developing management strategies.

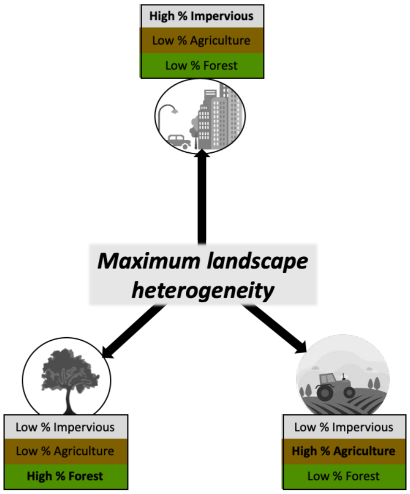

Figure 2.3: An example of the triangular distribution captured by a multi-dimensional landscape definition that differentiates between urban, agricultural, and natural portions of the landscape along dual axes of variation. Hard and soft portions of the landscape are sorted along the vertical axis, while brown and green regions along the horizontal. This results in a multi-dimensional perspective where heterogeneity is maximized at the center of both axes.

Landscape metrics that are transferable across ecosystem contexts are needed to improve understanding of human-dominated ecosystems and effectively synthesize local and regional conservation efforts. Attempts to produce universal metrics for human-footprint or urbanization have thus far failed to result in methodological consistency in part due to methodological complexity and data requirements. For example the HERCULES method (Cadenasso et al., 2007) requires users to classify the landscape into categories of building, surface cover, and vegetation using LiDAR data. Likewise, the method proposed by Seress *et al*. (2014) requires users to classify satellite imagery categorically as buildings, vegetation, or roads to train a semi-automated model. Metrics proposed as generalizable for use in human-natural systems also tend to focus on one axis of variation such as the built environment. Recently, a human modification gradient (Kennedy et al., 2019) was produced that incorporates all aspects of the human footprint, however, it results in a single metric making it difficult to decompose the relative effects of agriculture or urbanization. This multi-dimensional approach offers a flexible alternative that balances regional adaptability with local specificity and ecological realism to better understand mechanistic relationships between landscape structure and ecological process (Frazier & Kedron, 2017a; McDonnell & Hahs, 2008). We use an established multi-variate statistical approach to succinctly describe spatial heterogeneity and employ readily available NLCD data to incorporate complexity of the entire landscape into a clear and consistent dual axis of human-influence.

As the human population continues to grow, the urban, industrial, and agricultural infrastructure must be restructured to ensure future ecological integrity. Debate over how to do this in practice has led to sensitive concepts of land management such as land-sharing (the integration of natural systems into the mix of human land-uses) versus land-sparing (concentrating natural and human systems in large individualized blocks). Indeed, this discussion has typically focused on agricultural (Phalan et al., 2011), and urban (Norton et al., 2016) systems in isolation, when as demonstrated here, urban, agricultural, and natural landscapes represent three distinct aspects of landscape heterogeneity complex. Viewing the land-sharing versus land-sparing debate through a multi-dimensional lens of landscape heterogeneity views the landscape mosaic in a fully integrated agro-urban-natural system, highlighting the need for a fully integrated conservation landscape. Furthermore, the species that will benefit or suffer most from decisions related to how landscapes are managed is context-specific (Stott, 2016). Here the multidimensionality of that context is highlighted such that changes along one axis can result in unintended consequences as a result of responses to the other (Figure 2.4). Determining how to design a conservation strategy and manage a heterogeneous regional landscape for this species would require that the entire human-natural mosaic be considered and could be facilitated with a multi-dimensional approach to landscape context.

American robins are widely considered to be urban-adaptive and are thought to benefit from hard landscapes with human habitation (Evans et al., 2015; Morneau et al., 1995). However, my results consistently predicted higher occupancy in more forested (green) regions over areas predominantly agricultural (brown), while the effect of the hard-soft axis on robin occupancy varied by city both in terms of magnitude and direction (Figure 2.4). This regional variation in the effect of hard-soft on robin occupancy demonstrates the need to consider and decouple multiple dimensions of landscape heterogeneity. As a synanthropic species, it is reasonable to assume that robins would prefer hard regions of the landscape near human habitation, however, these results suggest that the synanthropic nature of robins is more nuanced. While highly adaptable and able to exploit many habitat types, natural areas in close proximity to urbanization (i.e., 'green' and 'hard') appear preferable over those in more agricultural landscapes. Prior research in heterogeneous temperate forested regions has reported higher presence and survival of robins in residential yards, woodlots and golf courses (Blair, 2004; Malpass et al., 2018), while studies in agricultural landscapes found that robins were more common in habitat fragments surrounded by urbanization than those surrounded by agriculture (Rodewald & Bakermans 2006).

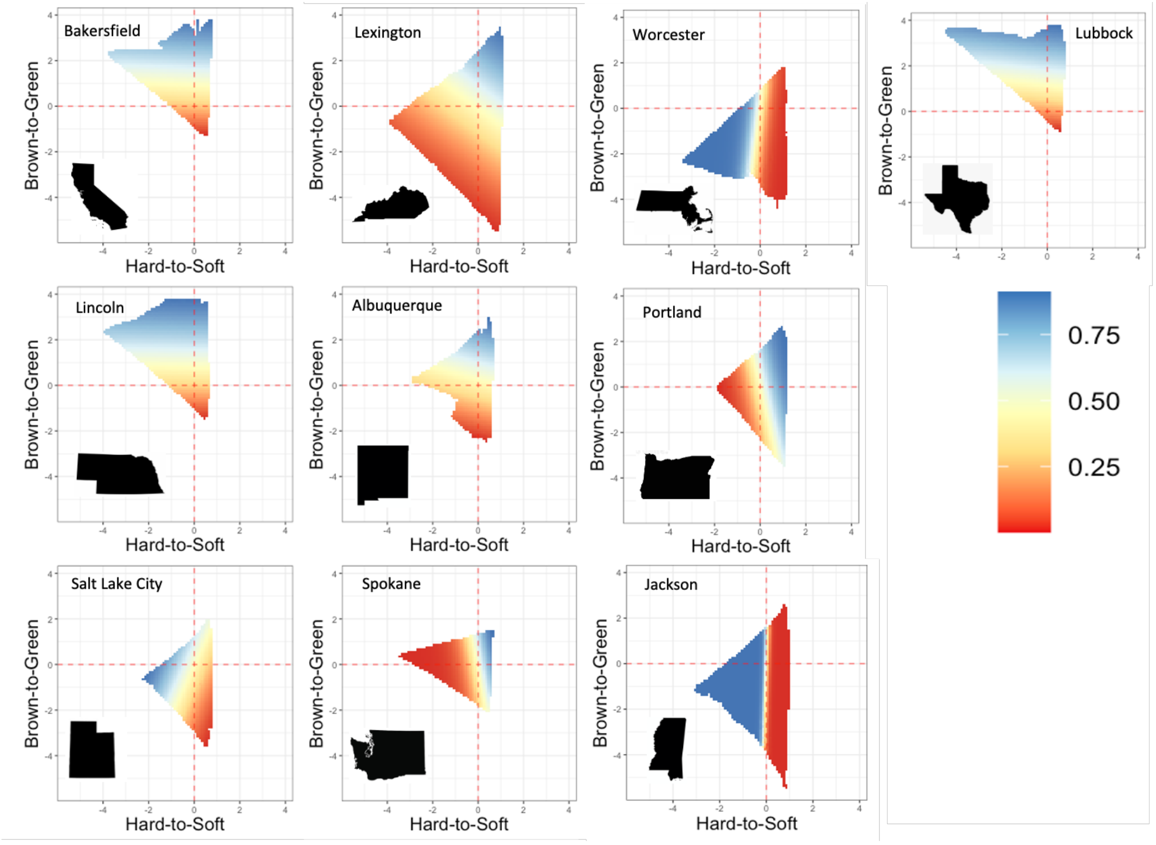

Figure 2.4: Surface plots depicting robin occupancy on both the brown-to-green (x axis) and hard-to-soft (y axis). Red portions represent areas of low occupancy, blue high occupancy. Variation in surface reflects values for the gradients in each city. Points represent sampling locations.

Robin occupancy was demonstrably influenced by dual axes of human-modification across the continental United States. This suggests that a continued reliance on one-dimensional landscape descriptors may result in ecosystem pattern being misinterpreted as inherent stochasticity (e.g., noise), when in fact it reflects unmodeled response to an overlooked component of the landscape. Bearing this in mind, management decisions that consider only a single aspect of the human-natural landscape may overlook or misinterpret ecological response and result in ineffective conservation plans (Fischer et al., 2006). A multi-dimensional framework mitigates this by offering complimentary metrics that provide more nuanced understanding of ecological response.

All measures of landscape heterogeneity are imperfect representations of reality and therefore fall short to varying degrees, and it is unlikely that any single metric will be ideally suited to every question of ecological pattern and process (Frazier, 2019). Adopting the multi-dimensional perspective can help move toward a more general understanding of landscape mosaics, and yet, oversimplified one-dimensional measures such as percent forest cover, or percent impervious surface continue to dominate the literature (Padilla & Sutherland, 2019). Identifying causal relationships between observed between spatial pattern and ecological process is often difficult, however, the multi-dimensional perspective of spatial heterogeneity has the potential to improve upon existing approaches and produce ecologically relevant landscape metrics that have the potential to provide valuable insight into the underlying ecological responses in human dominated landscapes.

CHAPTER 3

DRIVERS OF AVIAN COMMUNITY STRUCTURE ALONG A MULTI-DIMENSIONAL LANDSCAPE GRADIENT

3.1 Introduction

Spatial variation in the structure and composition of landscapes result in associated shifts in ecological communities. Identifying the drivers of geographic variation in community size and structure has been an enduring challenge in ecology since the days of Darwin (Roughgarden, 2009). In heterogenous landscapes disturbed by varying degrees and types of human influence, an improved understanding of the ultimate drivers of biodiversity is necessary to ensure long-term persistence of ecosystem function (Sol et al., 2014). Though human-dominated systems have long been considered as fundamentally distinct ecologically, numerous existing theories developed in natural systems are applicable in highly modified and fragmented landscape mosaics (Parris, 2018). The theory of island biogeography, for example, is applicable in both naturally and artificially fragmented systems and has been used to suggest that smaller habitat fragments more distant from “mainland” patches in space or due to an impermeable landscape matrix would be less species rich, following expected species area and isolation patterns (Davis & Glick, 1978; Itescu, 2018; Marzluff, 2008). Ultimately, however, the effects of habitat fragmentation on biodiversity remains a point of conflict because landscape mosaics often increase spatial heterogeneity of available habitat types at the landscape scale, which may increase species diversity (Fahrig, 2017; Roth, 1976; Turner, 2005).

The debate over whether the biodiversity of landscape mosaics is driven more by island biogeography theory or spatial habitat heterogeneity remains strong (Fahrig et al., 2019; Rybicki et al., 2020) as a growing body of literature has corroborated patterns in line with both hypotheses in mammals (Beasley & Maher, 2019), plants (Aronson et al., 2014), invertebrates (Bogyó et al., 2015) and birds (Chace & Walsh, 2006; Marzluff, 2008, 2017; Oliveira Hagen et al., 2017). Avian diversity in landscape mosaics has been particularly well studied, and broadly speaking has shown that as patches become smaller and more functionally isolated, species diversity, and functional and phylogenetic diversity shift toward more generalist and synanthropic species (Evans et al., 2018; La Sorte et al., 2018; Pagani-Núñez et al., 2019; Shochat et al., 2010). Others have reported a non-linear response of species diversity, abundance, and trait diversity such that bird diversity is greatest in heterogeneous landscape mosaics (Chace & Walsh, 2006; Marzluff, 2017) in support of the theory that habitat modification and fragmentation can increase habitat heterogeneity and species richness at the landscape scale (Fahrig et al., 2019). However, because much of this research has relied on relatively simple metrics to quantify structure and composition of the landscape mosaic that do not accurately represent true complexity of the landscape the reliability and generality of observed patterns is incomplete (McDonnell & Hahs, 2008; Padilla & Sutherland, 2019). Conventional metrics used to quantify landscape heterogeneity in human-dominated systems (e.g., percent forest cover Marzluff, 2008, human population Clucas & Marzluff, 2015, city size Batáry et al., 2018) tend to focus on the effects of a single aspect of the landscape, such as urbanization or agriculture, when in fact these are often interspersed as a mosaic that includes natural habitat. A recent effort to improve spatial metrics for ecological research in human-dominated landscapes (Padilla and Sutherland 2020) demonstrated that multi-dimensional landscape gradients better represent complex landscapes and can improve understanding of ecological process. As such, taking a multi-dimensional approach can offer a more nuanced understanding of the effects of patch size and isolation vs. habitat heterogeneity on biodiversity.

Here, I use a Bayesian multi-species hierarchical model for species abundance to identify patterns expected under two contrasting theories of the effects of heterogeneous landscape mosaics on bird biodiversity in human-dominated landscapes – island biogeography theory and spatial habitat heterogeneity. If patterns of species occurrence follow island biogeography (H1) I would expect biodiversity to decrease linearly from natural to more un-natural agricultural or urban landscapes as fragmentation and functional isolation of available habitat increases. Conversely, in the case of spatial habitat heterogeneity (H2) I expect biodiversity to be highest in mixed use mosaics where the diversity of available habitat is greatest. Using multi-dimensional spatial metrics to describe the effect of human-mediated landscape modification, I further explore variation in species-specific responses as community diversity and composition shifts along gradients of human-mediated landscape modification.

3.2 Methods

3.2.1 Study system

This study consisted of 42 forested study sites located along the Connecticut River valley in western Massachusetts, from the Connecticut border in the south *(*-72.5764, 42.0606) to the Vermont border in the north (-72.5408, 42.6523). My objectives were to analyze the composition of bird communities in remnant and regenerating forests rather than those within the surrounding urban, suburban, or agricultural landscape matrix. Therefore, only sampling locations that were located within forests were included. To ensure that I adequately captured sites that represented the full extent of landscape variation, sites were systematically selected by generating 1000 points in forests across the study landscape from which 50 sampling locations were probabilistically selected based on their values for two landscape axes (see section 3.2.2). Eight sites were subsequently removed because of accessibility issues, resulting in 42 sites sampled over three years (Figure 3.1).

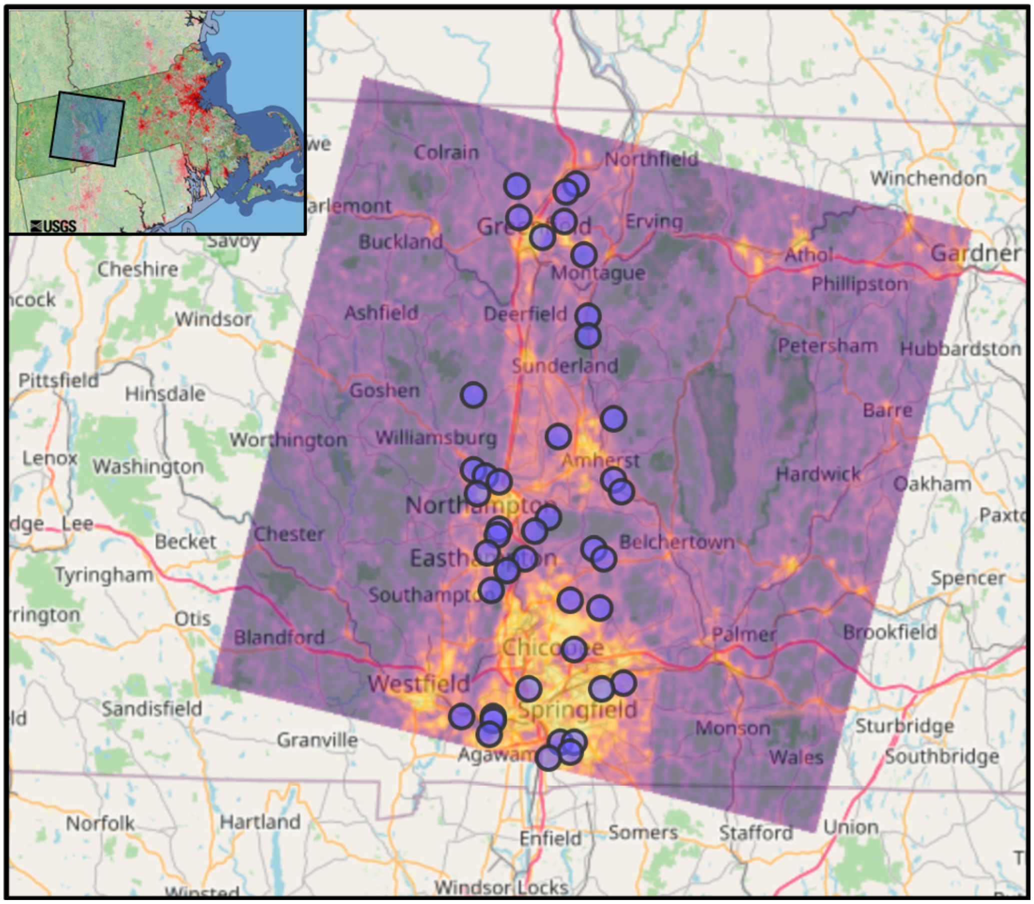

Figure 3.1: Map of study sites (points) with the regional context in Massachusetts (inset top-right). The gradient surface below sampling points represents the multi-dimensional landscape gradients.

Sampling locations were relatively in-tact mixed-deciduous eastern broadleaf forest fragments situated in a human-dominated landscape matrix of urban, suburban, and agriculture, and were dominated by overstory trees such as sweet birch (*Betula lenta*), white pine (*Pinus strobus*), red oak (*Quercus rubra*), and red maple (*Acer rubrum*). The understory tended to be relatively open and was dominated by leaf-litter cover, herbaceous growth such as ferns (e.g., *Dryopteris goldiena*), and small understory trees such as American witchhazel (*Hamamelis virginiana*) and ironwood (*Ostrya virginiana*). The matrix surrounding sites ranged from urban industrial and commercial, recreation (parks), and residential, to croplands or pasture.

3.2.2 Landscape quantification

Landscape analyses followed the landscape quantification framework and multivariate analysis used in Chapter 2. I used the 30-m resolution National Landcover Database (NLCD 2016) to analyze variation in modified (e.g., residential or agricultural) and un-modified (e.g., forests or wetlands) portions of the landscape. We extracted binary surfaces of each class (1 if focal class, 0 if otherwise) and, to account also for the landscape surrounding a given location, i.e., to quantify the landscape context, we computed the spatially weighted average for each pixel using a Gaussian kernel, resulting in a continuous surface ranging from 0 (no focal class within smoothing kernel) to 1 (smoothing neighborhood entirely focal class). This was done for each NLCD category, resulting in a smoothed surface for each. The width of the kernel, σ, was 1000 m which was chosen to capture the home range size of breeding birds and because it is a scale that has been linked to demographic processes in forest bird communities (Bakermans & Rodewald, 2006). To achieve an effective 1000-m smoothing scale with the 30-m pixel NLCD data, we set the smoothing parameter, σ, to span 16.67 pixels.

Finally, I used a Principal Components Analysis (PCA) to identify dominant patterns of variation in the smoothed NLCD data. Dominant principal components (≥10% variance explained) were identified and closely examined in order to properly interpret the ecological interpretation of component loadings. For these dominant components, I then produced spatial gradients where the value for each pixel is a PCA weighted average calculated as the sum of a cell's smoothed NLCD values multiplied by the corresponding component weight for each NLCD value.

Table 3.1: Dominant principal component axes produced from landscape analysis. The first two axes were used to create spatial gradients based on a 10% variance cutoff.

NLCD Layer		***PC1***	***PC2***	***PC3***
Std.Dev.		1.766	1.296	1.214
Variance Explained (%)		20.8	11.2	9.8
Water	11 - OpenWater	0.025	0.019	-0.005
Developed	21 - DevelOpen	0.406	0.001	-0.032
	22 - DevelLow	0.509	0.044	-0.039
	23 – DevelMid	0.493	0.188	-0.078
	24 - DevelHigh	0.369	0.201	-0.080
Barren	31 – Barren	0.023	-0.165	0.011
Forest	41 - ForestDeciduous	-0.292	0.382	0.511
	42 - ForestEvergreen	-0.155	-0.116	-0.607
	43 - ForestMixed	-0.261	0.044	-0.431
Shrubland	52 - Scrub/Shrub	0.057	-0.426	0.244
Herbaceous	71 -Grass/Herb	0.092	-0.385	0.256
Cultivated	81 - Pasture/Hay	0.010	-0.341	0.129
	82 - Crop/Cultivated	0.060	-0.159	0.117
Wetlands	90 - WoodyWetl.	0.017	-0.406	-0.055
	95 - HerbaceousWetl.	0.008	-0.311	-0.100

Multivariate analysis of landscape data resulted in two dominant axes of variation that together described 32% of the landscape variation (PC1 = 20.8%, PC2 = 11.2%). The first dominant axis described a transition from forested and agricultural (soft) regions of the landscape to suburban and urban (hard) regions. The second axis varied from open pastures and croplands (brown) to more structurally complex low-density residential and forests (green). Together, these two axes describe two dominant patterns of spatial variation in human-dominated landscapes. That is, component one distinguishes between built urban and suburban areas from undeveloped environment, while component two describes the transition in undeveloped areas from agricultural (brown) to forested (green) areas of the non-built landscape (Table 1). These axes (gradients) were used as predictor variables to understand variation in bird abundance, and are referred to as soft-hard (PC1) and brown-green (PC2) respectively.

