Scenarios of future changes in land use, open space, and habitat connectivity around the National Wildlife Refuge System and other protected lands

By

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Abstract

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Over the past year or so, I have been pondering the multitude of people who have helped me over the hurdles in graduate school and through those in my personal life. If I did everyone the justice they deserved, my acknowledgments would be far longer than my dissertation. I should have been adding to them weekly for the duration of my PhD and then maybe I would do everyone justice. *Maybe*.

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Executive Summary

Overview

Humans have directly influenced over 83% of the earth's land surface through land transformation activities that are one of the main threats to biological diversity (Sanderson et al. 2002). Globally land cover on the earth's ice-free surface crossed the threshold of "mostly wild" to "mostly anthropogenic" within the last hundred years with less than 25% remaining in a wild state and over 39% in use for agriculture and human settlement (Ellis et al. 2010). In the United States trends have been similar (Leu et al. 2008). The alteration of land cover and subsequent appropriation of the earth's resources is important to study because it entails impacts to climate, water quality and quantity, and biodiversity that affect management of our fish and wildlife resources (Vitousek and Mooney 1997, Williams and Jackson 2007, Theobald et al. 2009).

Conservation in the face of landscape change requires an understanding of key drivers of change, the threats the changes pose, and the potential tradeoffs associated with increased human presence (Heller and Zavaleta 2009, Wiens 2009). All of these impacts are exacerbated by human-induced climate change (Griffith et al. 2009). It is anticipated that we will see shifts in climate that include changes in the amount and timing of rainfall and the frequency of extreme events with likely impacts on ecological communities (Williams and Jackson 2007). While we are in the early stages of the projected changes in climate, there is already evidence of impacts to species, ecological communities, and ecosystems (Walther et al. 2002).

Adapting to change necessitates anticipating and evaluating impending changes to identify threats and appropriate responses (Smith et al. 2000). The incorporation of threat into conservation decisions is critical to maximizing conservation outcomes obtained from investing limited conservation funding (Merenlender et al. 2009). Identification of future threats has been recognized as a priority research area for the U.S. Fish and Wildlife Service National Wildlife Refuge System (Griffith et al. 2009). Further, the potential future effects of land use and climate change on protected areas has been identified as one of the most important research areas needed to guide conservation policy (Fleishman et al. 2011). Using predictive models in a scenarios-based approach can increase the value of ecological research for management application (Coreau et al. 2009), providing important information on the effects of potential alternate futures on biodiversity and other ecological resources (White et al. 1997, Gude et al. 2007).

Our current approach to conservation relies heavily on protected areas as refugia to safeguard biodiversity (Gaston et al. 2008). While protected areas alone are not sufficient for effective conservation, they are often the backbone of conservation (Margules and Pressey 2000). The global protected area network includes over 11% of the earth's land surface (Rodrigues et al. 2004). However, these protected areas, linked to their surroundings by ecological flows and processes, cannot be viewed in isolation (Hansen and DeFries 2007). Protected area effectiveness for conserving biodiversity is influenced by the surrounding landscape, which is often in other intensive uses such as agriculture or human settlement (Joppa et al. 2008, Griffith et al. 2009, Wade and Theobald 2010). These surrounding land uses threaten, and may be limiting, the value and effectiveness of protected areas as a conservation tool (Joppa et al. 2008, Radeloff et al. 2010).

The distribution and pattern of land use in the U.S. is such that large areas of the country are strongly affected by human activities (Hansen et al. 2005, Leu et al. 2008). The conversion of land for human use affects both ecological processes and biodiversity (Flather et al. 1998, Foley et al. 2005). Intensive land use impacts biodiversity through both habitat loss and fragmentation (Fahrig 2003, Damschen et al. 2006, Fischer and Lindenmayer 2007). In addition, current and historic land use affect water quality (Allan and Arbor 2004, Locke et al. 2006), community composition (Pidgeon et al. 2007, Attum et al. 2008), species range limits (Schulte et al. 2005), dispersal and movements (Damschen et al. 2006, Fahrig 2007, Eigenbrod et al. 2008), and invasion by non-native species (Predick and Turner 2008, Gavier-Pizarro et al. 2010).

Coupled human and natural systems, defined as those systems that incorporate interacting natural and human mechanisms and processes, are a product of human transformation of the earth (Liu et al. 2007b). Human choices and actions that affect the distribution and pattern of land use have direct consequences for biodiversity (Pidgeon et al. 2007, Peterson et al. 2008). As such, effective conservation requires balancing human use and biodiversity at the landscape scale (Wiens 2009). In order to advance conservation, we need to understand future land use scenarios, to incorporate human-driven processes of land use change, to identify opportunities for, and potential vulnerabilities to, biodiversity conservation and landscape connectivity (Liu et al. 2007a, Gude et al. 2007).

Land use change around the world has followed a general pattern beginning with agricultural production in areas of high primary productivity, followed by development of industrial and population centers removed from agriculture as a second phase, and, finally, an information stage where land use is somewhat independent of primary productivity and industrial development (facilitated, e.g., by telecommuting and working via remote desk top) (Huston 2005). The landscape transitions through these stages from dominance of natural ecosystems to intensive human use, and each stage has associated changes to ecosystem services such as fresh water, forest products, and food production (Foley et al. 2005). This pattern of land use change is evident in the United States (Brown et al. 2005). The specific pattern within ecoregions has been modeled based on the linkages between land use history and ecological and economic processes and land use change has been forecast at an ecoregional level (Sohl et al. 2010). The models can be used to assess the likely impact of different economic policies and scenarios on future land use patterns (Radeloff et al. 2012, Hamilton et al. 2013). Forecasting land use change is essential to effective conservation planning and is most effective when conducted across multiple scales (Merenlender et al. 2009b, White et al. 1997, Foley et al. 2005b).

One particularly problematic aspect of land use is intensification related to housing growth and exurban development because they often occur in a manner that results in high human-environment conflict (Radeloff et al. 2005a, 2005b). Housing is a particularly persistent form of land use; once land use converts to housing it tends to stay in housing (Radeloff et al. 2010). Exacerbating negative impacts from exurban development is the fact that residential development has effects that extend beyond the footprint of the house. In addition to the houses themselves, residential development is typically associated with increased infrastructure developments that have their own associated impacts including: decreased native species diversity and abundance (Friesen et al. 1995, Lepczyk et al. 2008, Fahrig and Rytwinski 2009), increased rates of predation (Wilcove 1985), and interference with species movements (Fahrig 2007). These issues are compounded by the density and pattern of exurban housing growth, which often results in impacts to biodiversity that far exceed the actual footprint of the structures and lawn (Hansen et al. 2005, Gagne and Fahrig 2010a, 2010b).