3.2.3 Bird surveys

The Bird community was monitored using unlimited radius 10-minute point count surveys. In each year from 2017 to 2019, three surveys were conducted at each site during the breeding season (June and July) to avoid periods of migration and dispersal and avoid systematic violations of closure required for occupancy and abundance estimation (see below). All surveys were conducted in the morning between the hours of 0500 and 0900, and were not conducted during periods of high winds or heavy rains. During each survey I recorded survey date and start time, wind speed according to a four-point Beaufort Scale, and precipitation and cloud cover using a six-point scale.

3.2.4 Community abundance model

Abundance and species richness of the avian community was estimated using a hierarchical-community abundance model (HCM), which has two key components: 1) an ecological *state* process model describing variation in the state variable, in this case species-specific abundance, and 2) an observation, or *detection* process model describing variation in detection probability which is conditional on the latent (Dorazio et al., 2015). To estimate species-specific effects on abundance and detection, respectively, the HCM assumes that species-level covariate effects are random effects from a shared community-level distribution. The use of the community random effects distribution allows for sharing of data across all species in the community making it possible to estimate species specific responses for data-sparse species and even species that may not have been detected at a given site due to very low detection rates (Dorazio et al., 2006; Hanioka et al., 2018). Our data were limited to three sampling seasons with relatively little species turnover, therefore, we were not interested in directly modeling processes of local extinction and colonization and did not use a dynamic- HCM, opting instead for an 'stacked' approach where every sampling location in each year is treated as a unique site and an effect of year included to account for dependencies.

I was specifically interested in explaining species- and community-level responses to variation in human influence using the improved multi-dimensional gradient representation described in Chapter 2. Specifically, I aimed to quantify the relative importance of each axis of human influence according to predictions that communities are richer in areas of highest heterogeneity. To account for potential non-linear responses over the heterogeneity gradient, I included both dominant gradients of human-mediated landscape modification to explain variation in detection, as well as their squared for abundance. In addition, a site-by-year intercept ($\beta_{0.Yr\ i}$) was also included in both process models to allow for variation between years. Abundance of species i at site j (λ_{ij}) was modeled as:

$$\log(\lambda_{ij}) = \beta_{0.Yr\ i} + \beta_{1ij} * SH_j + \beta_{2ij} * BG_j + \beta_{3ij} * SH_j^2 + \beta_{4ij} * BG_j^2$$

and the detection process as:

$$\text{logit}(p_{ijk}) = \alpha_{0.Yr\ i} + \alpha_{1ij} * SH_j + \alpha_{2ij} * BG_j + \alpha_{3ij} * day_{jk} + \alpha_{4ij} * time_{jk} + \alpha_{4ij} * day_{jk}^2$$

where SH_j, SH_j^2, BG_j, and BG_j^2 are the values for the linear and quadratic soft-hard and brown-green landscape axes at site j. Species level parameters for detection and abundance, α_i and β_i parameters, are drawn from a normally distributed community distribution governed by hyper-parameters, e.g., $\beta_{1i} \sim Normal(\mu_{\beta_1}, \sigma_{\beta_1}^2)$. The expected total abundance (M$_j$) and species richness (R$_j$) at each site was derived within the model as $M_j = \sum_{i=1}^{R} \lambda_{ij}$ and $R_j = \sum_{i=1}^{R} [1 - \exp(-\lambda_{ij})]$, respectively

Models were analyzed using MCMC methods using three chains each with 100,000 total iterations; 25,000 iterations were discarded as a burn-in and chains were thinned by every 10th iteration. We considered all chains to have converged when the Gelman-Rubin statistic ($\hat{R}$) were less than 1.1 and by visual inspection. All analyses were conducted in R version 3.6.2 (R Core Team, 2019). Spatial smoothing and mapping analyses were done using the 'smoothie' (Gilleland, 2013) and 'raster' packages (Hijmans & van Etten, 2015), respectively. MCMC analysis and evaluation of the HCM was conducted using the 'nimble' (de Valpine et al., 2017) and 'MCMCvis' packages, respectively (Youngflesh, 2018).

3.3 Results

A total of 83 species were observed over the three sampling seasons, with observed site level diversity ranging from a low of 6 to 33 species at a given site. Species were observed from a range of functional and taxonomic groups, including species characteristic of mature forests (Blackburnian warbler – *Setophega fusca*), wetlands (wood duck – *Aix sponsa*), residential or suburban habitats (American robin – *Turdus migratorious*), and scrubby secondary growth (willow flycatcher – *Empidonax traillii*). The mean expected number of occupied sites for each species across all years (126 total) was 41.1 and ranged from 2.8 (Nashville warbler – *Leiothlypis ruficapilla*) to the most frequently occurring 120.8 (tufted titmouse – *Baeolophis bicolor*). Mean estimated species richness at each site was 27.1 and ranged from 17.9 to 39.9, while model derived bird abundance (mean = 116.6) ranged from 45.3 to 269.9 birds per site. Both observed (2017 = 19.86, 2018 = 18.26, 2019 = 17.05) and model derived species richness (2017 = 29.54, 2018 = 26.81, 2017 = 24.92) decreased between years, and as expected was greater for detection corrected expected values.

3.3.1 Avian community response

Community hyperparameters reflected the underlying variability in species specific responses. Mean community detection probability increased annually from 2017 ($\mu.\alpha_{0,y1}$ = 0.073 [0.048, 0.107]) to 2019 ($\mu.\alpha_{0,y2}$ = 0.151 [0.107,0.204]). Neither axis of landscape heterogeneity had an effect on community mean detection probability. There was a negative trend in response to survey day ($\mu.\alpha_3$= -0.043 [-0.097, 0.06]) and survey time ($\mu.\alpha_4$ = -0.013 [-0.058, 0.032], Table 3.2). Annual increase in detection probability corresponded to a year-by-year decrease in the community mean abundance intercept (Table 3.2). Mean abundance showed a decreasing linear trend, and strong negative quadratic relationship along both the soft-to-hard ($\mu.\beta_1$ = -0.075 [-0.202,0.058]; $\mu.\beta_3$ = -0.115 [-0.193,-0.048]) and brown-to-green axes ($\mu.\beta_2$ = -0.115 [-0.246,0.017]; $\mu.\beta_4$ = -0.193 [-0.299,-0.105]). These results demonstrate that there exists a meaningful aggregate community response to one or both landscape axes, reiterating the value of a multi-dimensional landscape framework (Figure 3.2).

Predicted richness and total abundance of the avian community summed across all species, plainly reflect community level trends. Both richness and abundance increased toward the center of both gradients at locations where habitat heterogeneity is expected to be greatest (Figure 3.2). However, species richness declined more steeply than abundance toward the edges of the multi-dimensional landscape space, resulting in a "sphere" of maximal abundance occupying a larger portion of the landscape than that of species richness (Figure 3.2.c and 3.2.d). This is likely due to a subset of species with high estimated abundance in portions of the landscape that may be considered marginal in terms of species richness.

Table 3.2: Community hyper-parameters for detection (ρ) and detection (λ). Credible intervals for quadratic effects of landscape metrics ($\mu.\beta_3$ and $\mu.\beta_4$) did not overlap 0. All other hyperparameter estimates had credible intervals that overlapped 0 at 95% confidence.

	Parameter	***Posterior mean***	***2.5% credible***	***97.5% credible***
p	**$\mu.\alpha_1$ *Soft-Hard***	0.0108	-0.137	0.148
p	**$\mu.\alpha_2$ *Brown-Green***	0.0661	-0.067	0.065
p	**$\mu.\alpha_3$ *Julian Day***	-0.0430	-0.097	0.006
p	**$\mu.\alpha_5$ *Julian Day* ^{2}**	-0.0186	-0.066	0.027
p	**$\mu.\alpha_4$ *Time***	-0.0130	-0.058	0.032
λ	**$\mu.\beta_1$ *Soft-Hard***	-0.0750	-0.202	0.058
λ	**$\mu.\beta_3$ *Soft-Hard* ^{2}**	-0.1151	-0.193	-0.048
λ	**$\mu.\beta_2$ *Brown-Green***	-0.1148	-0.246	0.017
λ	**$\mu.\beta_4$ *Brown-Green* ^{2}**	-0.1928	-0.299	-0.105

3.3.2 Species-specific Response

Species specific variability in the magnitude and direction of response existed in spite of the relatively strong estimated community-level response to both the soft-to-hard and brown-to-green axes (Appendix C.1). As anticipated based on the strength of the community level quadratic coefficients (Table 3.2), most species showed a non-linear peaked or valleyed response. I categorized species on the basis of migratory status (long- and short-distance, residents) and explored patterns in species response, however there was little meaningful difference. There was, however, a slight difference in the response to the soft-to-hard axis (β_1) between long- and short-distance migrants with long-distance migrant species showing a more negative response based on an Analysis of Variance (p-value = 0.0023).

3.4 Discussion

3.4.1 Avian community richness and diversity

My results non-linear community-level response of avian species richness and total abundance in human dominated systems, specifically, strong quadratic effects of both soft-hard and brown-green gradients. Our results offer support for the hypothesis that spatial habitat heterogeneity drives patterns of species diversity and abundance in human-dominated landscapes, but provides a refined perspective about how these patterns emerge as a function of landscape complexity that can be intuitively described as variation across two intuitive axes of human influence. Accordingly, both diversity and abundance were highest in the most heterogeneous portions of the multidimensional landscape (Figure 3.2). Increased heterogeneity of habitat at the landscape scale provides more variety in the types of habitat and resources available, thereby providing niche space for a greater diversity of species to exploit. By evaluating species response to landscape structure in multi-dimensional framework I demonstrate that habitat heterogeneity rather than isolation due to permeability of the landscape matrix drive patterns of bird diversity in human-dominated landscapes.

3.4.2 Species-specific patterns

These results further demonstrated as expected under the habitat heterogeneity hypothesis, species-specific responses to landscape structure was somewhat variable and dependent on the ecology of the species in question. As the amount of human-modification to the landscape increases through fragmentation, urban development, or agriculture, species with more specialized habitat and resource requirement are expected to decrease in abundance while synanthropic species increase in abundance and generalists may be able to exploit habitats in all landscapes (Evans et al., 2018; Norton et al., 2016). These patterns were broadly recognized here, though this was not fully explained by migratory status, a common method of categorizing species specialization (Figure 3.3). The way in which ecology and life-history mediate species response is exemplified in the following representative species: brown-headed cowbird (*Molothrus ater*), blue jay (*Cyanocitta cristata*), red-bellied woodpecker (*Melanerpes carolinensis*), mourning dove (*Zenaida macroura*), veery (*Catharus fuscescens*), and the American goldfinch (*Carduelis tristis*, Figure 3.4).

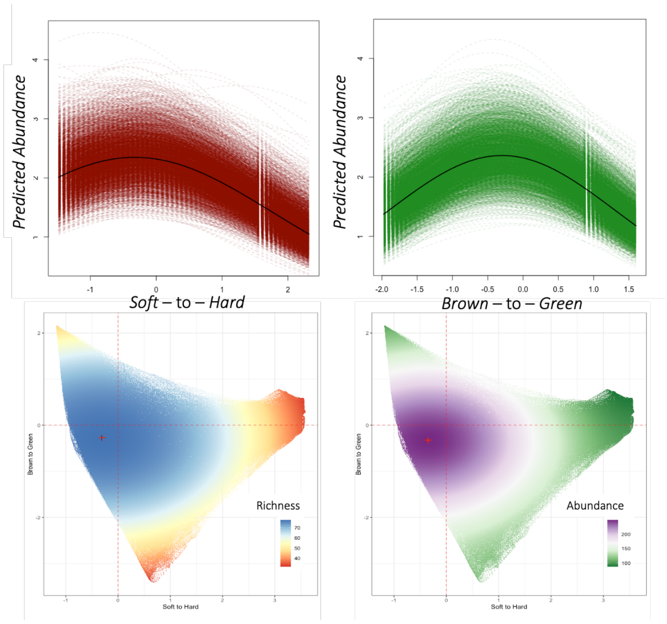

Figure 3.2: Community level hyperparameters for mean abundance. Response to the soft-to-hard (1.A) and brown-to-green (1.B) both showed a strong negative quadric relationship. This results in mean abundance highest near the center of both axes, where landscape heterogeneity is expected to be highest. This is visualized when expected site-level mean abundance for sampling

Two species, the mourning dove (Figure 3.4.*d*) and veery (Figure 3.4.*e*) had higher abundance at increased levels of heterogeneity. The veery is a primarily insectivorous long-distance migrant that nests and forages near the forest floor of damp mixed-deciduous forests with a dense understory (Heckscher et al., 2020). In spite of significant annual declines over the last several decades (Sauer et al., 2017), it can persist mixed-used and suburban landscapes that are not extensively fragmented or urbanized (Kluza et al., 2000). Like the veery, mourning dove abundance was highest in more heterogenous mixed landscapes. However, as a more adaptable species, mourning dove are able to inhabit a wide variety of environments including suburban regions with forest edge habitat where they benefit from supplemental food (Hayslette & Mirarchi, 2001).

Not all species shared the non-linear abundance pattern observed at the community level. The blue jay is a species emblematic of mixed forest ecosystems of eastern North America that is also common in residential areas where large masting trees (e.g., oaks) and supplemental food resources are present. Accordingly, the species has generally benefited from residential development, tending toward higher population density where housing density is moderate (Kluza et al., 2000). This analysis supported these patterns, showing that while the species is expected to be present in all landscapes (mean predicted abundance $\mu.\lambda = 6.4$), abundance was positively associated with mixed forest (green) landscapes and toward moderately modified (soft) landscapes. The red-bellied woodpecker, like the blue jay, is a relatively common generalist species. But, as an obligate insectivore reliant on standing snags for foraging and nesting, it is negatively affected by extensive urbanization and agricultural development where fragmentation is extensive and remnant patches are small (Zuckerberg et al., 2011). Predicted abundance was relatively consistent across the landscape ($\mu.\lambda = 2.8$) decreasing toward areas dominated by higher density urbanization and agriculture and increasing in mixed-use forested landscapes (3.4.*c*). Some highly adaptable species, however, may not be significantly affected by human-mediated landscape modifications, as seen in the American goldfinch (Figure 3.4.*d*). Goldfinch are known to inhabit cultivated fields, forests, floodplains, roadsides, and gardens near early-successional forests, and has benefitted from human presence and widespread supplemental feeding (A. D. Rodewald & Bakermans, 2006). These patterns were clearly reflected in the data, with the species consistently abundant throughout the study system, though it slightly decreased in landscapes that were extensively forested with less edge or successional habitat, or highly urbanized.

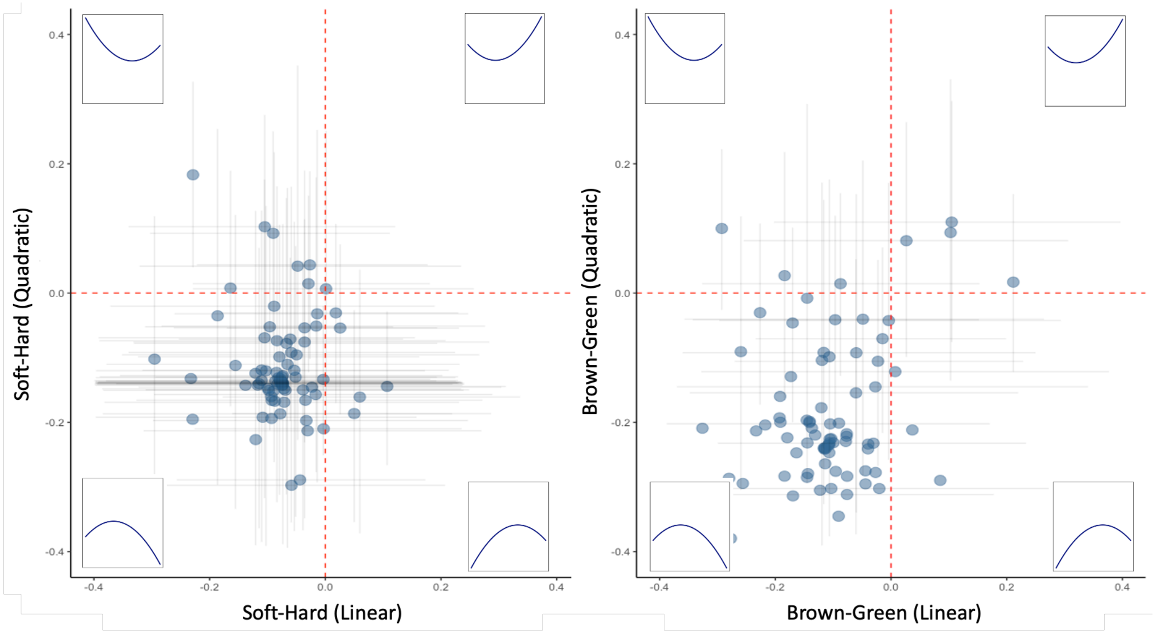

Figure 3.3: Species-specific regression coefficients for linear and quadratic effects of soft-to-hard (left) and brown-to-green (right). The majority of species reflected community level parameters (Table 3.2) and exhibited a negative response to linear and quadratic effects for both landscape metrics. Inset figures at the corners represent the expected effect of the landscape gradient on bird abundance for species within that plot quadrant.

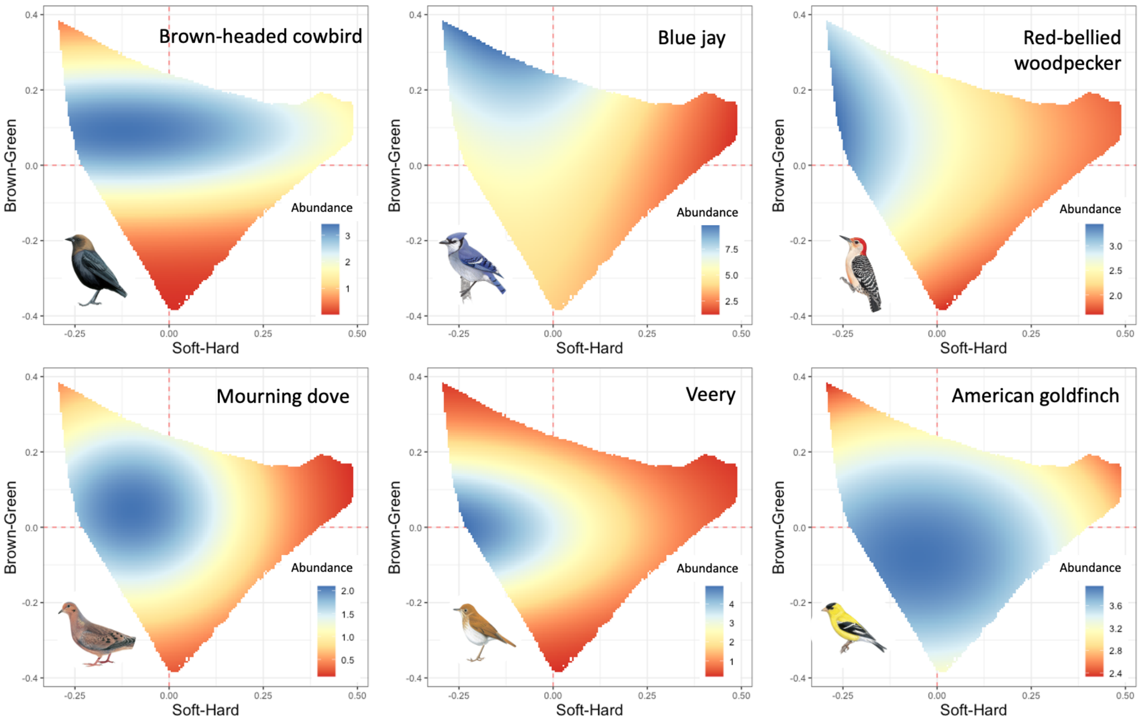

Figure 3.4: While the community-wide response to landscape metrics was quite strong, species-specific responses are governed by life-history and of the species in question. The brown-headed cowbird (a), a bird of open country that parasitizes songbird nests along woodland edges, is most abundant in locations that are entirely agricultural (no forest edge) or entirely wooded, however, they are equally abundant in all but the most urban (hard) habitats. Blue jays (b) and red-bellied woodpeckers (c) meanwhile, are fairly adaptable and can occupy most landscapes, however their abundance is maximized in softer-green regions dominated by forests. Species such as the mourning dove (d) and veery (e) can breed in secondary growth forests allowing them to persist in at higher abundance near the mid-point of both gradients where habitat heterogeneity is greatest. The veery, however, is far more sensitive than the mourning dove resulting in the zone of highest abundance constrained toward the soft end of the landscape. Highly adaptable synanthropic species such as the American goldfinch (f) are abundant in all but the most forested and urban regions.

3.4.3 Habitat heterogeneity and bird biodiversity

Analysis of bird communities in a human-dominated landscape reflected a clear peak in bird biodiversity mid-way along both axes of landscape modification where habitat heterogeneity is expected to be greatest. The effects of landscape modification and destruction in the Anthropocene on biodiversity are often thought to be inherently negative, however, an increasing body of empirical and theoretic work has highlighted the significance of the scale- and context-dependence of these relationships (Carrasco et al., 2018; Stein et al., 2014). With species under threat worldwide, the relevance of habitat-biodiversity relationships in conservation and management practices is clear.

In anthropogenic systems land-sparing versus land-sharing ideas reflect the controversy surrounding biodiversity in heterogeneous systems. The land-sparing approach leans on island biogeography theory to prioritize large remnant habitat patches while centralizing anthropogenic development (e.g., urbanization or agriculture) elsewhere. Increased habitat heterogeneity through land-sharing, meanwhile, suggests that integrating human and natural landscapes into a mixed-use mosaic is ideal (Droz et al., 2019). In this system, bird biodiversity declined as landscapes became more homogenous, whether that landscape was predominantly agricultural, urban, or forested, and was maximized in the more heterogeneous center both at the community (Figure 3.2) and species level (Figure 3.3) suggesting that the a wisely managed land-sharing paradigm will meet conventional conservation objectives such as the prioritization and maximization of biodiversity (Fahrig, 2017).

Biodiversity is thought to increase in spatially heterogeneous landscapes due to the higher diversity of available ecological niches (Carrasco et al., 2018). In human-dominated landscapes a mosaic of habitat fragments of varying sizes provides habitat for open, edge, and less sensitive interior species while supporting generalist and synanthropic species. However, because species with more specialized needs, those with large home ranges, or those of particular conservation concern may not be able to exist at sustainable densities in a mixed-use landscape, sufficiently large habitat fragments must still be present at the landscape scale. Though biodiversity is relatively high, habitat fragments in heterogeneous landscapes may act as sinks for some species while excluding others therefore, larger portions of natural habitat that are functionally connected are necessary. As an example, Acadian flycatchers, a species in decline over much of its range, breeds in urban forest fragments in central Ohio but suffers high rates of nest-predation and may persist only if they are supported by larger source patches (Padilla & Rodewald, 2015).

3.4.4 Conclusions

My results support for the hypothesis that biodiversity in human-dominated landscapes is driven by spatial habitat heterogeneity, and hence that in human modified landscapes, the maintenance of avian diversity would benefit from landscape management paradigms that adopt a land-sharing perspective. However, it is important to remember that in order to ensure the long-term persistence of all species on the landscape prioritizing spatial habitat heterogeneity alone is not sufficient. The species and ecosystem processes most likely to be lost under a habitat heterogeneity management approach must be identified, and appropriate measures taken to protect sufficient habitat on the landscape. As anthropogenic pressures on the ecosystem mount, my results highlighting the biological benefits of heterogeneous human-natural landscapes are encouraging because they not only provide quality habitat for a diverse suite of organisms, but also provide opportunity for people to reap the rich physical, psychological, and sociological benefits of nature.

CHAPTER 4

EVALUATING THE RED-BACKED SALAMANDER (*PLETHODON CINEREUS*) AS AN INDICATOR FOR BIODIVERSITY IN HUMAN-DOMINATED LANDSCAPES

4.1 Introduction

Effective conservation and management of natural resources requires accurate assessments of species population and ecosystem processes are both integral to effective conservation and adaptive ecosystem management (Lindenmayer et al., 2015). In most instances, however, financial and logistic limitations make it impractical to directly measure ecological targets such as complex biological processes, rare and endangered species, or biodiversity. Rather, focusing on indices of occurrence or abundance of proxy organisms offers a convenient alternative to directly measuring target species or processes (Lindenmayer & Likens, 2011). Individual species and taxonomic groups from a range of taxa have been used as environmental indicators, including fish (Bergerot et al., 2008), invertebrates (Walters et al., 2009), birds (Battisti & Fanelli, 2016), mammals (Sutherland et al., 2018), and reptiles (Bal et al., 2018; *reviewed by*, Caro et al., 2005; Lind et al., 2005; Lindenmayer & Likens, 2011). Although criteria for identifying indicators vary, in general an effective indicator species is one whose ecological state (e.g., occurrence, abundance, fecundity) provides a reliable assessment of habitat quality, the state of the local species community or ecosystem condition (Landres et al., 1988).

In contrast with umbrella or flagship species where managing a single species confers benefits to the entire ecosystem (Simberloff, 1998), the state of an indicator species is expected to be directly proportional to the state of an ecological target metric

(Lindenmayer & Likens, 2011). According to Noss (1990), an indicator species should be (1) sufficiently sensitive to environmental perturbations to provide early warning, (2) widely distributed (i.e., wide applicability), (3) capable of providing a continuous assessment to a range of stressors, (4) easy and cost effective to measure, (5) able to differentiate between effects of natural and anthropogenic stressors, and (6) relevant to the target ecological phenomenon. While indicators are often selected based on one or more of these criteria, the process remains vague with more than 40% of applications relying on citing prior literature and 17% failing to provide any selection criteria (Siddig et al., 2016). Generally qualitative assessments of candidate species as indicators has also resulted in further uncertainty in the development of best practices for indicator species selection (Bal et al., 2018; Lindenmayer & Likens, 2011). An indicator can be objectively assessed by demonstrating that changes in status of the indicator reliably reflect changes in the process of interest. This validation is essential but is often overlooked due to the challenges related to monitoring all ecological targets and the indicator simultaneously.

Amphibians are the most threatened class of extant vertebrate and are of high conservation priority globally (Sterrett et al., 2019). Accordingly, many species have the ecological and physiological traits characteristic of ideal indicator species (Cosentino & Brubaker, 2018; Siddig et al., 2019; Townsend & Driscoll, 2013). For example, anurans have been used as indicators of PCB contamination in Kentucky streams (DeGarady & Halbrook, 2006), and montane salamanders have been used to identify potential thermal refugia in the Cascade Mountains (Garcia et al., 2020). Among amphibians, terrestrial salamanders of the species rich family *Plethodontidae* are considered to be excellent indicators of forest condition throughout the Americas because they are dispersal limited, cutaneous respirators, and are sensitive to environmental changes (Clipp & Anderson, 2014; Welsh & Droege, 2001). In temperate forests of eastern North America, red-backed salamanders (*Plethodon cinereus*) are highly abundant with a broad distribution (Burton & Likens, 1975; Milanovich & Peterman, 2016); are effective indicators of environmental conditions such as soil mercury (Townsend & Driscoll, 2013) or forest disturbance (Siddig et al., 2019); are dominant predators of important soil macro-invertebrates; and are thought be top-down drivers of critical processes including leaf-litter decomposition and nutrient cycling (Homyack et al., 2010; Wyman, 1998). Their significant role in maintenance of ecosystem function and sensitivity to environmental changes, coupled with a well-established and standardized monitoring protocol that is relatively easy to implement, make red-backed salamanders excellent candidates for an indicator species (Cosentino & Brubaker, 2018; Gade & Peterman, 2019; Mossman et al., 2019; Pearce & Venier, 2009; Venier et al., 2007). Yet, there have been relatively few rigorous quantitative assessments of red-backed salamanders as indicators of ecosystem health (Siddig et al., 2019; Townsend & Driscoll, 2013).

The Indicator Value (IndVal) metric proposed by Dufrêne & Legendre (1997) is a conceptually appealing and easily implementable method for assessing indicator species that has been used in a range of theoretical and applied contexts (Urban et al., 2012). IndVal measures the degree to which the occurrence or abundance of a species is indicative of sites within a given typology or for points along a gradient of environmental variation (Dufrêne & Legendre, 1997). While perhaps effective for assessing indicators of site types or past disturbance, IndVal does not directly take the broader community into consideration in its estimation and therefore implicitly assumes that biological targets such as biodiversity respond to the same environmental categories as the indicator (Sattler et al., 2014). In forests of the northeastern United States where the invasive hemlock wooly adelgid (*Adelges tsugae*) are causing rapid decline of eastern hemlock (*Tsuga canadensis*) IndVal was used to demonstrate that red-backed salamanders were significant indicators of intact hemlock forests, while eastern newts (*Notaphthalmus viridescens*) were more indicative of experimental hemlock removal plots (Siddig et al., 2019). However, because no additional ecosystem components were considered in this case, the assertion that properties of ecosystem condition are related to salamander abundance is incomplete as there lacks a formal process model linking the two. Furthermore, IndVal requires course categorization of environmental changes that in reality exist along a continuum (see Chapters 2 and 3). Therefore, IndVal cannot quantify ecological responses over continuous gradients that are valuable in the context of applied species, biodiversity, or ecosystem management in a changing world.

In light of the many limitations of IndVal, improved methods for jointly assessing the response of indicator species and species communities across environmental gradients are needed to optimize the selection of, and assess the performance of, indicator species as biodiversity conservation tools. In general, the process of evaluating an indicator species should begin by identifying objectives including relevant ecological stressors (e.g., global climate change) and management goals (e.g., climate refugia, Figure 4.1). With these objectives in mind, appropriate indicator species are selected and evaluated according to how well the indicator links stressors to ecosystem targets (Bal et al., 2018; Lindenmayer et al., 2015; Siddig et al., 2016). This critical final step of scientific evaluation and assessment is often overlooked, but it is imperative to ensure that changes in indicator is related *both* to the ecosystem target and the environmental threat. If the relationships between the environment, indicator, and ecosystem targets are not formally tested, management decisions may be misdirected and risks inappropriate allocation of conservation and management resources (Lindenmayer et al., 2015).

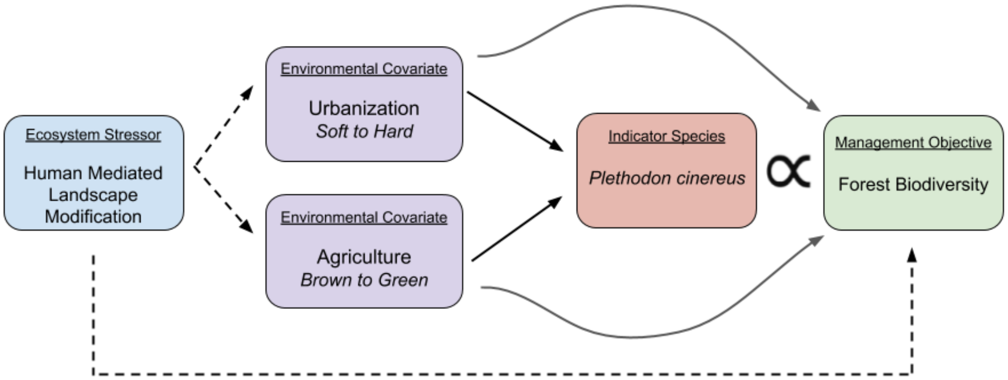

Figure 4.1: Conceptual diagram describing role of an indicator species in adaptive management. First, an ecosystem stressor of concern is identified (far left). Next, a desired management objective (far right) thought to be at risk due to ecosystem threats (hashed arrow). Finally, environmental factors thought to be mediated by the ecosystem threat (landscape gradients, middle left) are measured and directly related to the occurrence or abundance of an indicator species (red-backed salamander, middle right) whose response is assumed to be proportional to that of the management objective. Here we include the additional component of indicator assessment by directly measuring the impact of environmental covariates on the management objective (curved arrows). Hashed lines represent assumed or inferred relationships while solid lines represent those that are directly measured and assessed.

Here an indicator species conceptual process model (Fleming et al In Review) is adapted to empirically evaluate the red-backed salamander (*Plethodon cinereus*) as an indicator of the effects of anthropogenic landscape modification on biodiversity in northeastern forests (Figure 4.1) and compare such an approach to the widely applied IndVal metric. I use species richness as a measure of forest condition because biodiversity is an important aspect of ecological integrity and resilience and is known to be affected by human-dominated urban and agricultural mosaics (Beninde et al., 2015; Turrini & Knop, 2015). Variation of species richness and species associations (i.e., residual co-occurrence) for trees, birds, soil macroinvertebrates, and red-backed salamanders along a human-dominated landscape gradient are estimated using a joint species distribution modelling framework to evaluate the red-backed salamander's indicator potential. My approach to indicator assessment is centered on the premise that species within a community will exhibit a shared environmental response, in this case to gradients of human influence, and that an ideal indicator species represents an exemplar of the shared community response, i.e., will exhibit a stronger than average response and be measured with greater precision. Red-backed salamanders play are sensitive to environmental conditions such as temperature and moisture that have an effect on many species in the community. Therefore, I expect salamanders to indicate for changes in species diversity (*sensu* forest condition) as both are expected to change along gradients of human-influence.

4.2 Methods

4.2.1 Study System

The study system comprises forty-two forested study sites in western Massachusetts, USA, extending from the Connecticut border in the South (-72.5764, 42.0606) to the Vermont border in the North (-72.5408, 42.6523). All sampling locations were located in forest fragments situated along a range of landscape contexts defined by the degree of surrounding heterogeneity because my objectives were to identify indicators of biodiversity in forested habitats rather than the non-forested matrix. To ensure that the full extent of landscape variation was captured, I systematically selected sites by randomly generating 1000 points in forests across the study landscape in which access permission was likely to be granted and selecting 50 locations that ensured representative sampling of the two landscape axes of interest (see section 4.2.2

Landscape Quantification). Eight sites were removed because of accessibility issues, resulting in 42 sites sampled over three years (Figure 4.2).

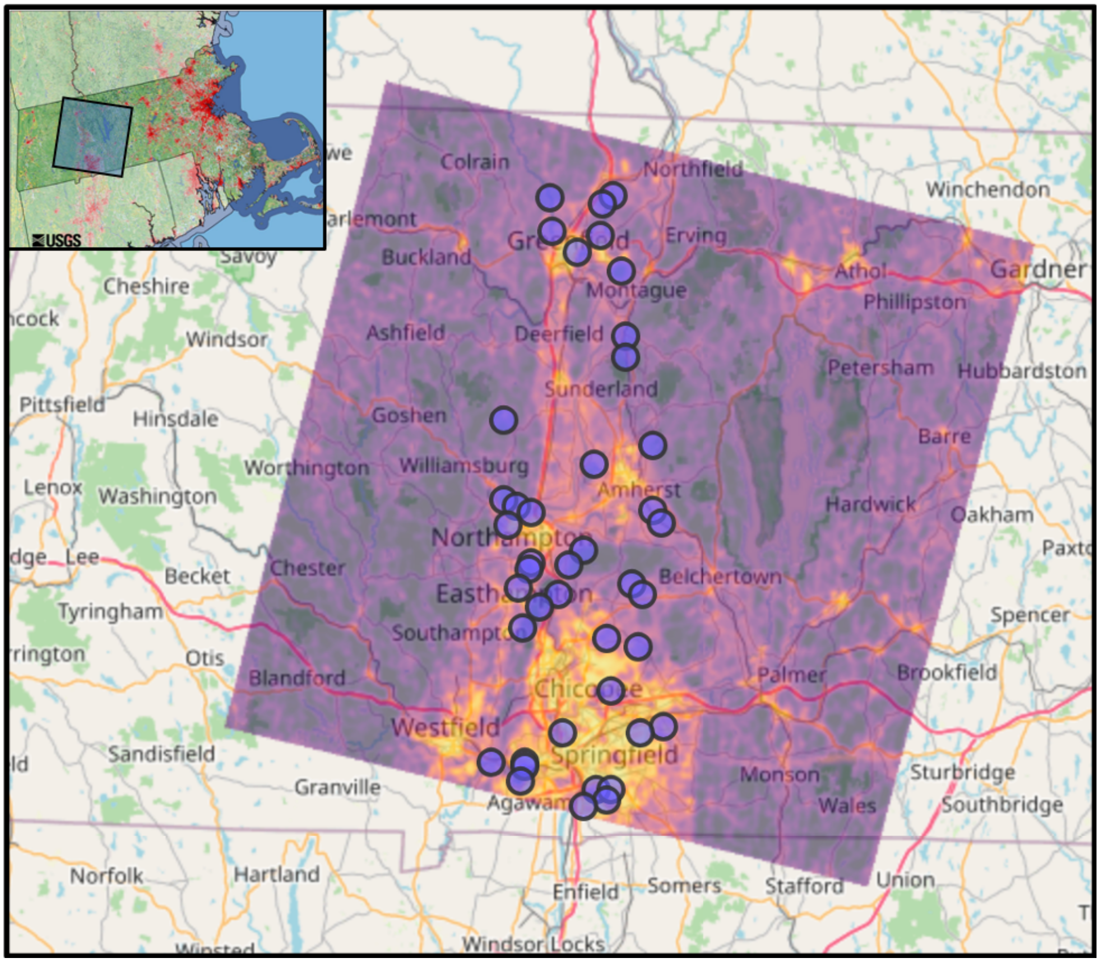

Figure 4.2: Map of study sites (points) with the regional context in Massachusetts (inset top-right). The gradient surface below sampling points represents the multi-dimensional landscape gradients.

Sampling locations were relatively in-tact mixed-deciduous eastern broadleaf forest fragments situated in a human-dominated landscape matrix of urban, suburban, and agriculture, and were dominated by overstory trees such as sweet birch (*Betula lenta*), white pine (*Pinus strobus*), red oak (*Quercus rubra*), and red maple (*Acer rubrum*). The understory tended to be relatively open and was dominated by leaf-litter cover, herbaceous growth such as ferns (e.g., *Dryopteris goldiena*), and small understory trees such as American witchhazel (*Hamamelis virginiana*) and ironwood (*Ostrya virginiana*).

4.2.2 Landscape Quantification

Landscape analyses followed the transparent landscape quantification framework of Padilla and Sutherland (2019). The 30-m resolution National Landcover Database (NLCD 2016) was used to analyze variation in modified (e.g., residential or agricultural) and un-modified (e.g., forests or wetlands) portions of the landscape. For each NLCD class, a binary raster surface (1 if focal class, 0 if otherwise) was created to which I applied a Gaussian kernel density spatial smoothing to estimate the spatially weighted average for each pixel. This resulted in a continuous surface ranging from 0 (no focal class within smoothing kernel) to 1 (smoothing neighborhood entirely focal class). The width of the smoothing kernel is set by a bandwidth parameter, σ, which should be determined by ecological process of interest (Boyce et al., 2017). I selected a 1000-m radius smoothing kernel as an appropriate scale of the surrounding landscape, because it relevant to the presence and abundance of the species included in the community monitoring (see section 4.2.3 Ecosystem Surveys). Using these smoothed raster surfaces, a pixel-by-NLCD class matrix of smoothed values, ranging from 0 to 1, was created.

Finally, I used a Principal Components Analysis (PCA) to identify dominant patterns of variation in the smoothed NLCD data. Dominant principal components (≥10% variance explained) were identified and closely examined in order to properly interpret the ecological interpretation of component loadings. For these dominant components, spatial landscape gradients were produced, where the value for each pixel is a PCA weighted average calculated as the sum of a cell’s smoothed NLCD values multiplied by the corresponding component weight for each NLCD value.

Multivariate analysis of landscape data resulted in two dominant axes of variation that together described 32% of the variation in the data (pc1 = 20.8%, pc2 = 11.2%). The first dominant axis of variation described a transition from forested and agricultural (soft) portions of the landscape to suburban and urban (hard) regions. Meanwhile, the second axis varied from open pastures and croplands (brown) to more structurally complex and forested landscapes with low or no residential areas (green). Together, these two axes describe intuitive patterns of spatial variation in human-dominated landscapes. That is, component one describes increasing dominance of the built urban and suburban environment, while component two distinguishes between the agricultural (brown) and forested (green) portions of the non-built landscape (Appendix D.2). These axes (gradients) were used as predictor variables to understand variation in bird abundance, and are here referred to as soft-hard (SH) and brown-green (BG) respectively.

4.2.3 Ecosystem Surveys

4.2.3.1 Red-backed Salamander

I used a natural cover object transect method to sample red-backed salamanders in the Spring and Fall 2017, 2018, and 2019. Salamanders were sampled along two 25-m long transects extending North (0 degrees) and West (270 degrees) from the site center. All cover objects, natural and unnatural, within 2-m of the transect line were searched, and any salamanders encountered were placed in an individual zip-top bag. For each salamander the individual's sex (male, female, juvenile), snout-to-vent (SVL) length, and color morph (red-backed or lead-backed phase) were recorded.

4.2.3.2 Avian Community

I measured composition of the breeding bird community using unlimited radius 10-minute point count surveys. In each year for 2017 through 2019, three surveys were conducted at each site during the breeding season months of June and July to avoid periods of migration and dispersal. All surveys were conducted in the morning hours between the hours of 0500 and 0900 eastern standard time and were not conducted during periods of high winds or heavy rains.

4.2.3.3 Soil Macro-Invertebrate Community

Macro-invertebrates were sampled at all sites once in 2017. At each site I removed 2 cores of leaf-litter and top 3-5 cm piece of 15-cm diameter PVC piping, each sample was placed in an individual Ziploc bag, and were then dried using Berlese-Tullgren funnels to extract macro-invertebrates. Samples were placed in individual funnels with reflector lamps set approximately 6-inches above, below each funnel a vial containing 70% ethanol was placed to collect macro-invertebrates. Mass in grams of all samples was taken before and after drying to compare the wet (pre) and dry (post) mass of soil. Finally, all macro-invertebrates in each sample were identified to Order under a 10-40x magnification dissecting microscope using a dichotomous key (Borror et al., 1989).

4.2.3.4 Tree Diversity

Dominant vegetation structure was sampled at all sites in 2017 and 2019. In 2017 I estimated percent canopy cover, leaf-litter cover, woody twig density, and identified all trees to species and measured tree DBH (diameter at breast height) in centimeters within an 11.3-m radius plot. In 2019 all trees were identified to species and measured DBH within a 2-m buffer width along the 25-m salamander transect lines. Detailed descriptions of field methods, including sample datasheets are available in the project handbook (Appendix D.1).