In addition to the effects of housing itself, natural ecosystems and protected areas are attractive amenities, with housing growth occurring more rapidly near protected areas than in the rest of the United States (Wade and Theobald 2010, Radeloff et al. 2010). Rapid growth at protected area boundaries means that our protected network is increasingly at risk of being fragmented into a series of smaller networks or into completely disconnected and isolated units.

This has serious implications for conservation because of disruption to ecological flows such as species movements and dispersal as well as the increasingly limited options it leaves for protected area management and adapting conservation to land use and climate change (DeFries et al. 2007, Griffith et al. 2009, Wiens 2009).

The question is how landscape connectivity can be retained in the face of land use change and housing growth. Connectivity reflects the degree to which the landscape facilitates or impedes flows among and between resource patches (Crooks and Sanjayan 2006). When viewed most broadly, connectivity includes the flow of nutrients, energy, disturbance, and species. Connectivity is affected by the overall reduction in the amount of habitat and the fragmentation of habitat. While habitat fragmentation has variable effects on biodiversity, habitat loss negatively impacts biodiversity maintenance, with well-connected landscapes better maintaining biodiversity (Fahrig 2003). Connectivity for wildlife provides opportunities for normal home range movements, dispersal, gene flow, and adjustments to species range in response to processes that occur at larger spatial and temporal scales (Crooks and Sanjayan 2006).

Connectivity in the context of wildlife movements has two components: structural and functional connectivity (Tischendorf and Fahrig 2000). The first component, structural connectivity, relates to the amount and spatial arrangement of habitat on the landscape. Functional connectivity incorporates a species' behavioral response to the structural landscape and is likely to differ among all but the most closely-related species (D'Eon et al. 2002). Connectivity among protected areas is a necessary component of any conservation planning or climate adaptation strategy (Margules and Pressey 2000, Griffith et al. 2009). Lands outside protected areas are critical for maintaining connectivity among protected areas, and ultimately, for maintaining biodiversity (Franklin and Lindenmayer 2009). Unfortunately, land use change negatively affects landscape connectivity both by increasing the isolation of habitat patches and by decreasing suitable habitat in the matrix (Goodwin and Fahrig 2002).

One of the primary strategies promoted to combat the effects of land cover and land use change leading to habitat loss and fragmentation is the creation, restoration, and management of corridors to maintain connectivity among protected areas (Noss 1987, Beier and Brost 2010). The effectiveness of corridors as a biodiversity conservation strategy has been questioned (Noss 1987, Simberloff et al. 1992), however, they have proven to be effective, at least in some applications (Beier and Noss 1998, Haddad et al. 2003, Haddad and Tewksbury 2005, Damschen et al. 2006, Gilbert-Norton et al. 2010). Given this, corridors are a key strategy for maintaining the resilience of biological systems to land use change and their adaptation to climate change. A well-connected landscape will facilitate the species movements and range shifts that are anticipated to be necessary as some species fail to thrive in their current range and need to colonize new areas in response to climate change to survive in nature (Griffith et al. 2009, Beier and Brost 2010).

A survey of decision makers, scientists, and policymakers identified as a top priority determining how changes in land use and climate will impact the effectiveness of protected areas (Fleishman et al. 2011). I worked with managers and policymakers to develop research questions to address this research need. The overarching goal of my dissertation was to develop projections of possible future conditions and evaluate the effect of those conditions on protected area management and quantify changes to connectivity among protected areas. First, I assessed the effect of three plausible economic policy scenarios on future land use around the U.S. Fish and Wildlife Service's (FWS) National Wildlife Refuge System (NWRS). Second, I quantified the effects of housing growth on open space pathways and habitat corridors around the NWRS.

Finally, I evaluated the effect of future landscape conditions on protected area suitability and landscape connectivity for the Blanding's turtle (*Emydoidea blandingii*), a species with limited dispersal capability that is declining throughout its range. I based future landscape conditions on combinations of economic policy and climate projections. Future land use around the NWRS was a major theme in my dissertation and the management need for this information was the driving force behind my dissertation. The nationwide distribution of the NWRS provided an excellent opportunity to evaluate the effects of different scenarios on a widespread protected area network.

Chapter Summaries

In Chapter 1, I quantified potential changes in land use around the NWRS using a previously-developed spatially explicit econometric model of land use change in the US under several economic policy scenarios (Radeloff et al. 2012). The study area for this chapter encompassed 461 refuges in the contiguous 48 states. I quantified land use transitions among 5 land use classes between the years 2001 and 2051 within 5, 25, and 75 km of refuges for 3 economic policy scenarios. The land use classes I evaluated were: forest, range, crop, pasture, and urban.

The first policy scenario I evaluated, which I called "business-as-usual", was a scenario that simply projected future conditions as a continuation of land use change patterns from 1992 to 1997, the period on which the model was calibrated. The second policy scenario, "preserve natural habitats", reflected a conservation policy whereby a landowner was levied a $100/acre tax for removing land from forest or range use. The final policy scenario, "restricted urban growth", reflected a scenario in which urban growth was restricted to already urbanized areas (those counties that are part of a metropolitan statistical area).

The main finding in this chapter was that the effect of policy scenarios varied widely across administrative regions, indicating that implementation of a single nationwide policy would have variable results across the NWRS. In addition, I found that restricting urban growth, a fairly draconian policy that is unlikely to be implemented at a nationwide scale, did more to conserve natural habitats surrounding refuges than a policy specifically directed to preserve natural habitats. This is a reflection of the very high economic return of converting land to urban use.

Continuing with the theme of future land use, I evaluated the effect of future housing growth on the NWRS in Chapter 2 of my dissertation. I chose housing growth because it is a persistent and particularly problematic land use. First, land use can easily transition into and out of most uses but that is largely untrue for urban use (i.e., housing). Once land has been converted to urban use, it remains in urban use. Second, the impact of urban use extends beyond the footprint of structures to include other things such as increased infrastructure (i.e., roads) and increases in subsidized predators (e.g., domestic cats). Once again, my study area was refuges in the contiguous 48 states (455 individual refuges in this instance).

In Chapter 2, I evaluated open space pathways within 5, 25, and 75 km of refuges in 1940, 1970, and 2000, and used projections of housing density change to evaluate potential open space pathways in 2030. I quantified the number and areal extent of open space pathways, defined as contiguous areas with < 6.19 houses/km^2 (< 1 house/40 acres), at each spatial extent. In addition, I used an 8-neighbor rule to quantify the number and areal extent of habitat corridors within each open space pathway from the year 2000 that extended outward 5, 25, and 75 km from each refuge boundary. I defined habitat corridors as contiguous areas of open water, forest, shrubland, grassland, and wetland as determined using the 2006 National Land Cover Dataset.