4.2.4 Indicator Species Analysis

4.2.4.1 Joint-species Distribution Model

In line with recommended approaches to indicator species selection (Bal et al., 2018; Lindenmayer et al., 2015), I first identified an ecosystem target of concern to be indicated. Species richness was selected as the target metric because it has been proposed as a proxy for ecosystem health (Ziter, 2016) and is known to be impacted by human-mediated landscape modification (Aronson et al., 2014). I analyzed the site- and species-specific abundance data using a hierarchical joint species distribution modelling (JSDM) framework that attributes variation in species abundance and co-occurrence to the environmental variation, and residual species-to-species associations (Ovaskainen et al., 2017a). These models enable simultaneous estimation of large communities by borrowing information across species by assuming species-specific regression coefficients that follow a multivariate normal distribution governed by shared community-level hyper-parameters. This method is also able to estimate positive and negative residual species associations by directly estimating pairwise elements of a latent covariance matrix, Ω (Ovaskainen et al., 2016). A single model was fitted in which the species abundance of species i at site j (λ_{ij}) was modelled as a function of two environmental covariates describing key diverging patterns of human-mediated modification to the landscape and their respective quadratic terms as follows:

$$\lambda_{\mathrm{ij}} = \beta_{0i} + \beta_{1i} * SH_j + \beta_{2i} * BG_j + \beta_{3i} * SH_j^2 + \beta_{4i} * BG_j^2$$

Where β_{0i} are the species specific intercepts, β_{1i} and β_{2i} the effects of soft-hard and its quadratic, and β_{3i} and β_{4i} estimates for brown-green and brown-green^2, and SH_j, SH_j^2, BG_j and BG_j^2 the scaled values of soft-hard and brown-green landscape gradients (and quadratics) at site j. Although multiple years and repeat visit surveys were available for some groups (i.e., birds and salamanders), I used the maximum observed abundance across all visits and years assuming that the collapsed three-year data set would more accurately reflect the system state than the single year alternative that is more susceptible to stochastic absences or turnover. Furthermore, by using a reduced dataset, this approach is able to assess whether a single season of rapid surveys could effectively evaluate an indicator species.

This model was fitted using a highly efficient MCMC sampler with 3 chains of 20000 effective post burn-in samples (iterations). Model convergence and fit were assessed by visual examination MCMC chains, and when the Gelman-Rubin statistic ($\hat{R}$) were less than 1.1.

4.2.4.2 Indicator Species Selection

Finally, I sought to use both methods to determine the value of the red-backed salamander as an appropriate indicator and identify alternative indicator candidates. Using the output from the joint-species distribution model, potential indicators were identified as those whose distributional pattern were best explained by the suite of environmental covariates selected to characterize anthropogenic stressors (Figure 4.1). This was done by calculating the proportion of total variance explained by the JSDM attributed to the four covariates (i.e., the soft-hard and brown-green gradients with polynomial terms). Specifically, species-specific R-squared values were multiplied by the percent of that variance explained by structural parameters which was calculated using the variance partitioning function in the HMSC package. I then ranked species by the absolute variance explained by the environment model.

The potential indicators identified in the JSDM were then compared to species-specific IndVal scores (Dufrêne & Legendre, 1997), which is the product of a species' specificity (i.e., mean abundance in sites of a given type in relation to all sites) and its *fidelity* (i.e., relative frequency of occurrence in a given site type). Because the ecological target metric was species richness, sites were grouped into categories of species richness based on the 30th and 70th percentile, resulting in categories of sites with 29 – 40 species (13 sites), 40 – 47 species (19 sites), and 48 – 54 species (10 sites). Indicators were ranked according to the *p*-value associated with the IndVal score, a relative measure of their ability to 'indicate' the most species rich category. Through this comparison, I seek to determine (1) whether there is support for red-backed salamander as an indicator of species richness in northern forests by either method, and (2) whether there is consistency in indicator species selection using both approaches.

All analyses were conducted in R version 3.6.2 (R Core Team, 2019). The package 'Hmsc' was used for JSDM analysis (Ovaskainen et al., 2016), and the 'indicspecies' package was used for IndVal analysis (De Cáceres & Legendre, 2009).

4.3 Results

4.3.1 Observed Data

In total I observed 151 species and species groups across all taxa, with 83 bird species, 39 species of tree, and 28 invertebrate groups in addition to red-backed salamanders. The number of species observed at each site ranged from 29 to 54 with a mean of 44.3 species per site. The most diverse site was characterized by a mixed stand of small to medium sized trees (mean DBH = 13.02), with a relatively high density of snags, while the least diverse site was a stand composed almost entirely of a single species (> 70% white pine). Indicator candidate, the red-backed salamander was observed in 36 of 42 sites, with a mean abundance of 2.3 salamanders per site and a maximum of 10 salamanders.

4.3.2 Community and Species Response

Evaluation of model fit confirmed convergence, with no significant autocorrelation in MCMC chains and an overall mean Gelman-Rubin statistic < 1.01. Most of the variation in species abundance across sites was explained by changes in abiotic landscape structure along dual axes of human-dominance (mean = 78.6%) rather than by biotic species associations or additional latent factors. Accordingly, there was very little support for species-to-species associations as significant drivers of abundance and diversity in the study system (mean posterior support = 0.018) and estimates for species associations were approximately equally split between positive (51.3%) and negative (48.7%). The 62 species-species associations with at least 95% posterior support were similarly fairly evenly split between positive (53.2%) and negative (46.8%). These results suggest that within the observed species community, abiotic environmental factors are, relatively speaking, more prominent predictors of community assemblage than biotic species interactions. Species-specific pseudo R-square values ranged from 0.07 to 0.96 with a mean of 0.159.

At the community level, variation in abundance reflected a clear quadratic response for both soft-hard and brown-green axes (Table 4.1). Accordingly, the majority of species in the data reflected similar non-linear patterns of abundance (Figure 4.2). Red-backed salamander abundance was strongly influenced by landscape structure, particularly along the soft-hard gradient (SH_j = 0.27 [-0.5, -0.03], SH_j^2 = 0.21 [-0.001,0.42]; Table 4.1). In contrast with the majority of the species in the community however, predicted salamander abundance was higher at the more extreme soft and hard ends of the gradient, rather than in the more heterogeneous center (Figure 4.3).

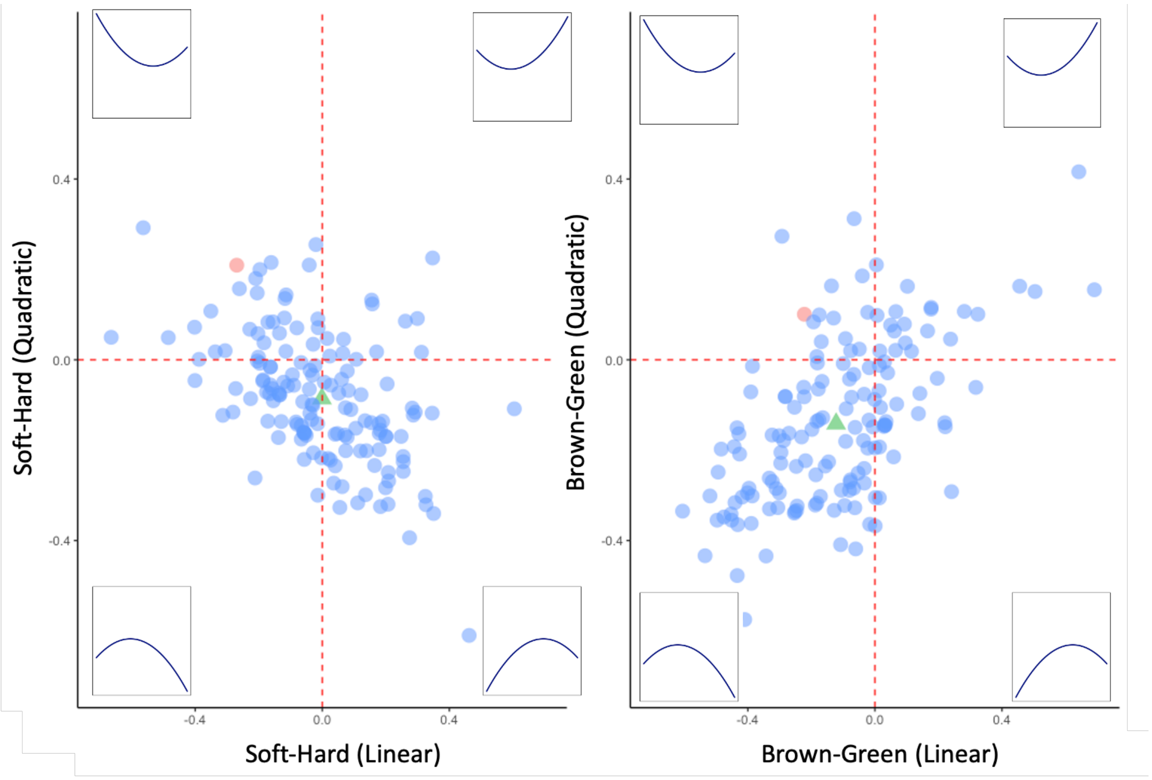

Figure 4.3: Species-specific estimates for soft-hard (left) and brown-green (right) landscape gradients and their respective polynomials. Though there was some variability, species generally followed a similar trend of increased abundance in the more heterogeneous center of the gradients. Red-backed salamander (shown by the red dot) response was somewhat of an outlier in comparison with the majority of the species community (community-estimates shown by green triangle) calling into question its function as an indicator of forest biodiversity.

4.3.3 Indicator Species Selection

Selection of indicators based on variance partitioning of the joint-species distribution model resulted in seven species with the portion of variance accounted for by the landscape gradients with four species in the top 2.5%, red oak (*Quercus rubra*), coopers hawk (*Accipiter cooperi*), black-and-white warbler (*Mniotilta varia*), and indigo bunting (*Passerina cyanea*, Table 4.2). Despite the fact that red-backed salamander abundance was strongly influenced by the environment (Table 4.1) it was not among the species identified as indicator candidates through variance partitioning.

IndVal analysis to identify indicator species for species richness revealed four species indicative of sites with species richness in the highest 30% (> 47 species), veery (*Catharus fuscescens*, IndVal = 0.803), chestnut-sided warbler (*Setophaga pensylvanica*, IndVal = 0.629), yellow-billed cuckoo (*Coccyzus americanus*, IndVal = 0.579), and the invertebrate order *Protura* (IndVal = 0.587, Table 4.1).

Table 4.1: Covariate estimates for the species community as a whole, red-backed salamander, and the four species identified by IndVal as potential indicators. Parenthetical values represent 95% of each estimate's posterior distribution. Larger IndVal scores suggest higher indicator potential (max = 1), and p-values show certainty determined through a permutation test. Veery, chestnut-sided warbler, yellow-billed cuckoo and the invertebrate order Protura were all identified significant indicators for the most species rich sites.

	Soft-Hard	***Soft-Hard^2***	***Brown-Green***	***Brown-Green^2***	***IndVal***
Community Estimates	-0.001 (-0.09,0.09)	-0.086 (-0.17,-0.01)	-0.122 (-0.24,-0.02)	-0.142 (-0.23,-0.05)	NA
red-backed salamander	-0.269 (-0.50,-0.03)	0.209 (-0.01,0.42)	-0.222 (-0.50,0.05)	-0.101 (-0.11,0.31)	
veery	-0.485 (-0.84,-0.14)	0.049 (-0.29,0.39)	-0.714 (-1.2,-0.29)	-0.435 (-0.78,-0.11)	0.803 ($p = 0.0025$)
chestnut-sided warbler	-0.129 (-0.63,0.38)	-0.137 (-0.62,0.30)	-0.44 (-1.0,0.10)	-0.316 (-0.79,0.12)	0.629 ($p = 0.0032$)
yellow-billed cuckoo	-0.171 (-0.66,0.31)	-0.136 (-0.58,0.29)	-0.44 (-1.0,0.10)	-0.316 (-0.79,0.12)	0.579 ($p = 0.009$)
Proturan	0.605 (0.1,1.13)	-0.109 (-0.47,0.25)	-0.409 (-0.94,0.12)	-0.575 (-1.0,-0.10)	0.587 ($p = 0.009$)

Table 4.2: The seven species in the top 5% of variance accounted for by the environmental landscape gradients along with associated covariate estimates for landscape axes. Values in parenthesis represent 95% of each estimate's posterior distribution.

	Soft-Hard	***Soft-Hard^2***	***Brown-Green***	***Brown-Green^2***
red oak	0.122 (-0.12,-0.37)	-0.077 (-0.27,0.12)	0.137 (-0.14,0.42)	-0.119 (-0.36,0.12)
coopers hawk	0.027 (-0.47,0.55)	-0.056 (-0.49,0.38)	-0.434 (-1.1,0.13)	-0.15 (-0.62,-0.30)
black-and-white warbler	-0.171 (-0.57,0.23)	-0.083 (-0.27,0.45)	-0.401 (-0.92,0.08)	-0.294 (-0.69,0.09)
indigo bunting	-0.014 (-0.42,0.41)	-0.09 (-0.26,0.45)	-0.418 (-.96,0.08)	-0.304 (-0.71,0.08)
eastern phoebe	-0.135 (-0.54,0.28)	0.059 (-0.29,0.41)	-0.301 (-0.78,0.17)	-0.168 (-.57,0.22)
cherry spp.	0.347 (-0.1,0.83)	0.225 (-0.1,0.57)	-0.034 (-0.59,0.52)	-0.241 (-0.71,0.21)
blue-winged warbler	-0.186 (-0.75,0.39)	-0.044 (-0.52,0.45)	-0.389 (-1.1,0.27	-0.362 (-0.92,0.17)

4.4 Discussion

4.4.1 Red-backed Salamanders as Indicators for Biodiversity

The red-backed salamander (*Plethodon cinereus*) has been widely promoted as an ideal indicator of ecosystem health, because of their significant ecological role and sensitivity to environmental variation (Welsh & Droege, 2001). Though this assertion has been established on firm conceptual and ecological grounds, and has propagated through the literature, the assumption has not been thoroughly evaluated in practice. I utilized an approach to evaluating the red-backed salamander as an indicator for biodiversity that was developed around the conceptual basis that a biological community would generally exhibit a shared response to environmental stressors, and that an ideal indicator would strongly reflect community-wide response (Figure 4.2). I used both joint species distribution modeling and the more commonly applied indicator metric, IndVal, and found that although salamander abundance was strongly influenced by gradients of landscape modification, the linear response was not consistent with the non-linear response exhibited by the majority of species in the forest community (Figure 4.3).

Furthermore, I found that red-backed salamanders were not among the species with the highest percent of the variance in abundance explained by landscape gradients (Table 4.2), and, contrary to previous findings, was not identified as an indicator of species rich sites according to IndVal scores (Table 4.1).

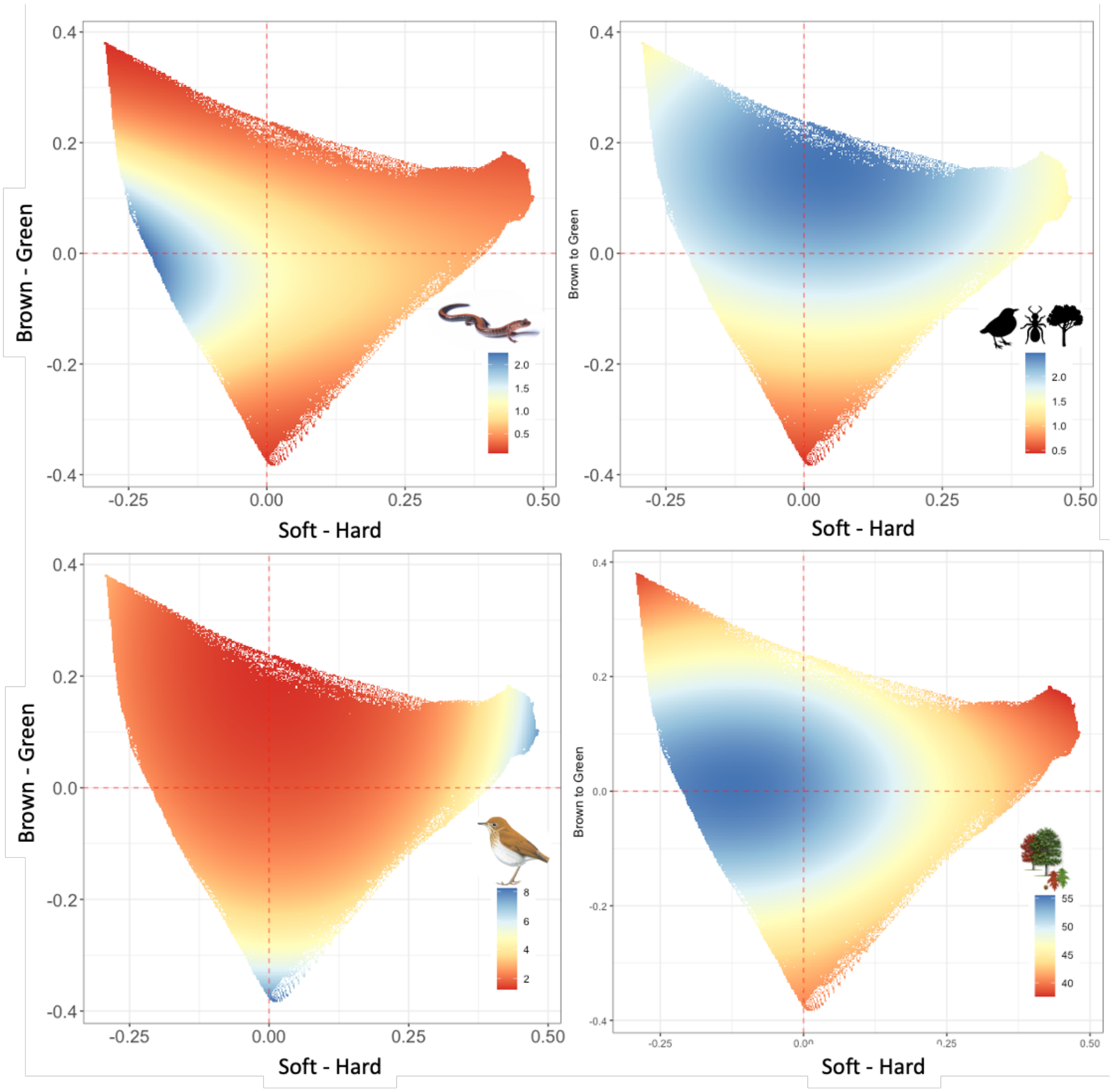

Figure 4.4: A comparison of indicator species for biodiversity in a heterogeneous human-dominated landscape. Biodiversity (top right) is maximized toward the midpoint of both landscape gradients, where habitat heterogeneity is greatest. Red-backed salamanders (top left) seem to be present at higher numbers in forest fragments situated in more homogenous agricultural (brown) and urban (hard) landscapes. Both the veery (bottom left) identified in IndVal analysis and the red oak (bottom right) identified through variance partitioning, were more emblematic of the biological community and are likely better candidates as indicators in my system.

At the community level human-modification of the landscape, as measured by multi-dimensional landscape gradients, strongly affected patterns of species-specific abundance (Table 4.1). The response to landscape heterogeneity was non-linear: species-specific abundances, and overall species richness were highest in the most heterogeneous regions of the landscape which fell approximately at the center of each axis (Figure 4.4). Encouragingly, the lack of residual species-species correlation suggests that the quadratic effects of both landscape gradients adequately captured species' habitat associations and allowed for a more informed evaluation of species-specific value as an indicator species (Appendix D.3).

Variation in patterns of species distribution and community assembly in heterogeneous and human-dominated habitats has been of considerable research interest for some time (McKinney, 2002). Biological communities are arranged by a suite of interacting biotic (e.g., competition/facilitation) and abiotic (e.g., temperature) filters (Ovaskainen et al., 2017b). In human-dominated landscapes where non-native species may outcompete native species (García-arroyo et al., 2020) and changes in temperature and moisture prevent the establishment of sensitive species (McLean et al., 2005), the biotic and abiotic filters differ from those in natural systems and the process of community structuring remains poorly understood (Mittelbach & Schemske, 2015). In spatially heterogeneous landscapes, increased diversity of habitat types may provide more available niche space, thereby reducing competition (Fahrig, 2017), conversely, the addition of new species (e.g., non-natives, generalists) that are able to exploit newly available niches in these habitats may increase the role of competition (Shochat et al., 2010). My results showed clear evidence that abiotic filters as described in the multi-dimensional landscape gradients were the most significant drivers of abundance at both the community and species level and provided very little evidence that positive or negative species associations influence the composition of biological communities in this system.

Members of the Plethodontid family, especially the red-backed salamander, are frequently promoted as ideal indicators because of their abundance, wide distribution, and ease of sampling (Ochs & Siddig, 2017; Welsh & Droege, 2001). It was surprising, therefore, that these results stand contrary to those predictions and suggest that red-backed salamanders are not the most ideal indicator of biodiversity in my system (Figure 4.2). Despite the fact that salamander abundance did show a strong response to environmental predictors, particularly along the soft-hard axis, it did not reflect the non-linear pattern of the community as a whole. In contrast to community diversity and species abundance, which are both maximized in more most heterogeneous areas mid-way along both landscape gradients, salamander abundance was highest in soft landscapes, decreasing as the mosaic becomes more heterogeneous, and again increasing slightly in more urban hard areas (Figure 4.4).

Red-backed salamanders are common across the landscape and are known to persist in small habitat fragments, even in inhospitable urban and agricultural landscapes (Noël & Lapointe, 2010; Wilk et al., 2020). At the same time, however, the small home range and cutaneous respiration of red-backs make them sensitive to small changes in the microclimate of the soil and forest floor (Ochs & Siddig, 2017; Pearce & Venier, 2009; Sugalski & Claussen, 1997), demonstrating that occupancy and abundance of red-backed salamanders is likely driven more by micro-scale rather than landscape-level factors. The species included in this analysis did not represent a comprehensive account of all species present in the community, but it does include species from a number of different taxonomic groups representing an array of life-histories and existing at a range of scales. The contrasting responses to landscape heterogeneity between salamanders and the broader community likely reflects these landscape-level versus micro-scale processes.