My major finding in this chapter was, once again, that conditions around the NWRS are regional in nature. There are extensive areas of habitat extending from refuges up to 75 km in the western refuges, where simply protecting existing areas would maintain habitat corridors. The Midwestern refuges have extensive areas of open space reaching up to 75 km, but those areas are in use for crop and pasture and thus they would require extensive restoration to provide habitat corridors through which many species could move. Perhaps most alarming, I found that housing growth has already eliminated, and precluded establishment of, habitat corridors throughout most of the eastern United States. Opportunities to provide connectivity for refuges east of the Appalachian Mountains are largely restricted to working with neighbors to establish connections at a more localized scale. Finally, while open space has been decreasing around the refuges, the overall rate of change in open space pathways has not been very rapid, indicating that implementation of conservation measures is still possible. However, any approach to improve and conserve connectivity should take regional conditions into consideration.

Finally, in my third chapter I evaluated current conditions and projections of future conditions to determine the effect of changes on a species with limited capacity to disperse through a highly modified landscape. I chose to evaluate functional habitat connectivity for the Blanding's turtle because, while it is a relatively widespread species, it is declining throughout its range and is a species of conservation concern to many conservation organizations (Mockford et al. 2006). I evaluated the relative effects of future land use and climate change on protected area suitability and landscape connectivity for the 250 most important protected areas for Blanding's turtle in Wisconsin. Computational limitations prevented me from evaluating the full extent of the turtle's range.

I identified current and future conditions most suitable for Blanding's turtle based on land use and climate data in a maximum entropy modeling framework, using Maxent (Phillips et al. 2006), a software program that predicts habitat suitability using presence-only data. I identified the 250 most important protected areas, and quantified current habitat suitability throughout Wisconsin for Blanding's turtle using the land use classes described in Chapter 1 (forest, range, crop, pasture, and urban) as well as open water, forested wetland, and herbaceous wetland, plus mean annual temperature from historic data. Using the econometric model from Chapter 1, I was able to project future land use under the "business-as-usual" scenario and a "pro-agriculture" policy scenario that reflects a 5% increase in economic returns every 5 years for land in agricultural use. I chose the pro-agriculture scenario based on discussions with land managers, who feel that this scenario is similar to recent trends. In addition, I used projections of mean annual temperature under low and high emissions scenarios as environmental layers. This gave me 4 scenario combinations (2 economic policy scenarios by 2 emissions scenarios), for which I evaluated future potential conditions.

I estimated future suitability of habitat within protected areas and throughout Wisconsin under each of the 4 potential scenarios. In addition, I quantified changes in connectivity for Blanding's turtle under the different scenario combinations. To conduct this portion of the analysis, I used Circuitscape, a software package that calculates landscape resistance to movement. The "resistance distances" that Circuitscape output provides scale linearly, so I was able to project relative future changes in landscape connectivity under the different policy scenario combinations.

My primary finding from Chapter 3 was that future changes in habitat suitability and landscape connectivity for Blanding's turtle are driven primarily by climate change. I also found that the land use scenarios I evaluated were minimally different from one another with regard to their effects on both connectivity and habitat suitability. My results indicate that under future conditions there will be substantial shifts in suitable habitat northward, with total amounts of suitable habitat for Blanding's turtle in Wisconsin under the low emissions scenario roughly equivalent to current totals, though largely restricted to the northern half of Wisconsin. Under the high emissions scenario, almost no suitable habitat remains in Wisconsin for the Blanding's Turtle in the 2050's. I did find that protected areas within Wisconsin tend to provide proportionally more suitable habitat than Wisconsin as a whole. Perhaps the most notable results from my analysis were the projections of future changes in landscape connectivity. I was able to demonstrate that resistance distance increases at an exponentially higher rate for connections between protected areas in southern Wisconsin than for connections among protected area in northern Wisconsin. My results provide a graphical representation of "trailing edge" effects related to climate change, in which habitat degradation occurs more quickly at the trailing edge of a shifting climate space than elsewhere in the climate space.

Significance

I focused my dissertation on predictions of future change around a nationwide protected area network, and used a scenarios-based approach to assess potential future changes to landscape connectivity. My first two chapters address the NWRS as a whole, while my third chapter is a regional analysis of the effects of change on landscape connectivity for an individual species of conservation concern. My dissertation makes scientific, methodological, and management contributions for protected area and landscape management in the face of global change.

The main scientific contributions in my dissertation are in Chapter 3 where I demonstrate the relative effects of land use change versus climate change for a species with limited dispersal ability. While many studies have projected shifts in suitable climate space for individual species, I was able to quantify relative changes in landscape resistance to movement, a measure of functional connectivity, as well as the relative effects of land use and climate change in predictions of future habitat suitability. My predictions of landscape resistance to dispersal provide an example of trailing edge effect, in which loss of habitat at the trailing edge of a shifting climate space occurs more quickly than elsewhere within the suitable climate space of a given species.

My methodological contributions are primarily found in Chapters 2 and 3. In Chapter 2, I used a housing growth dataset in a novel way. Based solely on a threshold of housing density, I quantified structural connectivity for protected areas in two ways. First, I quantified "open space pathways", which represent opportunities to protect existing habitat connectivity and/or restore habitat to improve habitat connectivity. Additionally, I provided a second quantification of structural connectivity by identifying existing habitat corridors within those pathways. In Chapter 3, I synthesized several existing methodolgies in a novel manner. I used a synthetic approach to provide predictions of future habitat suitability and landscape connectivity. First, I used a combination of a predictive econometric model, climate projections, and habitat suitability modeling to quantify changes for a species over time and to tease apart the relative importance of climate change and land use change for future suitability for the species. Second, I used a triangulated irregular network (TIN) to simplify analysis of landscape connections among a network of relevant neighbors, resulting in a computationally feasible technique to evaluate changes in protected area network connectivity. I combined the habitat suitability model outputs with connectivity analysis to predict relative changes in landscape connectivity for a subset of the relevant neighbors identified using the TIN surface. I was then able to quantify changes for each connection in the landscape and demonstrate increasing rates of landscape resistance along a north-south axis, an effect driven almost completely by climate change.

Finally, my dissertation contributes directly to management through both Chapters 1 and 2. First, the data generated for both of these chapters is available to FWS for use in conservation planning for the NWRS. The data from Chapter 1 were provided to FWS electronically, with metadata supplied to guide its use. The data include estimated landscape changes under 3 economic policy scenarios in the vicinity of each refuge in the lower 48 states, providing managers and planners the opportunity to evaluate the relative effect of economic policies on future landscape conditions around individual refuges. The open space pathway and corridor data from Chapter 2 are spatial in nature and are available to managers.