Experimental and observational research has shown red-backed salamanders to have small home ranges of 30-m^2 or less (Cosentino & Droney, 2016; Hernandez-Pacheco et al., 2019), with lifetime dispersal distances less than 10-m (Cosentino & Brubaker, 2018; Ousterhout & Liebgold, 2010), and are most sensitive to small changes in soil conditions, particularly moisture, temperature, and pH (Frisbie & Wyman, 1992; Petranka, 1998; Sugalski & Claussen, 1997). Accordingly, occurrence and abundance of salamanders across the landscape is likely governed by these fine scale features of the micro-habitat. While these may vary along gradients of urbanization and land-use change (Pouyat et al., 2008), they are more directly impacted by local variation in forest type, canopy cover, and availability of coarse woody debris and leaf-litter (Frisbie & Wyman, 1992; Homyack et al., 2010; Ochs & Siddig, 2017; Pearce & Venier, 2009). Because of their small home-range size red-backed salamanders may be buffered from the negative effects of urbanization where they are able to find suitable conditions in the soil micro-habitat (Norton et al., 2016). In urban parks of central Ohio, for example, the size of forest fragments did not affect local salamander abundance, however, there was very little evidence for movement between fragments (Wilk et al., 2020).

In addition to assessing the effectiveness of red-backed salamanders as indicators, I used two additional approaches to identifying potential indicators in my study system, IndVal, and variance partitioning. IndVal (Dufrêne & Legendre, 1997) is a metric that identifies indicators based on the specificity and fidelity of each species to site types. Based on this measure, four candidate species were identified as indicators for the sites with the highest species richness, with the veery, chestnut-sided warbler, and yellow-billed cuckoo most strongly supported (Table 4.1). These bird species all breed in early successional and disturbed habitats, particularly scrubby edges and regenerating forests (Hobson & Bayne, 2000), which are often readily available in human-dominated landscapes. The final species group, the invertebrate order *Protura* are small organisms that reside in moist soil and leaf-litter feeding on detritus and fungi (Galli et al., 2019), and are an important food resource for organisms, including red-backed salamanders (Homyack et al., 2010).

I also attempted to identify indicators based on the proportion of variance explained by environmental covariates in the community abundance model. Five of the seven species identified were birds, with three, the black-and-white warbler, blue-winged warbler, and indigo bunting known breeders in dense secondary growth and forested wetlands (Hobson & Bayne, 2000; Swift et al., 1984), and the remaining two, coopers hawk and eastern phoebe, common breeders in fragmented suburban habitats (McNair, 2016; A. D. Rodewald & Kearns, 2011). The red oak was the species whose response to the environment was most strongly supported by the model. This is a dominant species of eastern mixed deciduous forests, is a common species of residential neighborhoods, and generally has benefitted from human-mediated landscape alteration (Nock et al., 2013). Each of these species is characteristic of, or able to persist in, the forest types common in the heterogeneous landscape mosaic toward the center of the landscape gradients, and therefore are exemplars for the community wide response (Figure 4.3).

4.4.2 Indicators of Biodiversity in Human-Dominated Landscapes

My aims were to evaluate the ability of red-backed salamanders to act as an effective indicator of biodiversity in a human-dominated landscape, I found no support for the hypothesis that red-backed salamanders are an effective indicator species for biodiversity. However, several interesting candidate species were identified both through the joint-species distribution modeling (Table 4.2) and IndVal (Table 4.1) analysis. Species composition on the landscape is driven by multiple factors operating at a hierarchy of scales (Aronson et al., 2016). Many species, especially large charismatic or threatened vertebrate species, are more responsive to environmental filters at the landscape scale. This analysis included organisms operating at different scales – dominant structural vegetation, mobile vertebrate species, and small relatively sessile soil macro-invertebrates, and failure of red-backed salamanders likely reflects differential responses to micro- versus macro-scale environmental factors (Wilk et al., 2020). However, several interesting candidate species were identified both through the joint-species distribution modeling (Table 4.2) and IndVal (Table 4.1) analysis.

IndVal identified four species characteristic of damp, dense and scrubby forests including edge habitat and regenerating forests that are characteristic of heterogeneous mosaics in human-dominated landscapes where biodiversity is expected to be greatest. Of these, the veery (*Catharus fuscesens*) was the highest ranked indicator for the most species rich sites (Table 4.1). This species is a particularly good representative of community response to the ecosystem stressors and may be a good indicator of biodiversity (Figure 4.4). Veery are forest breeding birds that nest in forests with dense understory structure, and though sensitive to nest predation and parasitism, are able to persist in fragmented and residential landscapes because they lead to densification of forest vegetation structure (Kluza et al., 2000). As frequent vocalizers with a distinctive and song that is quickly learned, the veery is easy to monitor for occurrence or abundance. I also used variance partitioning of the joint-species distribution model to evaluate salamanders as indicators and found several species with habitat associations reflective of the broader community (Table 4.2). The red oak is a dominant component of the forest structure in the study region, and acts as a vital habitat and food resource for a number of species (Haynes et al., 2009). Unsurprisingly, oaks were more common in green rather than brown regions, but broadly speaking represented community response to the landscape (Figure 4.4).

4.4.3 Conclusions

My results provided no evidence in support of red-backed salamanders as indicators of biodiversity. While salamanders may be effective indicators of fine scale changes in the forest floor mesocosm and soil micro-environment, they are not able to reflect broad changes at the landscape scale (Figure 4.3). The suites of species we identified were characteristic of dense secondary growth forests that are typical of heterogeneous landscape mosaics. The veery is sensitive to structural (hard) landscape development, but is able to persist in forest fragments, while the red oak is most abundant in forested regions and is a critical food resource for many species (Figure 4.3), making species preferable to the red-backed salamander as indicators of biodiversity. In contrast to the veery whose habitat associations overlap with a majority of other species in the community, the red oak may act more as a keystone or foundational species because of the important role it plays in the food web. Using species such as these as indicators for biodiversity conservation in human-dominated landscapes prioritizes a mixed mosaic that includes scrubby forest edges while maintaining sufficient forest interior to preserve more sensitive species. Conversely, relying on the red-backed salamander as an indicator for the effects of anthropogenic stressors on biodiversity would lead to the incorrect assessment that biodiversity in heterogeneous landscape mosaics, where salamander abundance is lowest, is at risk.

While these results did not provide support for red-backed salamanders as indicators of biodiversity, I was able to identify several indicator candidates using joint-species distribution modeling and IndVal. One especially encouraging aspect of this is that although my data were collected by a single observer over time, the type of data used here could just as easily have been collected in a short time by a team of citizen scientists in a ‘bio-blitz’ making it possible for decision makers to use a data driven approach to indicator species identification and assessment, and ultimately make informed and adaptive management decisions. As the human footprint on the landscape continues to grow informed species conservation and management is imperative. I stress that critical and objective evaluation of proposed indicators is vital, and demonstrate the process using observational abundance data that are increasingly available through citizen science platforms such as eBird and iNaturalist and can be leveraged for the mutual benefit of human and natural ecosystems.

CHAPTER 5

CONCLUDING REMARKS

The initial aim of this dissertation research was to better understand the effects of habitat transformation, particularly urbanization, on a common and environmentally sensitive species. However, I immediately recognized that prior to understanding the effects of landscape pattern on ecological process, a clear understanding and measure of the landscape is required, something that was lacking in human-dominated systems. In recognition of this knowledge gap, I developed a transparent framework for standardizing landscape gradient quantification in human-dominated systems and applied this framework to find a consistent multi-dimensionality to the landscape that is often overlooked. Ultimately, however, my goals in this research were to better understand the ecological impacts of human-mediated landscape transformation such as urbanization or agriculture, I was able to use the multi-dimensional landscape gradients to test theories of community ecology and indicator species analyses. I truly hope that this research has an impact beyond the halls of academia. The multi-dimensional landscape gradients developed here can be used to better inform conservation and landscape management, while my own applications in forests of western Massachusetts has provided strong evidence that a mixed-use landscape mosaic is beneficial to biodiversity.

The ecological response of urban-rural landscapes has been extensively studied in recent decades. In spite of this, the lack of sound and consistent definitions of these landscapes has been repeatedly pointed out and attributed to the equivocal findings in the literature. I revisited the relevant literature to review the urban gradient concept, however, rather than aiming to illuminate inconsistencies, I sought to identify patterns in line with suggested best practices in landscape ecology. This review highlighted that despite observed variability, researchers consistently follow a general decision framework for landscape quantification, however, transparent forethought and ecological justification was often lacking in making these decisions. Accordingly, in order to improve standardization of urban gradients in practice, I called for transparent reporting and clear ecological justification for decisions made regarding (1) landscape structure, (2) spatial data, and (3) spatial scale. It is my hope that the transparency called for in this chapter will lead to methodological improvements and standardization in urban gradient definition and ultimately improve general understanding of ecological processes in a rapidly urbanizing world.

Chapter 2 applied the transparent framework outlined in Chapter 1 to quantify landscape gradients in 10 ecologically distinct US cities. I used freely available NLCD land-cover and land-use data to represent human-mediated and natural landscape features which were analyzed using a multivariate approach at a 500-m spatial scale to produce a pair of general and intuitive landscape gradients describing structural (soft-hard) and non-structural (brown-green) types of human-mediated landscape alteration. Together, these axes provide a complete multi-dimensional perspective of heterogeneous landscape mosaics and proved to be both consistent in various contexts, and effective at predicting ecological response. In short, this chapter acts as a critical proof-of concept for the transparent landscape gradient framework identified in Chapter 1. by using readily available remote-sensed data to represent a broadly applicable set of landscape features with an easily implementable analytical method, and demonstrating its reproducibility and ecological relevance, I hope that this work will encourage other researchers to follow suit.

In my third Chapter I focused my efforts exploring the multi-dimensional landscape gradient back to my local study system in western Massachusetts to investigate the effects of landscape heterogeneity on the structure and composition of bird communities. I tested two prominent theories describing how biological communities and biodiversity are impacted by habitat fragmentation and landscape mosaics. These theories, island biogeography and spatial heterogeneity, both have strong support in the literature and firm conceptual grounding. I used multi-dimensional landscape metrics in a hierarchical model for species abundances to test these theories and describe patterns of avian diversity in a human dominated landscape. My results showed that bird diversity is greatest near the center of both soft-hard and brown-green axes of the multi-dimensional gradient, the area of highest heterogeneity, and lends support to the hypothesis that biodiversity in fragmented landscape mosaics benefits from the greater habitat diversity and niche breadth heterogeneous landscapes provide. The debate over how to best manage fragmented landscapes has roiled for several decades and remains a relevant topic in ecology. By using a multi-dimensional perspective of the landscape, I demonstrated a general non-linear response of birds to the landscape and demonstrate that this landscape framework can be used to improve understanding of ecosystem process in other contexts as well.

For my fourth and final research chapter I simultaneously expanded my scope beyond bird communities to include tree and invertebrate species, while focusing on a single species, the red-backed salamander (*Plethodon cinereus*). I once again relied on the multi-dimensional landscape gradients to critically evaluate the red-backed salamander as an indicator species for biodiversity. The indicator species concept is widely used to rapidly assess habitat and prioritize conservation efforts, however, the species often used as indicators, including the red-backed salamander, are rarely explicitly tested. I used abundance data for red-backed salamanders as well as tree, bird, and invertebrate species at 42 sites in western Massachusetts to test the salamander's potential as an indicator of biodiversity. I used a joint-species distribution model on the conceptual basis that the biological community would exhibit a shared response, and that an ideal indicator would be one whose response to the landscape strongly represented that of the species community. Although my results showed a clear community wide quadratic response to the multi-dimensional landscape, salamanders did not share this pattern with the majority of species on the landscape, suggesting that it is not an effective indicator for biodiversity. However, my analyses did reveal several candidate indicators that are characteristic of dense forests and edges common in heterogeneous landscapes where biodiversity is high. Indicator species are most often selected based on prior use in the literature, not critical evaluation. I hope that this work will cause others to pause and take time to objectively relate the indicator in question to ecological targets rather than relying on even well-founded ecological assumptions.

Overall, my dissertation was inspired by, and ultimately concluded with the red-backed salamander. Along the way, the arc of this research provides several important contributions to ecological theory and conservation practice in the context of human-dominated landscapes. First, my review of the urban gradient literature describes a clear methodological framework calls for transparency and ecological justification for decisions made when quantifying spatial metrics. Second, within this framework I used readily accessible remote-sensed land-cover data and a multivariate statistical approach to describe an ecologically intuitive and widely applicable pair of landscape gradients that together provide a clearer, multi-dimensional, perspective of human dominated landscapes. Together, these can provide much needed methodological standardization and improvement to landscape gradient quantification, and to reduce the variability in spatial metrics and uncertainty in understanding of the effects on ecosystem process. Finally, my evaluation of the red-backed salamander as an indicator species and test of theories describing species diversity in heterogeneous systems have both shown that in human-dominated landscape mosaics, species diversity is greatest in the moderately disturbed regions where spatial heterogeneity of habitat is highest. These results are encouraging because they suggest that as the human population continues to expand, wisely managed integration of the urban, agricultural, and natural landscapes can provide habitat for a large number of species. While large relatively undisturbed habitat tracts will still be needed to ensure survival of all species, a land-sharing approach where commercial, residential, and agricultural land-uses are integrated in a mosaic with natural habitat has the potential to be a valuable conservation tool. Furthermore, by providing ready access to nature for men, women and children it has the potential to improve social, emotional and physical health, reduce the effects of environmental injustice, and most importantly to instill them with a love for the natural world and an ethic of environmental stewardship.

APPENDICES

APPENDIX A – CHAPTER 1: A STANDARDIZED FRAMEWORK FOR TRANSPARENT QUANTIFICATION OF URBAN LANDSCAPE GRADIENTS

Appendix A.1: Full list of search terminology used in Web of Science [5.2.1]

Search Query:

TS = ("Urban Gradient" OR "Urban Rural Gradient" OR "Rural Urban Gradient")

Web of Science Categories:

Environmental Sciences OR Ecology OR Biodiversity Conservation OR Parasitology OR Marine Freshwater Biology OR Environmental Studies OR Mycology OR Plant Studies OR Zoology OR Forestry OR Ornithology OR Entomology OR Biology OR Evolutionary Biology

Journal Categories:

Environmental Sciences; Ecology; Biodiversity Conservation; Parasitology; Marine Freshwater Biology; Environmental Studies; Engineering Environmental; Mycology; Plant Sciences; Zoology; Forestry; Ornithology; Entomology; Biology; Evolutionary Biology

Appendix A.2: Full citations list of 250 reviewed papers

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Appendix A.3: Names and counts of 121 journals represented in review

Journal Name		Journal Name	
Acta Oecologica	2	Diseases of Aquatic Organisms	1
Acta Ornithologica	1	Diversity and Distributions	4
American Midland Naturalist	1	EcoHealth	1
Animal Behavior	1	Ecological Applications	6
Animal Conservation	3	Ecological Indicators	6
Applied Herpetology	1	Ecological Modeling	1
Applied Soil Ecology	1	Ecological Research	1
Applied Vegetation Science	1	Ecology	2
Aquatic Microbial Ecology	1	Ecology and Evolution	4
Archives of Environmental Contamination and Toxicology	2	Ecoscience	4
Asian Herpetological Research	1	Ecosphere	2
Asian Myrmecology	1	Ecosystems	2
Austral Ecology	2	Ecotoxicology	1
Avian Biology Research	1	Emu	1
Behavior	1	Entomological Science	1
Behavioral Ecology	2	Environmental Biology of Fishes	1
Behavioral Processes	1	Environmental Entomology	1
Biodiversity and Conservation	5	Environmental Monitoring and Assessment	1
Biological Conservation	6	Ethology	1
Biological Invasions	3	European Journal of Entomology	3
Biology Letters	2	Evolutionary Applications	1
Bird Study	3	Experimental and Applied Acarology	1
Bulletin of Insectology	1	Florida Entomologist	2
Canadian Journal of Fisheries and Aquatic Sciences	2	Forest Ecology and Management	1
Canadian Journal of Forest Research	1	Freshwater Science	1
Canadian Journal of Zoology	2	Frontiers in Ecology and Evolution	1
Chelonian Conservation Biology	1	Frontiers in Zoology	1
Community Ecology	2	Global Change Biology	2
Comptes Rendus - Biologies	1	Global Ecology and Biogeography	1
Conservation Biology	2	Herpetologica	1
Conservation Genetics	1	Herpetological Journal	2
Contemporary Problems of Ecology	1	Ibis	1

Copeia	1	Insect Conservation and Diversity	1
Current Zoology	1	Integrative and Comparative Biology	2

Journal Name		Journal Name	
International Journal of Remote Sensing	1	Oecologia	1
International Journal of Sustainable Development & World Ecology	1	Oikos	1
Journal of Animal Ecology	2	Ornitologia Neotropical	1
Journal of Arid Environments	1	Pedobiologia	1
Journal of Avian Biology	2	Periodicum Biologorum	1
Journal of Biogeography	3	Philosophical Transactions of the Royal Society B: Biological Sciences	2
Journal of Comparative Physiology B	1	Physiological and Biochemical Zoology	1
Journal of Economic Entomology	1	Plant Ecology	3
Journal of Evolutionary Biology	1	Polish Journal of Ecology	1
Journal of Field Ornithology	1	Remote Sensing of Environment	1
Journal of Geophysical Research	1	River Research and Applications	2
Journal of Great Lakes Research	1	The Auk	3
Journal of Insect Conservation	1	The Condor	5
Journal of Insect Science	1	The Journal of Arachnology	1
Journal of Mammology	2	The Journal of Wildlife Management	1
Journal of Medical Entomology	2	The Lichenologist	1
Journal of Mountain Science	1	The Wilson Journal of Ornithology	2
Journal of Ornithology	3	Tropical Conservation Science	1
Journal of Raptor Research	1	Urban Ecosystems	28
Landscape and Urban Planning	21	Urban Forestry & Urban Greening	2
Landscape Ecology	10	Water Quality Research Journal of Canada	1
Mammalian Biology	1	Wetlands	1
Molecular Ecology	1	Wildlife Research	1
Neotropical Entomology	1	ZooKeys	2
North American Journal of Fisheries Management	1	Zoologia	1
Northeastern Naturalist	1	Zoological Studies	1
Northwest Science	1		

A.4 – Analysis of Review Data

We fit a Poisson generalized linear model to evaluate the hypothesis that the number of reviewed publications would show an increase over time. The model indicated a significant positive effect of ‘year’ ($p < 0.001$), with an increase on average of 1.13 publications per year.

Table 2: Model coefficients for analysis of number of publications reviewed per year. Parameter estimates are on the Poisson log scale.

	Estimate	Std. Error	P-value
Intercept	2.476	0.1612	<2e-16
Year Effect	0.1212	0.0230	1.42e-07

We fit a Negative Binomial generalized linear model to evaluate the effects of focal taxa size on the selection of a spatial scale. We expected that, because larger organisms tend to have larger home ranges, and thus respond to the landscape at a larger spatial scale, the choice of scale would be related to the size species under study. One significant outlier in the response (scale > 10000) was removed because it had a large effect on model estimates, taxon body size was categorized on a scale of 1 to 4 as follows:

1. insects and micro-organisms,
2. small to medium organisms,
3. medium to large organisms,
4. very large organisms, trees, or ecosystem level.

We found no relationship between chosen spatial scale and body size classes (est. scale for size classes 1-4: *1338.0*, *1339.7*, *1338.9*, *1341.4*)

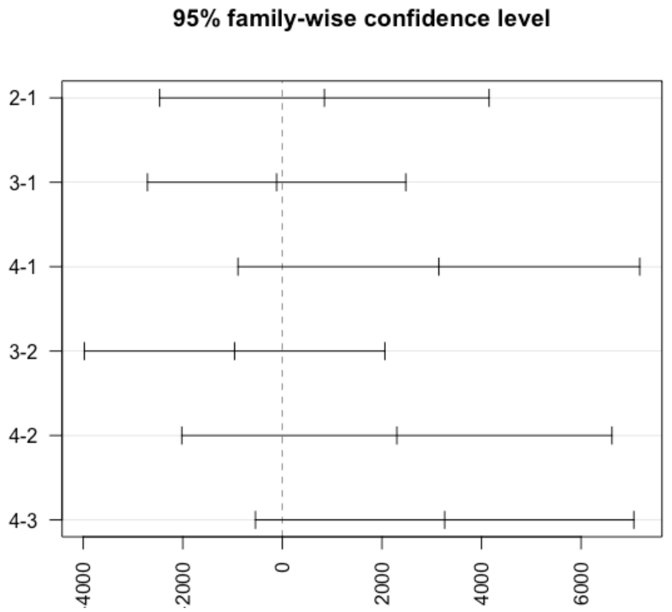


Figure 5: Pairwise comparison, derived from Tukey's honest significant difference test, of model coefficients for spatial scale for each size category. There was no significant difference in spatial scale for the largest (4) and smallest (1) sized species, respecively.

Table 3: Model coefficients for analysis of categorical body size and spatial scale. Parameter estimates are on the Negative Binomial (log-link) scale. Estimates for Size$_{2-4}$ correspond to the reference level Size$_1$. Starred p-value indicates significance at (alpha = 0.05).