In conclusion, my dissertation addresses a key management question regarding the future conservation effectiveness of the U.S. Fish and Wildlife Service National Wildlife Refuge System. The scenario-based projections of future landscape pattern and composition surrounding both individual refuges and the refuge system as a whole provide information needed by refuge managers and policy makers at local, regional, and national levels to advance conservation goals in light of changing land use and climate conditions. My work included important advancements in methodologies and science, enriching the published literature on the impacts of climate and land use change on protected area effectiveness and connectivity while using available data and software, such that analyses can be replicated in other locations and modified to address alternate or additional location-specific conservation concerns. I hope that findings of my dissertation will assist managers in maintaining, and improving where possible, the effectiveness of both individual refuges and of the entire National Wildlife Refuge System in achieving conservation goals.

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Chapter 1: Current and future land use around a nationwide protected area network

Abstract

Land-use change around protected areas can reduce their effective size and limit their ability to conserve biodiversity because land-use change alters ecological processes and the ability of organisms to move freely among protected areas. The goal of our analysis was to inform conservation planning efforts for a nationwide network of protected lands by predicting future land use change. We evaluated the relative effect of three economic policy scenarios on land use surrounding the U.S. Fish and Wildlife Service's National Wildlife Refuges. We predicted changes for three land-use classes (forest/range, crop/pasture, and urban) by 2051. Our results showed an increase in forest/range lands (by 1.9% to 4.7% depending on the scenario), a decrease in crop/pasture between 15.2% and 23.1%, and a substantial increase in urban land use between 28.5% and 57.0%. The magnitude of land-use change differed strongly among different USFWS administrative regions, with the most change in the Upper Midwestern US (approximately 30%), and the Southeastern and Northeastern US (25%), and the rest of the U.S. between 15 and 20%. Among our scenarios, changes in land use were similar, with the exception of our "restricted-urban-growth" scenario, which resulted in noticeably different rates of change. This demonstrates that it will likely be difficult to influence land-use change patterns with national policies and that understanding regional land-use dynamics is critical for effective management and planning of protected lands throughout the U.S.

Introduction

Humans have modified over 83% of the Earth's land surface due to land-use (Sanderson et al. 2002). Changes in land-use practices, and more specifically, conversion of land from more natural conditions to less natural conditions is one of the main threats to biological diversity

(Vitousek and Mooney 1997, Fischer and Lindenmayer 2007). The alteration of land cover and subsequent appropriation of the Earth's resources has major effects on climate, water, and biodiversity, and these in turn affect management of fish and wildlife resources (Vitousek and Mooney 1997, Williams and Jackson 2007, Theobald et al. 2009). Intensive land use, which we defined as areas where natural cover has been converted into pasture, crop, or urban use, affects biodiversity through both habitat loss and fragmentation (Fahrig 2003, Damschen et al. 2006, Fischer and Lindenmayer 2007), altering community composition (Pidgeon et al. 2007, Attum et al. 2008), limiting species ranges (Schulte et al. 2005), restricting animal dispersal and migration (Damschen et al. 2006, Fahrig 2007, Eigenbrod et al. 2008), and facilitating invasion by non-native species (Predick and Turner 2008, Gavier-Pizarro et al. 2010).

Land use also threatens the value and effectiveness of protected areas as a conservation tool (Joppa et al. 2008, Radeloff et al. 2010). Conservation efforts rely heavily on protected areas to provide refugia that safeguard biodiversity (Gaston et al. 2008). However, protected areas are linked to their surroundings by ecological flows (i.e., of energy, organisms, material) and processes and do not exist in isolation (Hansen and DeFries 2007a). The effectiveness of protected areas for conserving biodiversity is therefore influenced by the surrounding landscape, which is often altered by land use such as agriculture and settlements that typically eliminate, degrade, and fragment habitats (Joppa et al. 2008, Griffith et al. 2009, Wade and Theobald 2010). On the other hand, abandonment of agricultural lands can provide opportunities for habitats to be restored, with a potential positive effect on populations of native species.

Given that surrounding land use affects the function of protected areas, it is important to understand drivers of change, as well as threats and opportunities that those changes may pose to the maintenance of biodiversity (Franklin and Lindenmayer 2009, Heller and Zavaleta 2009, Wiens 2009). Furthermore, understanding future land use around protected areas is crucial to effectively mitigating potential effects of climate change given that many climate change adaptation strategies call for establishment of corridors to allow for species migration as suitable habitat and environmental conditions shift location (Griffith et al. 2009, Heller and Zavaleta 2009). Future land-use change is a vital consideration when investing limited conservation funds (Smith et al. 2000, Merenlender et al. 2009).

Understanding land use and land-use change around protected areas at different spatial scales (i.e., buffers) is important to have a better understanding of human pressures on protected areas (Burgman et al. 2005, Heller and Zavaleta 2009). It is also important because species relate to the landscape in different ways. Species differ in their home range size requirements, movement and dispersal capabilities, and perception of the environment. Therefore, it is important to understand land-use change at different scales that correspond to the range of scales at which species relate to landscapes (Sutherland et al. 2000, D’Eon et al. 2002, Olden et al. 2004, Wiens 2009).

Land-use change very broadly follows a trajectory from natural land cover to frontier clearing, subsistence agriculture, and ending in intensive land use where the majority of land has been converted for agricultural and urban use. Different regions of the world are at different points along this trajectory and the time required to pass through the different stages varies widely, with some regions remaining in the frontier and subsistence stage (Foley et al. 2005). The United States, however, has progressed through the stages, beginning with agricultural production, followed by growth of population centers, and finally urbanization and has established regional land use patterns (Brown et al. 2005, Huston 2005). Because these patterns are predictable to some degree, future land use can be simulated. Regional patterns may vary considerably and changes in land use are affected by regional economic, demographic, and ecological forces which, when modeled, allow us to fine-tune simulations of future land use (Sohl et al. 2010). Past changes in land use provides information that can be exploited to quantify the likely effects of different economic policies and scenarios on future land-use patterns (Radeloff et al. 2012). In the United States, past land-use trends suggest that land use is likely to continue to intensify rapidly, with urban use growing faster than other land-use classes (Radeloff et al. 2010). This means that the United States protected area network may be at risk from the effects of land-use intensification surrounding protected areas.

In the U.S., the only federally owned network of protected areas designed primarily for the protection of fish, wildlife, and plants is the U.S. Fish and Wildlife Service's (USFWS) National Wildlife Refuge System (NWRS). Other Federal lands (e.g., those owned by U.S. Forest Service, Bureau of Land Management, or National Park Service) are managed for multiple purposes. The main goal of the NWRS is to maintain the biological integrity of the refuge system (Meretsky et al. 2006) yet this goal may be compromised by intensifying land use in the surroundings of the refuges (Scott et al. 2004). Furthermore, given concerns that climate change will likely exacerbate current land-use effects on wildlife and the refuge system, it is of great interest to the USFWS to assess future land-use change as a major step in determining what climate change adaptation measures are indicated (Griffith et al. 2009). Predictive models of future land-use change can help managers explore plausible outcomes of different policy or economic scenarios and are thus an important tool for maintaining biological integrity. Future scenarios generated from such models can provide land managers with a better understanding of the full range of potential futures, and of the possible effects of alternate futures on biodiversity and other ecological resources (White et al. 1997, Gude et al. 2007, Coreau et al. 2009, Fleishman et al. 2011). Managers may be able to use the scenario outcomes to identify important pre-emptive actions for lands outside protected area boundaries which, if managed appropriately can be important for maintenance of biodiversity (Franklin and Lindenmayer 2009, Cox and Underwood 2011).