Size Category	Estimate	Std. Error	p-value
Size$_1$	7.199	0.243	<2e-16*
Size$_2$	0.489	0.389	0.2095
Size$_3$	-0.090	0.306	0.7675
Size$_4$	1.209	0.475	0.0109
theta (θ)	0.6014	0.0698	

A framework for transparent quantification of urban landscape gradients

Benjamin J. Padilla and Christopher Sutherland

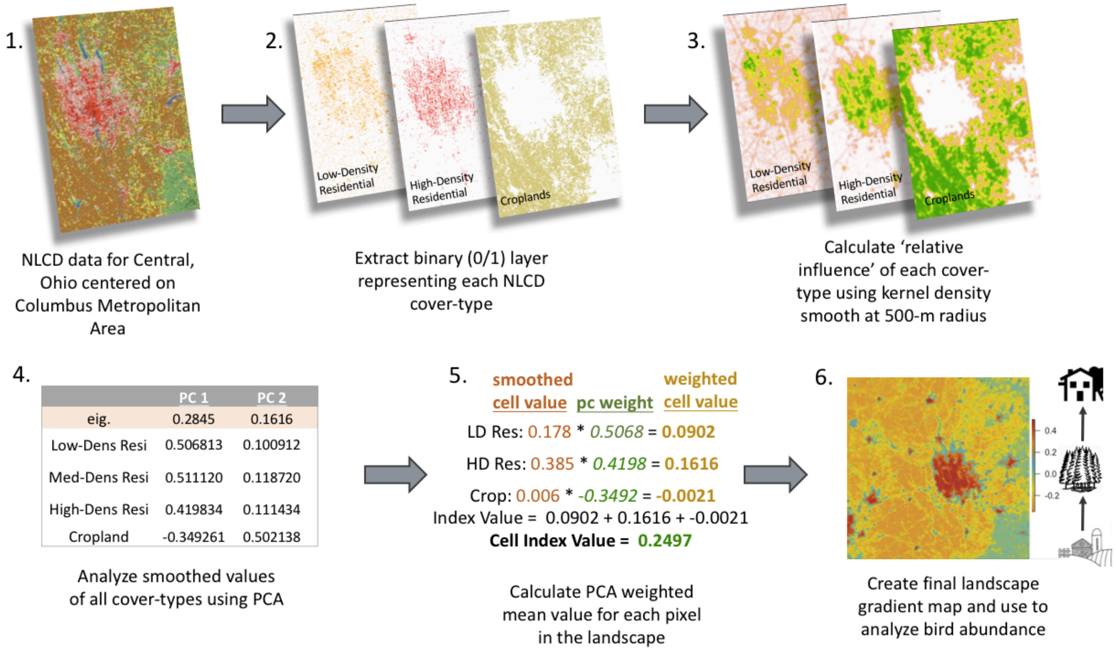
Appendix A.5 - Application of Framework in Context

We analyzed the landscape surrounding the urban centers of Springfield, MA and Columbus, OH to demonstrate the value of analyzing urban-exurban landscapes using a candid standardized framework. Urban-exurban landscape gradients were quantified for a 150-km *x* 150-km region surrounding Springfield, Massachusetts (42.1015° N, 72.5898° W) and Columbus, OH (39.9612 ° N, 82.9988° W) following the three step standardized landscape gradient framework (Figure 2.2 *in text*) for a hypothetical analysis of ecological response to landscape change in two common bird species (Northern Cardinal, *Cardinalis cardinalis* and Ovenbird, *Seiurus aurocapilla*). Decisions made at each step of the framework were identical in both regions in order to demonstrate the framework's ability to standardize landscape definition. A step-by-step diagram of our process and accompanying table of decisions made within landscape gradient framework can be found in Figure A.5.1 and Table A.5.1 respectively.

Coverage of natural habitat types, and human land-use and approximate density were identified as important features of both landscapes. Land-cover data from National Land Cover Database were selected to represent these features because it includes all relevant natural and human dominated cover types, and can approximate population density through categories of residential development (i.e. *High Density Residential* vs. *Low Density Residential*). Each NLCD cover type was then extracted as a binary map layer, and was subsequently 'smoothed' using a moving window kernel-density function resulting in the 'relative influence' of each cover type at every pixel on the landscape. Spatial scale of the smoothing kernel (500-m radius) was determined by the home range size of the known home range of focal species based on the established literature. The smoothed values of each cover type for every pixel were then analyzed using Principle Components Analysis to estimate dominant trends in land cover across the landscape. We examined the dominant component that explained majority of variance, and interpreted its application in the landscape context. Finally, the landscape gradient was calculated as a PCA weighted index of land cover across the landscape by multiplying the smoothed pixel value by PC weights for individual cover types and summing across cover types (*Equation 1*), where SLG_i is the Standardized Landscape Gradient value for cell i, LC_{ij} is the smoothed value for NLCD cover-type j in cell i, and pcw_j is the principle component weight of cover-type j.

$$SLG_i = \sum_j LC_{ij} * pcw_j$$

In both regions, the Standardized Landscape Gradient approach described an ecologically meaningful pattern in the landscape that differentiated different types of human land use (i.e. urbanization and agriculture) from natural habitat (forest; Figure 2.5).



NLCD data for Central, Ohio centered on Columbus Metropolitan Area

Extract binary (0/1) layer representing each NLCD cover-type

Calculate 'relative influence' of each cover-type using kernel density smooth at 500-m radius

	PC 1	PC 2
eig.	0.2845	0.1616
Low-Dens Resi	0.506813	0.100912
Med-Dens Resi	0.511120	0.118720
High-Dens Resi	0.419834	0.111434
Cropland	-0.349261	0.502138

Analyze smoothed values of all cover-types using PCA

smoothed cell value | pc weight | weighted cell value

LD Res: 0.178 * *0.5068* = **0.0902**

HD Res: 0.385 * *0.4198* = **0.1616**

Crop: 0.006 * *-0.3492* = **-0.0021**

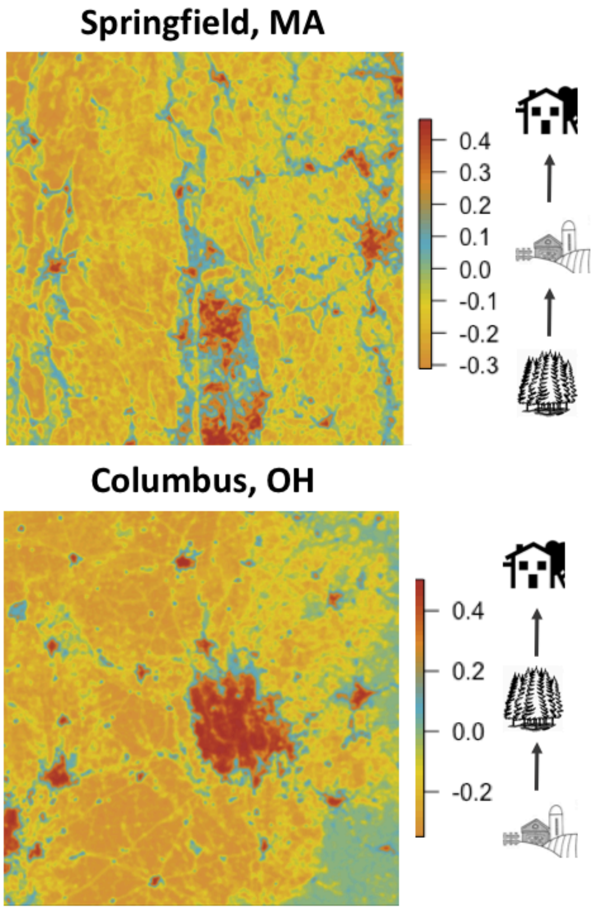
Index Value = 0.0902 + 0.1616 + -0.0021

Cell Index Value = 0.2497

Calculate PCA weighted mean value for each pixel in the landscape

Create final landscape gradient map and use to analyze bird abundance

Figure A.5.6: The process for quantifying the urban-exurban landscapes in Springfield, MA and Columbus, OH. Decisions made within the landscape gradient framework were consistent between regions, and are outlined in Table 2. Each panel represents a step in the process used to implement the gradient framework, and illustrates that implementation of decisions made within the framework may not occur 'chronologically' in the analytical process.


Springfield, MA

Columbus, OH

Figure A.5.7: Landscape gradients produced using the three step standardized gradient framework. In both regions the framework produced highly meaningful and intuitive gradients of landscape variability. Table 3 includes PCA variable weights for both regions.

Table A.5.1*: Decisions made within landscape gradient framework for analyzing urban landscapes in Springfield, MA and Columbus, OH. The corresponding step-by-step implementation of these steps is outlined in Figure 4.*

SLG Step	Decision	Justification
1) Landscape Features	Physical land-cover and demographic land-use	'Land-cover' categories (i.e. forest, shrub) track changes in 'natural' landscapes, while 'land-use' (devel., crop) tracks the human footprint and approximate population density
2) Spatial Data	Remote-sensed, National Land Cover Data	NLCD land-cover data in freely accessible and highly vetted. Benefits of accessibility and reproducibility outweigh potential pitfalls of errors in the data
3) Spatial Scale	500-m radius	Scale of analysis was determined by mean home range size of our two focal species (Northern Cardinal and Ovenbird) in the established literature
4) Analytical Methods	PCA weighted index	Principle Components Analysis incorporates variability of all landscape features over the landscape and extracts meaningful patterns of variation. A weighted index incorporates variability of all components into a single metric

Table A.5.2: Principle component weights for each NLCD cover type in Columbus, OH and Springfield, MA. PC1 explained the most variation in the data, and was used to create landscape gradient (seen in Figure D.5).

NLCD Cover Type	**Ohio PC1**	**Mass. PC1**
Std. Dev	1.773	1.850
Open Water	0.0617	0.0358
Developed Open	0.4154	0.4201
Low Developed	0.5068	0.4941
Med Developed	0.5111	0.4756
High Developed	0.4198	0.3751
Barren/Waste	0.0361	0.0662
Forest Decid.	- 0.0147	- 0.3117

Forest Everg.	- 0.0014	- 0.1054
Forest Mixed	-0.0339	- 0.2469
Scrub/Shrub	0.0005	0.0598
Grass/Herb	- 0.0339	0.1392
Pasture	- 0.0563	0.0375
Crop	- 0.3493	0.0819
Wet Woodlands	0.0184	0.0583
Wet Herbaceous	0.0032	0.0556

APPENDIX B – CHAPTER 2: MULTI-DIMENSIONAL LANDSCAPE GRADIENT DEFINITIONS FOR HUMAN DOMINATED LANDSCAPES

B.1 – Effects of smoothing scale: 1,500-m scale

To test for sensitivity of landscape quantification approach to choice of smoothing scale, we conducted landscape analysis at two kernel scales, 500-m and 1,500-m described here. Extending the size of the smoothing parameter increases the "neighborhood" surrounding each focal pixel influencing the smoothed value. In this way, a larger portion of the surrounding landscape is considered to have a significant contribution on the smoothed value of a given pixel. We analyzed all ten study cities in a joint analysis at a 1,500-m smoothing scale using the same methods described for 500-m.

Quantification of landscape heterogeneity at a 1,500-m smoothing scale yielded results that were highly comparable with the 500-m scale (Table A.1). The first principal component explaining the largest proportion of data variation (σ_{1500} = 19.2%) was also strongly negative for developed land-cover classes (e.g, Devel-Mid = -0.531), with neutral or positive loadings for forested (Forest-Deciduous = 0.034), open, and agricultural (Crop = 0.133) classes. The second principal component (σ_{1500} = 12.9%) showed a strong divergence between non-impervious (i.e., *soft*) landscape types, differentiating between those that are highly modified by human activity. Forested regions had strongly negative loadings (Forest-Deciduous = -0.481) while croplands had strongly positive loadings (Crop = 0.424), and distinguishes between types of non-structural landscapes. Finally, as in the 500-m analysis, the third principal component also distinguished between non-structural landscapes. However, while PC2 separated predominantly deciduous forests and wetlands (common in eastern US) from agriculture, PC3 separated mixed forests and scrublands (common in western US) from agriculture.

While the component weights and NLCD land-use eigen values differed between 500-m and 1,500-m analyses, the ultimate ecological interpretation of the resulting landscape gradients was consistent. In both cases the first component represented a gradient from heavily built to non-built environments along *hard*-to-*soft*, while the second and third represented variation in the non-built environment along an axis of *green*-to-*brown*.

B.2 – Effects of local environment

In addition to our joint (i.e., all cities) analyses, we quantified landscape gradients in all study cities independently (Table A.2). Results for city specific analyses were remarkably consistent in spite of regional variation in the composition and configuration of natural and human-dominated landscapes. This was especially true in the case of the first principal component describing the most significant portion of the variation in landscape data. In all cities the strongest component described a gradient of variation from *hard* regions characterized by the human-dominated built environment from non-built *soft* regions (Table A.2).The second component, however, was more variable and depended on the city specific landscape composition. Nevertheless, with the sole exception of Albuquerque, where PC2 differentiated wetland habitats from developed areas, the interpretation of the second component consistently described variation between *brown* and *green* regions, respectively.

B.3 – American Robin Occupancy Analysis

Table B.3.4: Total number and final number of sampling locations for each study city. In cases where cities had > 250 locations, we thinned the sampling pool with a random sample of 250 locations. Number of sampling events reflects the total number of visits to all sampling locations in a given city, and Frequency of Presence is the proportion of those visits where a Robin was observed.

	Bakersfield, California	Lexington, Kentucky	Worcester, Massachusetts	Jackson, Mississippi	Lincoln, Nebraska	Albuquerque, NM	Portland, OR	Lubbock, TX	Salt Lake City, UT	Spokane, WA
Total Num. Sampling Locations	31	181	**593**	56	165	**581**	**831**	46	**581**	224
Final Num. Sampling Locations	31	181	250	56	165	250	250	46	250	224
Final Num. Sampling Events	110	632	791	200	596	853	869	158	830	740
Freq. of 'Presence'	0.4818	0.4430	0.4349	0.4650	0.4463	0.4431	0.4325	0.4620	0.4289	0.3865

Table B.3.5: Parameter estimates for Robin detection probability (ρ) and occupancy (Ψ) for the best supported model: $logit(\rho_{ij}) = city_i * date_{ij} + date_{ij}^2 + HS_i + BG_i$ *and for occupancy,* $logit(\psi_i) = city_i * HS_i + BG_i$ *. All parameter estimates are on the logit scale.*

Parameter (p)	Estimate	Std. Error	p-value	Parameter (Ψ)	Estimate	Std. Error	p-value
(Intercept)	0.5437	1.077	0.614	***(Intercept)***	0.6216	0.959	0.517
city.KY	0.9950	1.099	0.365	***city.KY***	0.5677	0.993	0.568
city.MA	0.0150	1.087	0.989	***city.MA***	1.8075	1.186	0.127
city.MS	-1.4501	1.116	0.194	***city.MS***	3.5543	7.334	0.628
city.NE	1.2558	1.097	0.252	***city.NE***	0.7465	0.992	0.452
city.NM	-0.4088	1.127	0.717	***city.NM***	-0.8356	1.009	0.408
city.OR	-0.8127	1.082	0.453	***city.OR***	1.1564	1.138	0.309
city.TX	-1.4047	1.114	0.207	***city.TX***	0.4815	1.072	0.653
city.UT	-0.0671	1.082	0.950	***city.UT***	0.6174	1.017	0.545
city.WA	-0.148	1.094	0.989	***city.WA***	0.9677	1.077	0.369
date	-0.0187	0.113	0.869	***BG***	0.5176	0.143	*0.00029*
$date^2$	-0.0122	0.0015	$6.7e^{-17}$	***HS***	0.0394	0.571	0.945
BG	0.1421	0.0528	*0.007*	***city.KY:HS***	0.2868	0.640	0.654
HS	-0.0379	0.0422	0.369	***city.MA:HS***	-1.7202	0.765	0.025
city.KY:date	0.1160	0.112	0.302	***city.MS:HS***	-3.8444	5.004	0.442
city.MA:date	0.0678	0.112	0.547	***city.NE:HS***	-0.0307	0.594	0.958

city.MS:date	0.1259	0.115	0.276	***city.NM:HS***	-0.7110	0.623	0.254
city.NE:date	0.1018	0.112	0.363	***city.OR:HS***	1.1928	0.912	0.191
city.NM:date	0.0545	0.117	0.642	***city.TX:HS***	0.0138	0.792	0.986
city.OR:date	0.1002	0.1114	0.368	***city.UT:HS***	-0.9415	0.628	0.134
city.TX:date	0.2958	0.113	*0.008*	***city.WA:HS***	1.6107	0.819	0.049
city.UT:date	0.0940	0.1112	0.398				
city.WA:date	0.0857	0.1124	0.446				

APPENDIX C – CHAPTER 3: DRIVERS OF COMMUNITY STRUCTURE ALONG A MULTI-DIMENSIONAL LANDSCAPE GRADIENT

C.1 – Species-specific parameter estimates

Table C.1: Parameter estimates for abundance (lambda) for all species. For each parameter, the posterior mean and 95% credible intervals are reported.

Species Name	**Common Name**	**Soft – Hard**			**Soft – Hard^2**			**Brown – Green**			**Brown – Green^2**		
Anas platyrhynchos	mallard	-0.075	-0.398	0.237	-0.138	-0.46	0.16	-0.109	-0.547	0.33	-0.235	-0.682	0.162
Aix sponsa	wood duck	-0.075	-0.39	0.229	-0.13	-0.445	0.159	-0.107	-0.537	0.331	-0.247	-0.695	0.148
Corvus brachyrhynchos	American crow	-0.115	-0.361	0.117	-0.14	-0.364	0.07	-0.26	-0.576	0.038	-0.091	-0.305	0.119
Carduelis tristis	American goldfinch	0.018	-0.18	0.23	-0.031	-0.17	0.107	-0.097	-0.343	0.152	-0.041	-0.204	0.119
Setophaga ruticilla	American redstart	-0.048	-0.321	0.235	0.042	-0.227	0.352	0.103	-0.217	0.432	0.094	-0.135	0.331
Turdus migratorious	American robin	0.107	-0.094	0.312	-0.144	-0.266	-0.029	-0.015	-0.234	0.199	-0.071	-0.217	0.071
Icterus galbula	Baltimore oriole	-0.054	-0.316	0.213	-0.119	-0.368	0.11	0.007	-0.328	0.377	-0.122	-0.422	0.174
Strix varia	barred owl	-0.036	-0.332	0.283	-0.076	-0.348	0.189	-0.077	-0.51	0.374	-0.222	-0.665	0.179
Mniotilta varia	black-and-white warbler	-0.067	-0.331	0.193	-0.078	-0.312	0.147	-0.28	-0.659	0.056	-0.287	-0.591	-0.014
Coccyzus erythropthalmus	black-billed cuckoo	-0.078	-0.385	0.219	-0.187	-0.521	0.107	-0.091	-0.51	0.335	-0.345	-0.821	0.042
Poecile atricapillus	black-capped chickadee	-0.061	-0.253	0.134	-0.071	-0.198	0.054	-0.087	-0.327	0.153	0.014	-0.128	0.154
Ceryle alcyon	belted kingfisher	-0.103	-0.396	0.172	-0.12	-0.391	0.135	-0.078	-0.461	0.311	-0.23	-0.59	0.095
Polioptila caerulea	blue-gray gnatcatcher	-0.088	-0.372	0.189	-0.02	-0.262	0.218	-0.145	-0.499	0.194	-0.008	-0.294	0.292
Molothrus ater	brown-headed cowbird	-0.016	-0.283	0.276	-0.051	-0.277	0.179	0.049	-0.319	0.462	-0.41	-0.83	-0.056
Vireo solitarius	blue-headed vireo	-0.05	-0.351	0.266	-0.096	-0.404	0.207	-0.077	-0.512	0.384	-0.218	-0.652	0.183
Dendroica fusca	blackburnian warbler	-0.117	-0.454	0.182	-0.143	-0.464	0.143	-0.123	-0.545	0.302	-0.305	-0.747	0.071
Cyanocitta cristata	bluejay	-0.004	-0.182	0.181	-0.134	-0.251	-0.02	0.211	-0.067	0.459	0.017	-0.122	0.153
Certhia americana	brown creeper	-0.034	-0.326	0.271	-0.166	-0.477	0.115	-0.145	-0.544	0.238	-0.232	-0.608	0.105
Dendroica caerulescens	black-throated-blue warbler	-0.084	-0.39	0.208	-0.074	-0.323	0.165	-0.193	-0.615	0.199	-0.193	-0.543	0.123
Dendroica virens	black-throated-green warbler	-0.232	-0.585	0.047	-0.132	-0.415	0.131	-0.277	-0.686	0.092	-0.38	-0.727	-0.072
Vermivora pinus	blue-winged warbler	-0.11	-0.432	0.18	-0.135	-0.446	0.15	-0.144	-0.579	0.278	-0.279	-0.727	0.103
Branta canadensis	Canada goose	-0.072	-0.386	0.235	-0.148	-0.471	0.144	-0.192	-0.623	0.207	-0.16	-0.554	0.233
Thyothorus ludovicianus	Carolina wren	-0.031	-0.314	0.27	-0.213	-0.532	0.06	-0.066	-0.445	0.343	-0.413	-0.869	-0.04
Bombycilla garrulus	cedar waxwing	-0.186	-0.521	0.084	-0.035	-0.297	0.254	0.037	-0.305	0.431	-0.212	-0.539	0.091
Spizella passerine	chipping sparrow	-0.033	-0.298	0.246	-0.197	-0.47	0.036	-0.027	-0.37	0.34	-0.145	-0.439	0.141
Chaetura pelagica	chimney swift	-0.065	-0.378	0.232	-0.11	-0.394	0.163	-0.044	-0.457	0.397	-0.275	-0.718	0.115
Quiscalus quiscula	common grackle	0.001	-0.229	0.256	0.007	-0.218	0.251	-0.218	-0.517	0.074	-0.204	-0.486	0.079

Accipiter cooperii	coopers hawk	-0.071	-0.382	0.231	-0.169	-0.498	0.12	-0.191	-0.621	0.207	-0.2	-0.572	0.142
Geothlypis trichas	common yellowthroat	-0.229	-0.517	0.023	-0.195	-0.421	0.007	-0.308	-0.625	-0.011	-0.309	-0.546	-0.082
Dendroica pensylvanica	chestnut-sided warbler	-0.12	-0.433	0.154	-0.227	-0.55	0.039	-0.326	-0.762	0.043	-0.209	-0.567	0.128
Junco hyemalis	dark-eyed junco	-0.083	-0.399	0.22	-0.141	-0.456	0.155	-0.096	-0.525	0.339	-0.276	-0.737	0.122
Picoides pubescens	downy woodpecker	-0.036	-0.262	0.193	-0.054	-0.231	0.114	-0.061	-0.348	0.22	-0.154	-0.373	0.052
Tyrannus tyrannus	eastern kingbird	-0.074	-0.398	0.237	-0.143	-0.479	0.154	-0.115	-0.568	0.318	-0.24	-0.686	0.161
Sayornis phoebe	eastern phoebe	-0.073	-0.355	0.202	-0.128	-0.388	0.106	-0.233	-0.61	0.115	-0.213	-0.538	0.083
Pipilo erythrophthalmus	eastern towhee	-0.039	-0.31	0.248	-0.15	-0.367	0.049	0.085	-0.29	0.521	-0.29	-0.655	0.034
Contopus virens	eastern wood-peewee	-0.027	-0.222	0.177	0.044	-0.102	0.188	0.105	-0.202	0.396	0.11	-0.076	0.297
Sturnus vulgaris	European starling	-0.09	-0.409	0.213	-0.152	-0.468	0.133	-0.076	-0.497	0.354	-0.283	-0.726	0.1
Spizella pusilla	field sparrow	-0.099	-0.425	0.203	-0.147	-0.485	0.158	-0.04	-0.468	0.433	-0.234	-0.691	0.181
Myiarchus crinitus	great-crested flycatcher	-0.079	-0.324	0.162	-0.099	-0.312	0.106	-0.049	-0.357	0.265	-0.04	-0.282	0.205
Regulus satrapa	golden-crowned kinglet	-0.077	-0.392	0.234	-0.137	-0.461	0.164	-0.113	-0.564	0.326	-0.241	-0.699	0.161
Bubo virginianus	great-horned owl	-0.078	-0.399	0.229	-0.136	-0.466	0.163	-0.1	-0.54	0.342	-0.231	-0.675	0.174
Dumatella carolinensis	grey catbird	-0.044	-0.256	0.173	-0.289	-0.499	-0.097	-0.076	-0.335	0.177	-0.312	-0.526	-0.108
Picoides villosus	hairy woodpecker	-0.105	-0.392	0.155	-0.069	-0.317	0.176	-0.107	-0.449	0.244	-0.099	-0.376	0.176
Catharus guttatus	hermit thrush	-0.138	-0.466	0.145	-0.143	-0.439	0.125	-0.103	-0.503	0.3	-0.302	-0.706	0.042
Carpodacus mexicanus	house finch	-0.074	-0.397	0.24	-0.14	-0.468	0.16	-0.106	-0.542	0.332	-0.226	-0.657	0.164
Passer domesticus	house sparrow	-0.023	-0.323	0.304	-0.146	-0.475	0.159	-0.027	-0.439	0.438	-0.278	-0.757	0.132
Troglodytes aedon	house wren	-0.058	-0.327	0.207	-0.297	-0.609	-0.041	-0.146	-0.487	0.184	-0.197	-0.486	0.075
Passerina cyanea	indigo bunting	-0.086	-0.379	0.192	-0.136	-0.425	0.121	-0.256	-0.672	0.106	-0.295	-0.655	0.016
Charadrius vociferus	killdeer	-0.078	-0.401	0.227	-0.133	-0.452	0.162	-0.106	-0.537	0.327	-0.232	-0.675	0.168
Empidonax minimus	least flycatcher	-0.077	-0.398	0.231	-0.139	-0.474	0.163	-0.137	-0.577	0.283	-0.209	-0.632	0.179
Seiurus motacilla	Louisiana waterthrush	-0.017	-0.296	0.289	-0.157	-0.457	0.117	-0.179	-0.579	0.195	-0.224	-0.601	0.12
Zenaida macroura	mourning dove	-0.003	-0.226	0.235	-0.21	-0.41	-0.025	-0.105	-0.388	0.171	-0.202	-0.415	0.005
Vermivora ruficapilla	Nashville warbler	-0.084	-0.405	0.223	-0.123	-0.441	0.173	-0.09	-0.519	0.353	-0.201	-0.615	0.182
Cardinalis cardinalis	northern cardinal	0.05	-0.161	0.287	-0.186	-0.354	-0.026	-0.031	-0.299	0.233	-0.232	-0.425	-0.044
Colaptes auratus	northern flicker	-0.051	-0.294	0.193	-0.13	-0.346	0.073	-0.06	-0.36	0.25	-0.092	-0.339	0.153
Seiurus noveboracensis	northern waterthrush	-0.076	-0.397	0.225	-0.136	-0.462	0.164	-0.115	-0.563	0.331	-0.241	-0.698	0.156
Seiurus aurocapilla	ovenbird	-0.09	-0.303	0.111	0.092	-0.068	0.25	-0.226	-0.486	0.02	-0.03	-0.173	0.108
Dendroica pinus	pine warbler	0.06	-0.177	0.337	-0.161	-0.372	0.036	-0.116	-0.419	0.195	-0.092	-0.326	0.144
Dryocopus pileatus	pileated woodpecker	-0.059	-0.34	0.224	-0.092	-0.355	0.164	-0.173	-0.55	0.184	-0.129	-0.465	0.208
Dendroica discolor	prairie warbler	-0.098	-0.429	0.205	-0.151	-0.49	0.153	-0.04	-0.47	0.426	-0.241	-0.695	0.16
Pheucticus ludovicianus	rose-breasted grosbeak	-0.11	-0.408	0.161	-0.119	-0.385	0.128	-0.119	-0.469	0.232	-0.104	-0.391	0.171

Sitta canadensis	red-breasted nuthatch	-0.069	-0.384	0.239	-0.15	-0.483	0.146	-0.114	-0.553	0.328	-0.264	-0.727	0.133
Melanerpes carolinus	red-bellied woodpecker	-0.164	-0.417	0.072	0.008	-0.175	0.189	-0.004	-0.297	0.293	-0.043	-0.258	0.17
Vireo olivaceus	red-eyed vireo	-0.229	-0.45	-0.01	0.183	0.04	0.327	-0.293	-0.542	-0.032	0.1	-0.026	0.223
Buteo lineatus	red-shouldered hawk	-0.073	-0.394	0.235	-0.139	-0.468	0.157	-0.116	-0.567	0.328	-0.24	-0.695	0.16
Archilochus colubris	ruby-throated hummingbird	-0.076	-0.394	0.238	-0.139	-0.471	0.157	-0.141	-0.593	0.286	-0.2	-0.612	0.173
Agelaius phoeniceus	red-winged blackbird	-0.014	-0.261	0.247	-0.032	-0.293	0.252	-0.42	-0.802	-0.05	-0.193	-0.51	0.104
Piranga rubra	scarlet tanager	-0.105	-0.34	0.121	0.103	-0.07	0.275	-0.184	-0.465	0.09	0.027	-0.162	0.218
Melospiza melodia	song sparrow	-0.155	-0.42	0.084	-0.112	-0.334	0.121	-0.17	-0.463	0.112	-0.314	-0.554	-0.089
Melospiza georgiana	swamp sparrow	-0.092	-0.41	0.2	-0.166	-0.49	0.123	-0.044	-0.457	0.401	-0.295	-0.749	0.09
Tachycineta bicolor	tree swallow	-0.073	-0.395	0.24	-0.141	-0.47	0.161	-0.131	-0.582	0.299	-0.22	-0.652	0.172
Baeolophus bicolor	tufted titmouse	0.026	-0.17	0.231	-0.054	-0.187	0.075	-0.023	-0.27	0.228	-0.106	-0.267	0.051
Catharus fuscescens	veery	-0.295	-0.622	-0.013	-0.102	-0.328	0.119	-0.486	-0.874	-0.107	-0.376	-0.647	-0.122
Vireo gilvus	warbling vireo	-0.108	-0.397	0.158	-0.192	-0.473	0.054	-0.121	-0.461	0.217	-0.177	-0.489	0.114
Sitta carolinensis	white-breasted nuthatch	-0.096	-0.311	0.117	-0.052	-0.213	0.102	0.026	-0.255	0.306	0.081	-0.099	0.264
Empidonax traillii	willow flycatcher	-0.093	-0.413	0.202	-0.16	-0.483	0.127	-0.145	-0.587	0.271	-0.285	-0.729	0.094
Meleagris gallopavo	wild turkey	-0.081	-0.397	0.225	-0.131	-0.453	0.16	-0.104	-0.547	0.34	-0.225	-0.659	0.168
Troglodytes troglodytes	winter wren	-0.087	-0.405	0.215	-0.167	-0.5	0.126	-0.163	-0.598	0.247	-0.247	-0.662	0.116
Hylocichla mustelina	wood thrush	-0.029	-0.229	0.181	0.014	-0.122	0.151	-0.17	-0.431	0.074	-0.046	-0.2	0.101
Coccyzus americanus	yellow-billed cuckoo	-0.093	-0.41	0.2	-0.194	-0.533	0.094	-0.184	-0.617	0.21	-0.283	-0.705	0.084
Sphyrapicus varius	yellow-bellied sapsucker	-0.076	-0.397	0.237	-0.139	-0.47	0.167	-0.141	-0.574	0.286	-0.198	-0.603	0.164
Dendroica petechia	yellow warbler	-0.121	-0.425	0.156	-0.124	-0.39	0.127	-0.02	-0.374	0.37	-0.302	-0.667	0.018
Vireo flavifrons	yellow-throated vireo	-0.077	-0.393	0.228	-0.139	-0.469	0.159	-0.107	-0.544	0.333	-0.235	-0.69	0.166

APPENDIX D – CHAPTER 4: EVALUATING THE RED-BACKED SALAMANDER (PLETHODON CINEREUS) AS AN INDICATOR FOR BIODIVERSITY IN HUMAN-DOMINATED LANDSCAPES

Appendix D.1 – Project Field Handbook

Pioneer Valley Forest Community Assessment Project
2017 Field Handbook

For more information, please contact:

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Project Overview:

Purpose: Ecological communities are facing increasing pressure from anthropological advances and land-use change. In the Pioneer Valley, threats from urbanization and agriculture in particular, abut natural and protected land. As these changes progress, tools for rapid and reliable assessment of the health of ecological communities is required. This project exists to:

1. Assess the ecological health of forest communities in the Pioneer Valley
2. Evaluate the value of the red-backed salamander (*Plethodon cinereus*) as an ecological indicator species
3. Validate the reliability of the Anthropological Index in predicting ecological changes

Defining Urbanization: There is surprisingly little consistency among ecologists when it comes to describing how urban, or not-urban a place is. For example, if you and I were both to give an urbanization score from 1-10 of a particular forest patch, we would likely give very different scores depending on what factors we considered. Using readily available GIS data, we have produced a numeric gradient of land-use from forested to urban in order to make the process of defining urban landscapes more consistent and objective. The purpose of this field project is to evaluate how well this scale actually predicts expected changes in ecological communities in the Connecticut River Valley.

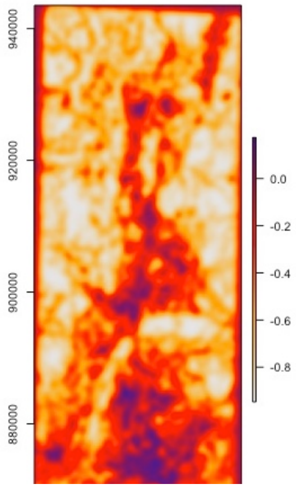


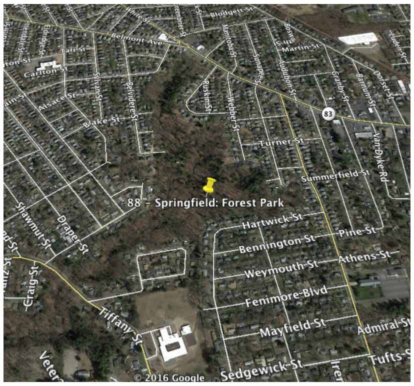
Figure 8: A "heat map" of urbanization for the study region

Indicator Species: Ecological indicator species are used to assess the efficacy of management, and provide warning signals for significant ecological shifts and pressures that may influence the ecosystem as a whole. Because ecological data is often difficult, or expensive to collect, the ability to gain an understanding of overall ecosystem health by looking at one species is extremely valuable. The red-backed salamander (*Plethodon cinereus*) is often considered to be an indicator of overall forest health, however, the true extent to which it does this is not fully known. This project will collect detailed data on salamander condition to see how salamander condition correlates to forest condition as a whole.

Figure 9: The red-backed salamander

Study System and Sites:

Forest communities are evaluated at a total of 50 randomly selected predominantly forested study sites on publically accessible land in the Connecticut River Valley of Western Massachusetts. The region is a mosaic of forests, agriculture, and urban/sub-urban regions; forests are diverse, including both bottomland and upland forests. Several significant urban areas exist, including Springfield in the south, Northampton and Amherst in the center, and Greenfield in the north. Study sites were selected in order to oversample transition zones between landscapes (i.e. forest – agriculture, or forest – urban), where values of the landscape index exhibit the most variance across spatial scales.



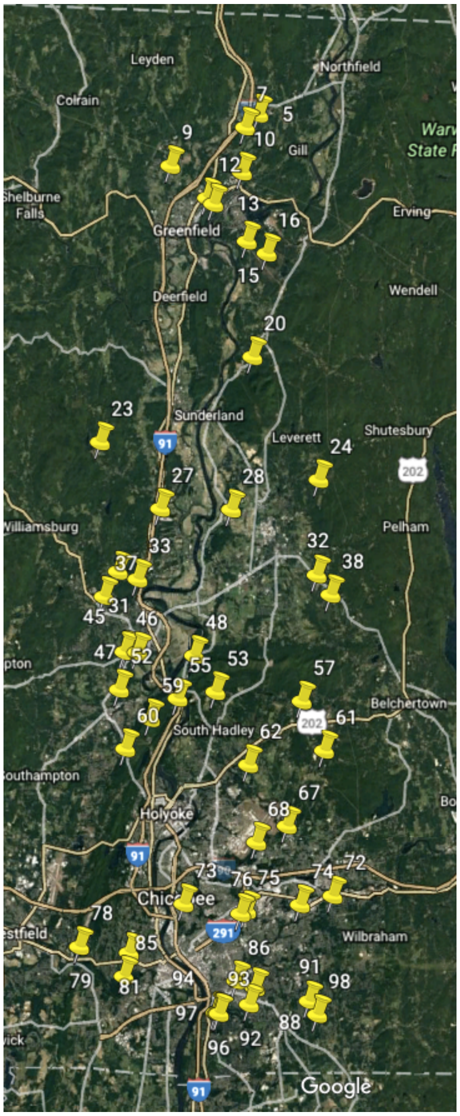


Figure 11: 50 forested study sites spanning the pioneer valley from Gill to Ludlow

Figure 10: Three examples of study sites in different landscapes. Springfield's Forest Park (TOP), Chicopee State Forest near the airforce base (MIDDLE), and Mt Toby (BOTTOM)

General Site Visit Protocol:

When planning site visits utilize the *Site Locations and ID* document to identify sites located in close proximity to each other. Park as far off the road as possible, being considerate of private land owners and neighbors. Navigate to site using GPS waypoint and descriptions in *Site Locations an ID.* Site locations are marked with brightly colored flagging tape and marked with the project ID and site name. Site names include a number from 1-50 ordered sequentially from north (1) to south (50) followed by town name (often abbreviated) and the conservation property on which the site is located (See figure below for example). Replace site flagging if it is missing, torn, or otherwise unreadable. Parking locations in *Site Locations* *and ID* are suggested, if you think there is a better location to park and access the site, that is OK, but remember to be respectful of properties and landowners.

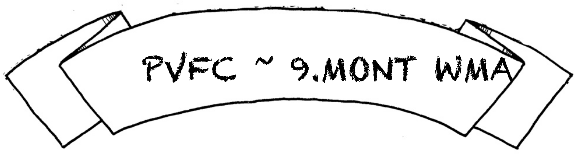


Figure 12: Sample Site flagging with project ID (Pioneer Valley Forest Communities) and site name. MONT is abbreviated Montague (town name) followed by WMA for specific conservation property (Wildlife Management

Remember, although all of our sites are located on publically accessible land you may have to navigate through, or closely beside privately owned land in order to access the site. If a land owner questions you **politely** explain what it is that you are doing and why you are there. If they ask you to leave, do so. Project managers will make communication. **Please, do not be confrontational or rude!!**

Being in the woods collecting data is an excellent opportunity to talk to the public. You may be asked who you are, why you are there, and what you are doing. More often than not they are genuinely curios! Be ready to share, explaining the data you are collecting, why it is important, and what it will be used for. Practice those science communication skills!

Safety is our number one priority. Counting salamanders and trees is much less important than your own personal safety. If you don't feel safe at a site leave, and tell us what happened. If you do not want to return, others can sample that site. Be smart, be kind, be safe, and ***have fun!***

Figure 14: Parking location and route to 3.GREEN GTD

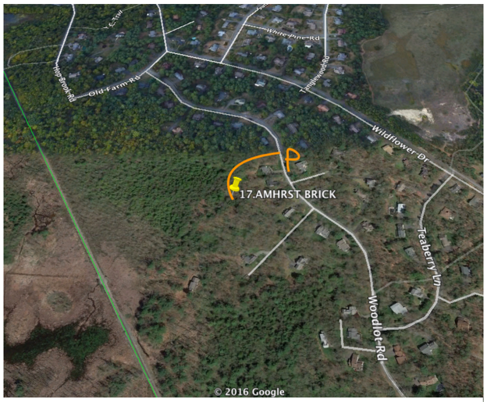


Figure 13: Parking location and route to 17.AMHRST BRICK

Field Methods and Protocols

Vegetation Surveys

Objectives: To describe species diversity and structural complexity of vegetation. Some organisms may respond most directly to the fine scale changes in habitat structure and composition rather than large scale landscape factors such as urbanizations. Furthermore, the diversity and composition of forest plant communities, as well as structural complexity, is known to change as anthropogenic pressure increases.

Equipment List:

- GPS unit
- Binoculars
- Clip board with data sheets with veg survey protocol
- Tree ID guide
- Biltmore Stick and DBH tape
- Compass
- Densiometer
- Survey ropes with stake (marked at 3m, 6m, 9m)
- Veg survey pole (marked at 3m, 6m)

Protocol:

- From the site's center point extend ropes in each of the four cardinal directions (N, S, E, W) using compass.
- Record site ID, observers, date, etc.
- Site Characteristics. Within each quarter of the 11.3-meter radius plot estimate the following:
  - Percent canopy cover – Using densiometer
  - Percent cover of shrubs (woody vegetation < 2-m in height), herbaceous plants, leaf litter, and bare rock/soil.
  - Percent slope and aspect (directional compass bearing of slope)
  - ***Be Sure*** to record in the Notes section of the data sheet if you observe any common exotic shrubs such as multiflora rose, honeysuckle, or privet.
- Measuring understory density with pole
  - At each marked 3-m interval extending from the center of the plot count the total number of "hits" on the pole between marks 0.5 – 1.5-m and 1.5 – 3-m. A "hit" is any point where a leaf, woody twig, stick, or branch makes contact with the pole. All woody vegetation, such as shrubs or trees are recorded as "stem" hits, while herbaceous vegetation recorded as "forb."
- Tree identification
  - Beginning in one quarter of the 11.3-m radius plot identify all trees to species and record the number of in each of 4 DBH (diameter at breast height) categories

  - DBH can be recorded using a DBH tape wrapped around the tree, or, estimating with a Biltmore stick.
- Eastern Hemlocks infestation
  - Within a larger (est. 30-m radius) plot, all Eastern hemlock should be identified and checked for presence of wooly adlegid infestation.
  - Upon identifying a hemlock examine a branch for presence of adlegid infestation. Adelgids appear as small clusters of white along the stems/needles on the underside of branches. If Adelgids are not observed on first branch, examine *one* additional branch for evidence of infestation.
  - The percentage of infested trees in each size class will be calculated as $N_{infected}/N_{observed}$
  - Only Eastern hemlocks with branches within reach without a ladder are to be examined for adelgid infestation. A *maximum* of 100 trees are to be examined.

Figure 15: Eastern hemlock infested with wooly adelgid

Figure 16: Densiometer used for measuring canopy cover

Site Characteristics						
%	CANOPY	SHRUB	HERB/FORB	LITTER	BARE / SOIL	OTHER (write in):
NE						
NW						
SE						
SW						
	EST SLOPE		**ASPECT**			

Understory Density										
NE	STEM 1.5-m	STEM 3-m	FORB 1.5-m	FORB 3-m	**NW**	STEM 1.5-m	STEM 3-m	FORB 1.5-m	FORB 3-m	*Dominant Ground Cover*
3-m					3-m					**NE:**
6-m					6-m					
9-m					9-m					**NW:**
12-m					12-m					
12-m					12-m					

Field Methods and Protocols

Amphibian Transect Surveys

Objectives: The red-backed salamander (*Plethodon cinereus*) is often considered to be an indicator for overall ecosystem health. However, the degree to which the health and condition of salamander populations actually correlates to overall forest health is not fully known. Two 25-m transects will be systematically searched at each study site.

Equipment:

- GPS unit
- Measuring tape
- Clip board with data sheets
- Ziploc bags
- Sharpie Markers
- Flashlight
- Ruler with millimeter scale
- Cooler with ice packs
- Tally Counter

Establishing the Transect:

- From the site's center point identify north (0°), and extend meter tape 25-m from center point following north (0°).
- After sampling first transect, repeat following western bearing (270°).