Our goal here was thus to evaluate current and future (yr. 2051) land use around the National Wildlife Refuges in the contiguous 48 United States. Specifically, we asked four questions:

- First, what is the current land use in the areas surrounding the National Wildlife Refuges?
- Second, what will the likely differences in surrounding land use be in 2051 under different economic and policy scenarios?
- Third, how do future conditions under these scenarios vary among regions or extent of analysis?
- Finally, what are the primary threats and opportunities to the NWRS in each of the seven USFWS administrative regions in the contiguous 48 states?

Methods

Study Area

We focused on USFWS National Wildlife Refuges in the conterminous United States (hereafter the refuges). We excluded NWRS lands that were not directly managed by USFWS (i.e., cooperatively managed lands) or specifically designated as refuges in the USFWS Cadastral database (http://www.fws.gov/GIS/data/CadastralDB/), which resulted in 461 refuges for our analyses.

We modeled land-use change at different scales around the refuges to assess whether the scale of analysis affected the land-use change trends. Changes were analyzed within 5, 25, and 75 km of each refuge. Some areas fell within the analyzed distances for more than one refuge (e.g., some areas were within 75 km of two or more refuges). These areas were counted more than once when calculating values for each of the 461 refuges, but were counted only once when calculating values for the refuge system as a whole. We chose these buffer distances because they approximate movement distances during the three main annual habitat use stages of the mallard (*Anas platyrhynchos*), a species that benefits a great deal from NWRS management. This choice reflects our effort to link our analyses to something biologically meaningful to managers in most of the NWRS, but we do not mean to imply that all refuges are managed for mallards only. The 5-km distance encompasses most brood movements (Mauser et al. 1994), 25 km approximates the daily foraging movements of overwintering ducks (Davis and Afton 2010), and 75 km is representative of the post-breeding/pre-migration movements (Gaidet et al. 2010). The maximum distance also equates to the distance within which many private land habitat restoration projects supported by the USFWS have been completed. The USFWS has implemented a private lands habitat restoration program called "Partners for Fish and Wildlife" for 25 years, which names as one of its priorities projects that benefit the NWRS and includes over 1,000,000 acres of restored wetlands as of 2010 (for further information see http://www.fws.gov/partners/).

Analyses

We quantified future land-use change around the refuges using an econometric land-use model (Meretsky et al. 2006, Lubowski et al. 2006). The model used observed land-use changes from the National Resources Inventory (NRI) between 1992 and 1997, measures of soil productivity, and county-level net economic returns to estimate land-use transition probabilities for urban, forest, range, crop, and pasture lands from 2001to 2051. Sets of transition probabilities were estimated separately for each county and soil quality class, and account for feedback effects of land-use changes on commodity prices and, thus, the net economic return to each use. The transition probabilities were combined with the National Land Cover Dataset (NLCD, 2001) to develop fine-scale projections of land use. The range category in the NRI was matched to the grassland/herbaceous and shrubland categories in the NLCD. An important advantage of using an econometric model as a basis for predicting change around refuges is that it permits us to evaluate the effect of different economic policy scenarios on land-use change. For instance, a subsidy for afforestation will alter the net return for forested land and, thus, the transition probabilities among the different land uses.

We considered three different scenarios of future land-use change in our analyses. The scenarios were designed to represent ambitious but potentially plausible policies that have already been implemented in some areas (e.g., some metropolitan areas have urban growth boundaries comparable to the restricted-urban-growth scenario). The first was “business as usual”, which applied the transition probabilities of the base model. These transition probabilities reflected the land-use change that occurred between 1992 and 1997, the time period on which the econometric model parameters were estimated. The second scenario, referred to as “preserve-natural-habitats,” was a conservation policy that levied a $100/acre tax on land that leaves forest or range use (i.e., a tax on land leaving natural vegetation). In this case, we assumed forest and range lands to be in a natural state. The third scenario, “restricted-urban-growth,” was a policy scenario in which urban growth was restricted to already urbanized counties (specifically, counties that are part of a metropolitan statistical area). The land-use model assumed no transition out of urban use since there were no such transitions observed in the NRI data (Nusser and Goebel 1997). In addition, the model did not include a transition into or from barrens or open water, as these areas normally remain in the same use. Also, wetlands were assumed to not transition to other uses since these areas also tend to remain in the same use, being protected by state and Federal regulations. Only private lands were subject to change in our analyses, i.e., land use in protected areas remained constant for the period of study. An assumption of the model was that responses by private landowners to changing economic conditions in the 1990s provide a basis for predicting responses to future economic conditions.

We evaluated the land use changes for our three scenarios in three major land uses: natural (NLCD classes 41, 42, 43, 52, and 71), agriculture (NLCD classes 81 and 82), and urban (NLCD classes 21-24). We conducted these analyses for the refuge system as a whole as well as for the 7 different administrative regions of the USFWS in the contiguous United States.

We looked at change in three ways. The first was the absolute change in area that occurred for a particular land use. The second was the change in the percentage of the buffer area represented by each land use. The final value was the rate of change for each land use over the 50 year span of our analysis.

Our projections of land-use accounted for endogenous feedbacks on the prices of market outputs from land, a key improvement over the Radeloff et al.(2012) land-use projections. The feedbacks resulted from land-use induced shifts in the supply of key outputs produced from land: agricultural products, timber, and housing. For example, if the amount of cropland declined, then the resulting decrease in the supply of crops induced an increase in crop prices. Any change in the price of an output from a particular land-use thus altered the net returns to that use, and affected future land-use change. We adopted the approach originally developed by Lubowski et al. (2006) to incorporate endogenous price feedbacks for the key land-uses in our analysis: crops, pasture, range, forest, and urban uses.

Results

Current use

Forest/range was the dominant land use surrounding the refuges in 2001, encompassing 57.4% (58.3 million ha) of the area within 25 km of all refuges, with crop/pasture following at 24.6% (34.2 million ha) and urban use the lowest at 6.5% (8.9 million ha). The remaining 24.4% of land use consisted of open water, wetlands, barrens, and non-natural woody cover such as orchards or vineyards. The dominant land use around NWRS lands varied both regionally and by the scale of analysis (Table 1, Figure 1). For example, along the coasts, urban use dominated within 5 km of some refuges but at 25 and 75 km forest/range or crop/pasture were the dominant land cover types (Figure 1). The proportion of refuges for which forest/range was the dominant use increased with increasing scale of analysis, while the proportion of crop/pasture remained relatively stable and dominance by urban land use decreased with increasing scale of analysis. For many individual refuges, the dominant land use changed across the scales of analysis (Table 1, Figure 1). The median proportion of land around the refuges in urban use and crop/pasture remained relatively stable across scales (between 25% and 30%), while the median proportion of land in forest/range use increased slightly with increasing scale from 49% to 56% (Figure 2). Increasing the scale of analysis smoothed the variability in the range of predicted urban use values, where the median value remained approximately 7%, but the range of values decreased with increasing scale (Figure 2). However, the scale of analysis had minimal effect on the proportion of refuges dominated by a particular use and on the median value for most land uses

(Table 1, Figure 1, Figure 2). Because this was true for starting conditions as well as conditions in 2051 for each scenario, we report further results only at the 25-km scale.

NWRS overall

In each of the three future scenarios, forest/range and urban land use increased while crop/pasture use declined. In all scenarios, the rate of urban growth, which was between 28.5% and 57.0%, far outstripped the rate of change of either forest/range or crop/pasture. The scenarios affected the particular land uses differently (Table 2). Forest/range land use experienced similar increases under both the preserve-natural-habitats and the restricted-urban-growth scenarios but a smaller increase under the business-as-usual scenario. Crop/pasture loss was highest under the preserve-natural-habitats scenario (Table 2). Most notably, urban land use grew at the lowest rate under the restricted-urban-growth scenario, exhibiting a nearly 50% reduction in the rate of increase, relative to other scenarios. In terms of area, crop/pasture losses were the greatest change followed by urban land use increases and, finally, forest/range increases (Table 2). Those changes, however, were not evenly distributed among the refuges.

Regional patterns

Clusters of refuges surrounded primarily by forest/range in 2001 were located mainly in the western half of the U.S., as well as near the Appalachian mountains in both the southeast and northeast, whereas refuges surrounded primarily by crop/pasture in 2001 were concentrated in the Midwest and along the Mississippi River (Figures 1, 3, and 4). The classification scheme we used for percent land use somewhat obscured urban land use, because it is relatively less prevalent, but several clusters were apparent in the Western U.S., as well as on the Atlantic and Gulf coasts of Florida and in the mid-Atlantic states (Figure 5).

The increase in forest/range land was greatest in terms of absolute change, proportion of surrounding area, and rate of change in the Upper Midwest, while losses of forest/range were less frequent with no regional pattern (Figure 3). This increase in forest/range use came at the expense of crop/pasture (Table 2). Forest/range land change was most prevalent in the Midwest (Figure 3). The increase in forest/range change strongly coincided with decreases of crop/pasture (Figure 4). Urban land use is unique in that it is persistent and did not decrease under any scenario (Figure 5). Total area and percent of buffer area increased in urban land use also coincided with areas of crop/pasture loss. However, while areas of high growth rates for urban use included the areas of crop/pasture loss, the areas with the highest rates of growth were much more widely distributed owing to the fact that rates of change can be relatively higher in areas with low urban land use (Figure 5).

We also found pronounced differences among FWS administrative regions in percent of total area that changed land use under the different scenarios. Our analyses indicated that region 3 (Upper Midwest region of the United States) stands out as the most dynamic, while changes were relatively similar across the other regions (Figure 6). This pattern occurred in all scenarios. The business-as-usual scenario resulted in the most dynamic change for all but region 3. The land-use response to restricted-urban-growth and preserve-natural-habitats scenarios varied among the regions.

The most notable gains in forest/range use area occurred in FWS region 3. Substantial forest/range loss, as a proportion of the surrounding area within 25 km, occurred within FWS regions 4 and 5 under all scenarios (Figure 4, Figure 7). Similarly, the biggest loss in crop/pasture area occurred in region 3, but loss was also notable in the Central Valley of California, and loss of this land use occurred in all regions. Urban growth by absolute area was remarkably similar within regions and when comparing the business-as-usual and restricted-urban-growth scenarios. However, the restricted-urban-growth scenario substantially reduced urban land use increases in area.

The rate of change in forest/range area was slightly higher under both the preserve-natural-habitats and restricted-urban-growth scenarios, but the most striking difference was by geographic region. Region 3 exhibited a much greater rate of increase than the other regions (Figure 7). Most noteworthy was the difference in growth rates among land uses. Urban use increased at a much higher rate than the other uses, nearly doubling in several regions under the business-as-usual and restricted-urban-growth scenarios. Crop/pasture loss rates were very similar under the business-as-usual and restricted-urban-growth scenarios and highest under the preserve-natural-habitats scenario.

Discussion

We predicted substantial future land-use change in the areas surrounding the National Wildlife Refuge System in the United States by 2051 and identified important threats and opportunities at a regional scale. These threats are relevant to regional managers, and to budget allocations at the federal level, because they show that most of the changes are regional in nature and any attempt to respond to anticipated threats will require a regional response through both policy establishment and budget allocation. While the models indicated that gains and losses will occur in forest/range and crop/pasture, the largest areal changes will be crop/pasture land-use loss. Urban land use was predicted to experience the highest rate of change, though the total urban areal change is likely to be smaller than changes in forest/range or agricultural cover. These trends varied among the scenarios that we analyzed, with forest/range largely gaining at the expense of crop/pasture, simply because land never leaves urban use. The only way to gain forest/range is thus through abandonment of crop/pasture. The most significant difference from the business-as-usual scenario occurred in the case of the restricted-urban-growth scenario, where reductions in housing growth rates were substantial and resulted in as much forest/range increase as under a scenario designed to preserve natural habitats. Our findings were similar to forecasts of crop/pasture loss and forest and urban gain trends forecast by other researchers (Pijanowski and Robinson 2011, Radeloff et al. 2012).

Our regional analyses indicated that forest/range land use will likely decrease in the Northeastern U.S., which also agreed with previous findings (Drummond and Loveland 2010). The forest/range will likely be lost to urbanization. Finally, the high rate of urban growth was in agreement with other studies reporting high rates of housing growth around protected areas (Radeloff et al. 2005, 2010, Wade and Theobald 2010).

Given that many studies indicate intensive land use encroaching on protected areas (Hansen and DeFries 2007b, Leinwand et al. 2010, Radeloff et al. 2010), including the NWRS (Scott et al. 2004, Griffith et al. 2009), it was a surprise to find that much of the land surrounding the NWRS is currently in forest/range land use. While we considered these to be relatively "natural", this assumption may not always hold. Low levels of intensively used land can impact the quality of wildlife habitat in nearby areas (Gagne and Fahrig 2010a, 2010b, Gavier-Pizarro et al. 2010).