Sampling the Transect:

- Record site visit data, including date, time, temperature, weather, etc.
- Systematically turn and replace all cover objects (rocks, logs, etc) > 6-cm in length within 1-m of each sited of the transect. Click Tally Counter for each piece of cover flipped in order to count total number of cover objects flipped on each transect.
  - If two observers are present, each can sample on one side of the transect line
- When a red-backed salamander is encountered, place into a Ziploc bag and mark with **plot code**, **transect direction** (N or W), **meter distance** from transect start, and **cover type**.

- Place salamander in cooler to prevent overheating.
- All other amphibians and reptiles encountered during the survey should be recorded, including transect location.
- All Scat encountered (mammalian) during transect survey should be recorded and identified, including transect location. If scat cannot be identified in the field photograph as best as you can.

Working with Salamanders:

- Transfer salamander data to salamander data sheet.
- Record salamander morph with “S” for red-striped, and “L” for lead-backed
- Measure snout-to-vent length (SVL) and total length (TL) in mm. This should be done two independent times, ideally by two different observers.
- Determine gender via candling with a headlamp/flashlight. Record males as “M” and females as “F”. If sex cannot be determined, record as unknown “U”. Juvenile salamanders should be recoreded as “J”.
  - If male, check snout for cirri
  - If female record number of eggs
- In Notes section of data sheet record status of tail (if stubbed etc.), and any other important observations.
- After measuring and recording data release salamanders under the **same cover** they were caught under.

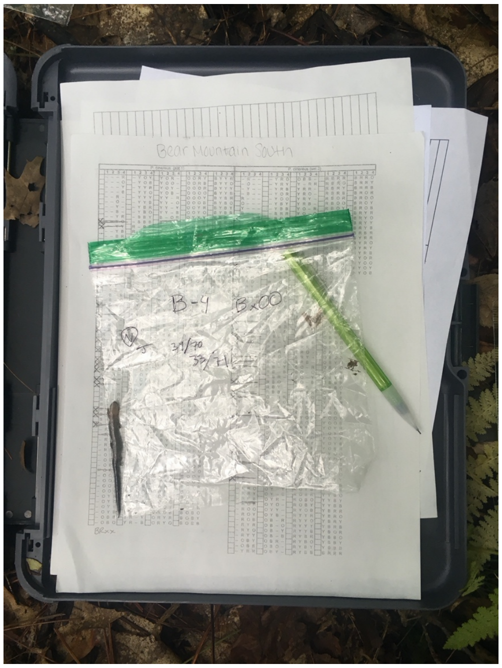


Figure 18: Salamander in Ziploc bag being measured and recorded

Figure 17: Checking natural cover objects

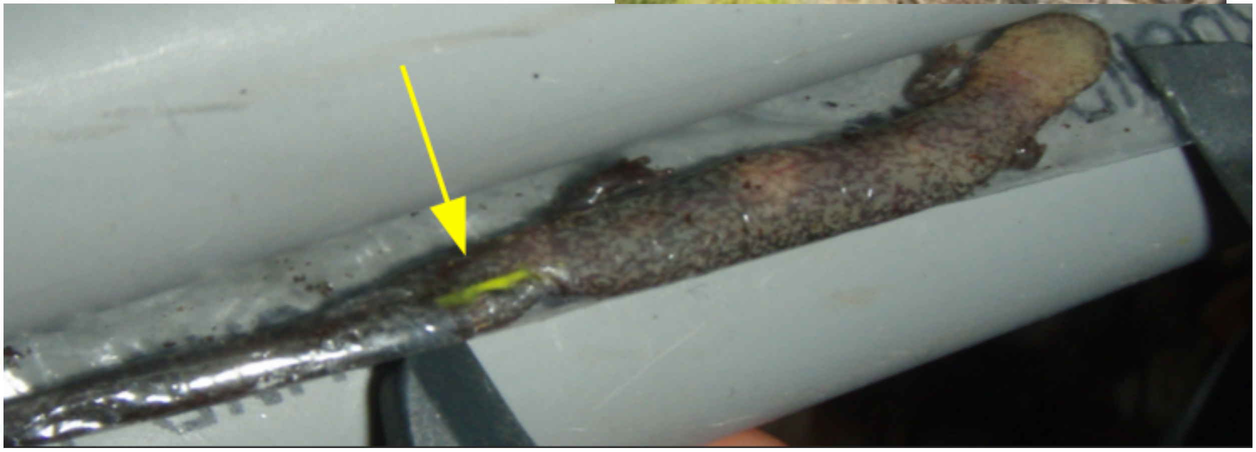


Figure 19: Total length is the length of the salamander from tip of the nose to the tip of the tail. Snout to vent length is length from tip of the snout to the vent, indicated by the yellow arrow

Field Methods and Protocols

Terrestrial Invertebrate Sampling

Objectives: Terrestrial invertebrates living in the leaf litter and first soil horizon play an integral role in the ecology of forest communities, particularly in regards to nutrient and energy cycling. Additionally, these organisms are the primary source of food for small vertebrates such as the red-backed salamander. Invertebrate sampling will serve to describe changes in arthropod communities across landscape gradients, and an estimate of resource availability for red-backed salamanders.

Equipment List:

- Compass and GPS
- 4" PVC soil corer
- Gallon Ziploc bags
- Sharpie Markers
- Rulers
- Rubber Mallet
- Tullgren funnel (in lab)
- Storage container (in lab)
- 70% Ethanol solution (in lab)
- Digital balance (in lab)
- Invertebrate identification key
- Dissecting microscope

Sampling Protocol:

- Field Protocol
    - Three sample cores will be taken at two visits throughout the sampling period
    - Standing at center of the plot, spin compass for 15-seconds, stopping on a specific bearing. Follow compass bearing from plot center for a total of 15 paces.
    - Using rubber mallet, hammer PVC soil corer into the ground, trying to get the corer approximately 8-inches into the ground.
    - Slice open duct tape and measure leaf litter depth
    - Place sample in Ziploc gallon bac and label with plot and sample number
    - Repeat three times per plot
- Lab Protocol
    - Samples may be stored in refrigerator for a maximum of 48-hours
    - Mass each sample in grams prior to placing in Tullgren funnel
    - When placing sample in funnel, **invert** sample so that top layer (leaf litter) is at the bottom of the funnel. Record drying start date and time.
    - Place sample in funnel for a minimum of 72-hours.
    - Preservative ethanol mixture will be labeled with plot and sample information. All specimens in ethanol mixture at end of this time may be stored until they are identified and recorded at a later date.

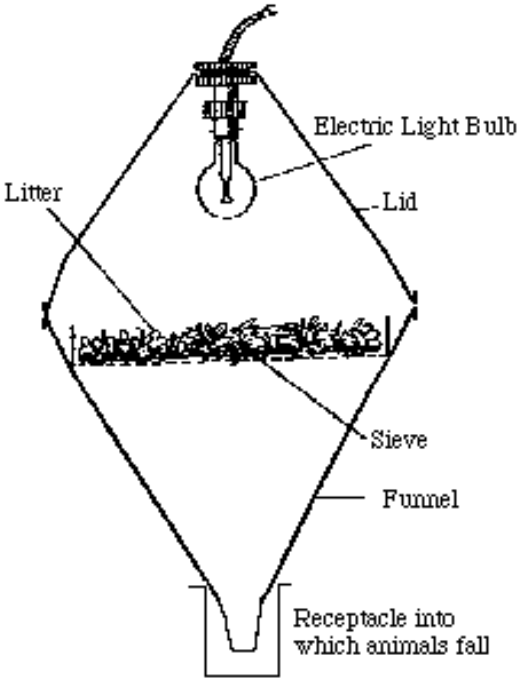
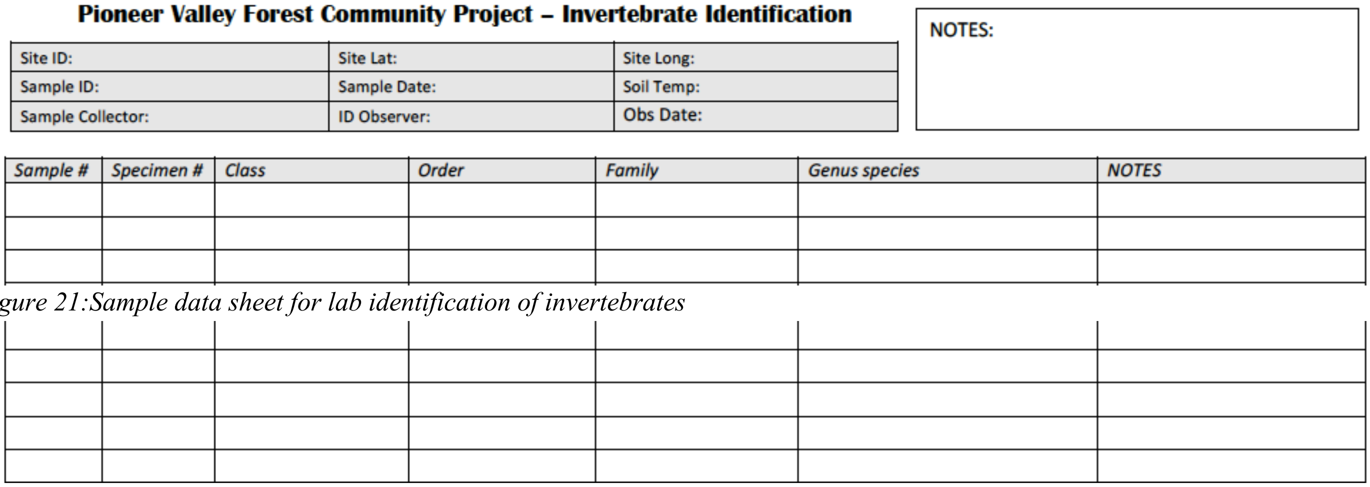


Figure 20: Diagram of Tullgren Funnel.

Field Methods and Protocols

Avian Point Count Surveys



Pioneer Valley Forest Community Project – Invertebrate Identification

Site ID:	Site Lat:	Site Long:
Sample ID:	Sample Date:	Soil Temp:
Sample Collector:	ID Observer:	Obs Date:

NOTES:

Sample #	*Specimen #*	*Class*	*Order*	*Family*	*Genus species*	*NOTES*

Figure 21:Sample data sheet for lab identification of invertebrates

Objectives: To assess breeding bird diversity and abundance at each study site. Many bird species exhibit differing responses to environmental degradation and ecosystem changes, and respond to landscapes at a variety of spatial scales. Point count surveys will be used to describe patterns of bird community diversity and abundance across changes in the landscape.

Equipment:

- GPS unit and compass
- Binoculars
- Clipboard with data sheets
- Thermometer

General Protocol:

- Each study site location (n=50) will be surveyed a total of **three** times during the peak breeding season when territorial behaviors and singing are most prominent.
- Surveys will take place after peak migration time, during the months of June and July 2017 to ensure true assessment of breeding bird communities.
- Surveys may begin half hour before sunrise, and no later than three hours after sunrise.
- Surveys are not to be conducted in high winds (>18 mph) or heavy rain.
- Each survey will be 10-minute 50-m radius point counts divided into two, 5-minute sub survey intervals.

10-Minute Point Count Method:

- Navigate to site coordinates using GPS
- Wait for a minimum of 10-minutes after arriving at a site before beginning point count
- Record Site ID, Observer ID, date, temperature, and weather codes and survey start time on data sheet
- Begin Survey: Track all observations from the first time of detection through the end of the time interval, being sure not to double count individual birds.
- All birds seen or heard will be recorded as either within 50-m radius, beyond 50-m, or fly-over observations.
- Individual bird movements may be tracked and recorded on the survey area diagram, using reference symbology to indicate species, sex, behavior, and movement.
- All species will be recorded using AOU alpha codes (i.e. red-eyed vireo – *REVI*)
- Record any relevant information and observations in the provided *Notes* area of data sheet
- Record survey end time

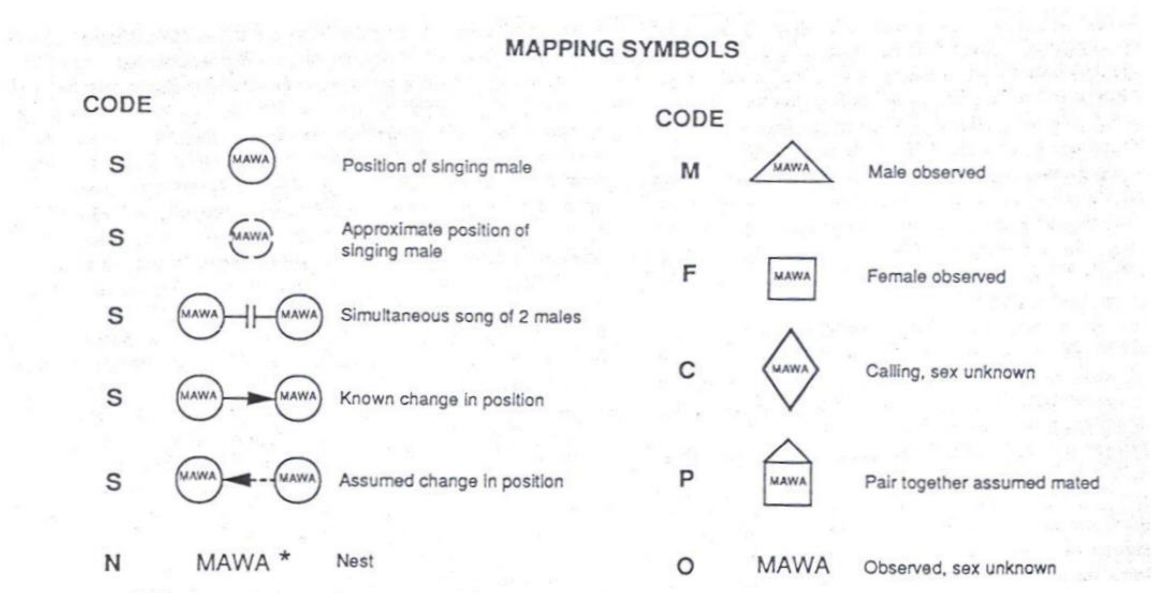
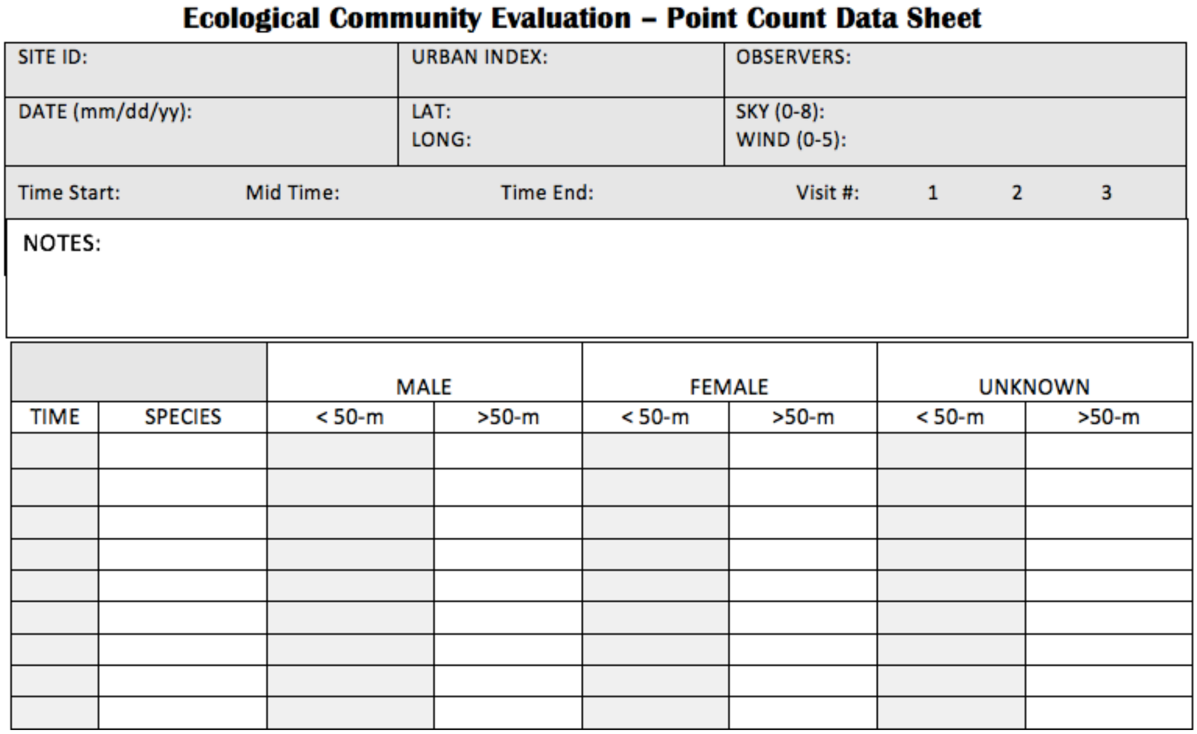


Figure 22: Symbols for indicating behaviors and movements of individual birds in survey diagram



Ecological Community Evaluation – Point Count Data Sheet

SITE ID:	URBAN INDEX:	OBSERVERS:
DATE (mm/dd/yy):	LAT: LONG:	SKY (0-8): WIND (0-5):

Time Start: Mid Time: Time End: Visit #: 1 2 3

NOTES:

		MALE		FEMALE		UNKNOWN	
TIME	SPECIES	< 50-m	>50-m	< 50-m	>50-m	< 50-m	>50-m

Figure 23: Point Count Survey data sheet. Environmental observations and visit information above, and species recordings below.

D.2 – Principal Components Analysis Results

Table D.1: Dominant principal component axes produced from landscape analysis. The first two axes were used to create spatial gradients based on a 10% variance cutoff.

NLCD Layer		PC1	PC2	PC3
Std.Dev.		1.766	1.296	1.214
Variance Explained (%)		20.8	11.2	9.8
Water	11 - OpenWater	0.025	0.019	-0.005
Developed	21 - DevelOpen	0.406	0.001	-0.032
	22 - DevelLow	0.509	0.044	-0.039
	23 – DevelMid	0.493	0.188	-0.078
	24 - DevelHigh	0.369	0.201	-0.080
Barren	31 – Barren	0.023	-0.165	0.011
Forest	41 - ForestDeciduous	-0.292	0.382	0.511
	42 - ForestEvergreen	-0.155	-0.116	-0.607
	43 - ForestMixed	-0.261	0.044	-0.431
Shrubland	52 - Scrub/Shrub	0.057	-0.426	0.244
Herbaceous	71 -Grass/Herb	0.092	-0.385	0.256
Cultivated	81 - Pasture/Hay	0.010	-0.341	0.129
	82 - Crop/Cultivated	0.060	-0.159	0.117
Wetlands	90 - WoodyWetl.	0.017	-0.406	-0.055
	95 - HerbaceousWetl.	0.008	-0.311	-0.100

D.3 – Species Associations Figure

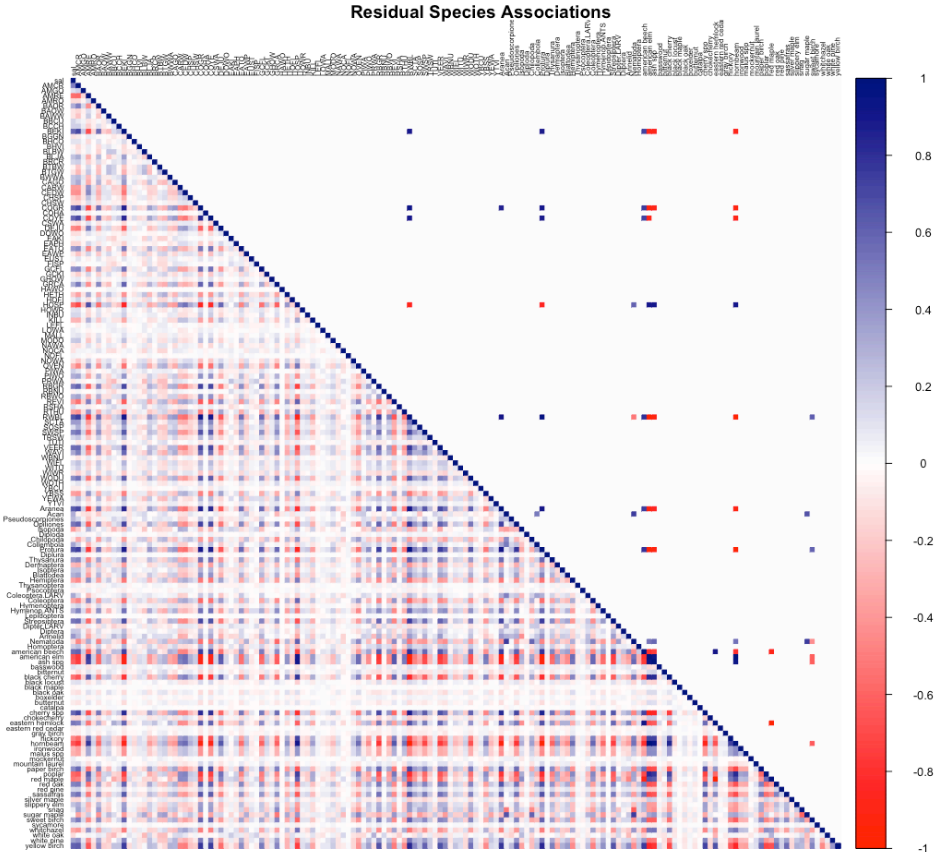


Figure D.2.1: Estimated species associations for all 151 species in the model. The lower triangle shows the mean parameter estimate, while the upper includes only those with greater than 95% posterior support. Red indicates a negative association, while blue a positive association.

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