We were also surprised to find that the different scenarios had a notable effect on land-use change around the NWRS given that previous analyses using this model found minimal change among scenarios for nationwide projections (Radeloff et al. 2012). However, the land-use projection method that we used was updated to incorporate endogenous price feedbacks and lower rates of urbanization, and we simulated different scenarios that resulted in more notable differences than those reported by Radeloff et al. (2012). In our analyses, the most notable contrast to business-as-usual occurred under the restricted-urban-growth scenario where urban land use growth was restricted to metropolitan counties. It is interesting that restricting urban growth resulted in similar increases in forest/range land use as the preserve natural habitat scenario. This suggests that the effect of unrestricted sprawl on habitat loss is so strong that a policy which restricts urban development, while unlikely to be widely implemented, could deliver similar conservation results as the direct preservation of natural habitat.

The regional variation that we found in terms of the percent of area around refuges that is likely to change concurred with other studies that indicated that protected areas are often protected more by their location than by policies (Joppa et al. 2008). The other major result was that urban land use will likely be a continuing management challenge for the NWRS. This result is in agreement with other studies predicting continued urban expansion around protected areas and into areas of natural vegetation, thus exacerbating biodiversity loss (Seto et al. 2011). Urban growth is a land use that can be difficult to address with incentive-based policies simply because the economic returns are much higher than for other land uses (Radeloff et al. 2012). However, state-adopted urban containment policies that employ strict growth boundaries have been shown to significantly reduce sprawl and preserve open space, with Portland, Oregon being an example of successful containment of urban sprawl (Nelson and Moore 1996, Woo and Guldmann 2011).

The similarity of the proportion of land currently in each use across the different scales of analysis for the NWRS was surprising to us. However, while our analyses did not suggest significant differences across the U.S., there were substantial regional and contextual differences in dominant land use as well as land-use change. Land-use change was forecasted to be most dynamic in the Midwestern region, followed by the Northern Great Plains region. While previous studies indicated stability in crop use in these regions (Brown et al. 2005), recent studies have found loss of crop land throughout here (Pijanowski and Robinson 2011). The changes are the result of a transition from crop/pasture use to either urban or forest/range use (Pijanowski and Robinson 2011, Radeloff et al. 2012). Our prediction of reduced land area in crop/pasture may not reflect increasing demands for food and biofuels production though, which are rapidly increasing and can only be met through either agricultural intensification or expansion (Tilman et al. 2011). In fact, other studies predict increases in crop as well as urban land use worldwide as well as in the Upper Midwest, an area where our models predict decreases in crop land use (Nelson et al. 2010, Sohl et al. 2012).

Perhaps the most striking result of our analyses was the rate of urbanization. Even with strong policies to restrict urban growth, many regions (1, 2, 5, and 8) are likely to experience high rates of growth in urban land use. While the predicted rates of urban growth under the restricted-urban-growth scenario were substantially reduced when compared with the other scenarios, those rates of growth were still high, matched only by rates of afforestation in the Upper Midwest.

It is worth noting that many of the National Wildlife Refuges are found along the coasts. These areas have a great deal of open water and wetlands, which we excluded from our analyses. Some of our results can give the misleading impression that those refuges are surrounded by urban land use when, in fact, much of the neighboring area is open water or wetland. We suggest though that exclusion of those areas was appropriate given the model goals of evaluating the effect of policies on terrestrial land use.

Model limitations

As any model, our land use model is an abstraction of reality, and our results have thus to be interpreted in the context of model assumptions and limitations. First of all, it is important to state that our “business-as-usual” scenario reflects “business-as-of-the-1990s”. The model was parameterized using data from land-use change between 1992 and 1997. The economic climate in the U.S. in the early 2010s is much different, with higher crop prices and much slower housing growth. However, our scenarios simply reflect adjustment of the model outputs through changing the net economic return for a particular land use. The main assumption in this approach is that human behavior has not changed and is focused on maximizing economic return from land use. The best use for the model is thus the comparison among scenarios and we treat conditions from the 1990s as a scenario that simply reflects what was occurring during a particular period of time.

Second, our model did not calculate confidence intervals for the predictions. Our predicted land use changes were made for the entire conterminous U.S., not just a sample of locations. As such, *any* difference in land use among scenarios is statistically significant, but that does not mean of course that any difference would be significant for management or policy considerations, or that our predictions were free of uncertainty. There are two sources of error that affect our predictions. The first is that the NRI data, upon which the econometric model was based, represents a sample, and as such the land use transition have confidence intervals. The second is that the land cover data (NLCD) has classification error. Given the nature of these types of error, confidence intervals could potentially be derived by simulating many instances of each scenario and sampling the input data from a distribution. Practically, this was not feasible though for two reasons. First, the computational resources required to simulate many instances of each scenarios were far beyond what was available to us. Second, errors in the land cover data are not spatially random (Comber et al. 2012), but the NLCD provides only aggregate accuracy values, and that makes it impossible to simulate realistic land cover maps based on the available accuracy data.

Third, we recognize that climate change is likely to affect future changes in land use to some extent. The same projection model we used was also used to investigate the effects of future changes in climate on land-use changes in the U.S. by incorporating into the model trends in population, income, agricultural prices, and forestry and crop yields as projected in two IPCC scenarios (Haim et al. 2011). Relative to a reference scenario with no changes in climate, climate change had only a small effect on the area of land in broad land-use categories (crops, pasture, forest, urban, and range). For example, across the conterminous U.S., the areas of land in crops and forest were 2.1% and 1.3% lower under the IPCC A1 scenario compared to the reference case, though somewhat larger differences are found in some regions. Within a land-use category, climate change could affect landowner choices such as the types of crops and trees to plant (Sohngen and Mendelsohn 1998), but the findings suggest no large shifts in broad land-use categories (Haim et al. 2011). Nevertheless, climate change, or other changes such as new technologies, could result in novel conditions in the future that our model, which was based on past land use trends, could not capture.

Conclusions

This was, to our knowledge, the first analysis of its kind providing spatially explicit predictions of economic policy scenarios for a nationwide system of protected areas. We have presented these results to managers in the USFWS from the field level to the national level and they have been well-received, most likely because we included managers from the USFWS in the formulation of our proposal, conducting our analyses and compiling results. In addition, our results have been provided in spreadsheet form to the managers in USFWS, stressing though in the accompanying documentation that the results should be used with caution when attempting to establish local policy since any national land use simulation will have limitations when applied at much finer scales. These data include estimates of land-use change for each of the NWRs under each scenario and is easily interpreted for direct use by managers, who possess local knowledge of surrounding land-use pressures, to assess changes in land use that may threaten the lands they manage. Armed with this knowledge, managers can encourage development of policies that address regional and local land-use change concerns. It should be noted that the model was used was developed specifically for the 48 contiguous United States, which has already reached the "intensive" land-use stage. This type of model would not be appropriate for areas which are still in the frontier stage of land-use change (Foley et al. 2005). However, we see great possibilities for comparable models to provide similar insights outside the 48 contiguous United States in regions that are in the intensive land-use stage.

Our results indicated that managers will be faced with both opportunities and challenges. Some regions experienced an increase in forest/range lands under all scenarios, which we considered to be more compatible with habitat and biodiversity conservation. In light of the anticipated need for improved habitat connectivity and corridors to mitigate the effects of climate change (Griffith et al. 2009), this is good news for conservation efforts in those regions. Forest regrowth provides valuable habitat and, consequently, conservation opportunities (Bowen et al. 2007, 2009). In fact, our findings are somewhat reassuring for conservationists given that land-use change is currently the main driver of biodiversity loss, and will remain so at least until the mid-century (Sala et al. 2000, van Vuuren et al. 2006). However, the general increase in forest cover is accompanied by the likely large increase in urban land use under all scenarios. Even with potential improvements in habitat connectivity, the overall implications for biodiversity are not clear. The biodiversity threats posed by urban development are likely to reduce, or even overwhelm, any gains through increased habitat area and connectivity. In fact, managers need to prepare for the challenges of working with increasing numbers of neighbors in a landscape of forest with an understory of houses. Further research on the quality of natural habitat with an intermix of houses and on identifying thresholds of housing density beyond which land ceases to support biodiversity will be important to assist managers of the future (Gagne and Fahrig 2010a, 2010b).Additionally, our results indicated that there are serious limitations to "one-size-fits-all" approaches to policy development and implementation. Our finding that regional differences were as strong as differences among policy scenarios has important implications for management of large networks of lands. This should serve as a caution to policy makers that regional context is critical for land management and that national policies need to be flexible enough to incorporate these differences. At a minimum, managers and policy makers need to assess threats and opportunities to inform optimal allocation of resources. Given these regional differences, it will be critical for managers to work with local and regional governments and partners to minimize the impact of future land use change on their lands. Finally, we suggest that it would be useful to identify buffer zones around refuges within which managers could focus additional conservation efforts through work with neighboring land owners. Managers could work with partners to delineate buffer zones appropriate to conserving those species and their habitats on which a refuge's management focuses, with particular consideration given to the threats likely to occur within that zone.

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Table 1. Percent of National Wildlife Refuges dominated by different land-use categories, at three different scales (buffer distances) and the proportion of each use category on all private lands nationwide.

	Distance around Refuge (km)			
Land use	5	25	75	National percentage
Forest/Range	53.2	56.9	63.6	57.8
Crop/Pasture	36.8	34.8	33.0	34.6
Urban	10.0	8.3	3.5	7.6

Table 2. Land area (million ha) and percent areain different land uses within 25 km of the National Wildlife Refuges in 2001 and 2051 under each scenario.

			Business-as-Usual		Preserve-natural-habitats		Restricted-urban-growth	
Land Use	Area 2001	% Area 2001	Area 2051	% Change	Area 2051	% Change	Area 2051	% Change
Forest/Range	58.3	57.4	59.4	1.9	61.0	4.7	60.9	4.5
Crop/Pasture	34.2	24.6	28.0	-17.0	25.9	-23.1	29.0	-15.2
Urban	8.9	6.5	13.7	52.2	14.2	57.0	11.6	28.5

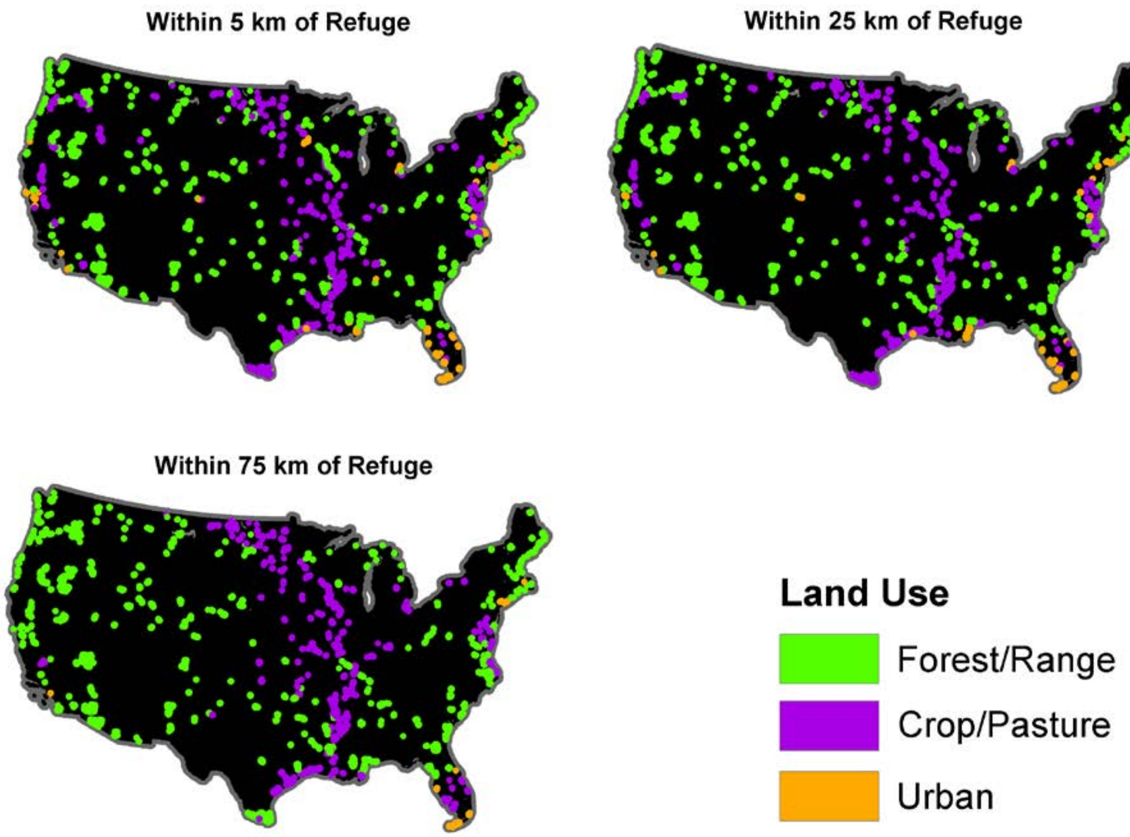

Figure 1. Current dominant land use around each National Wildlife Refuge in the contiguous 48 states.

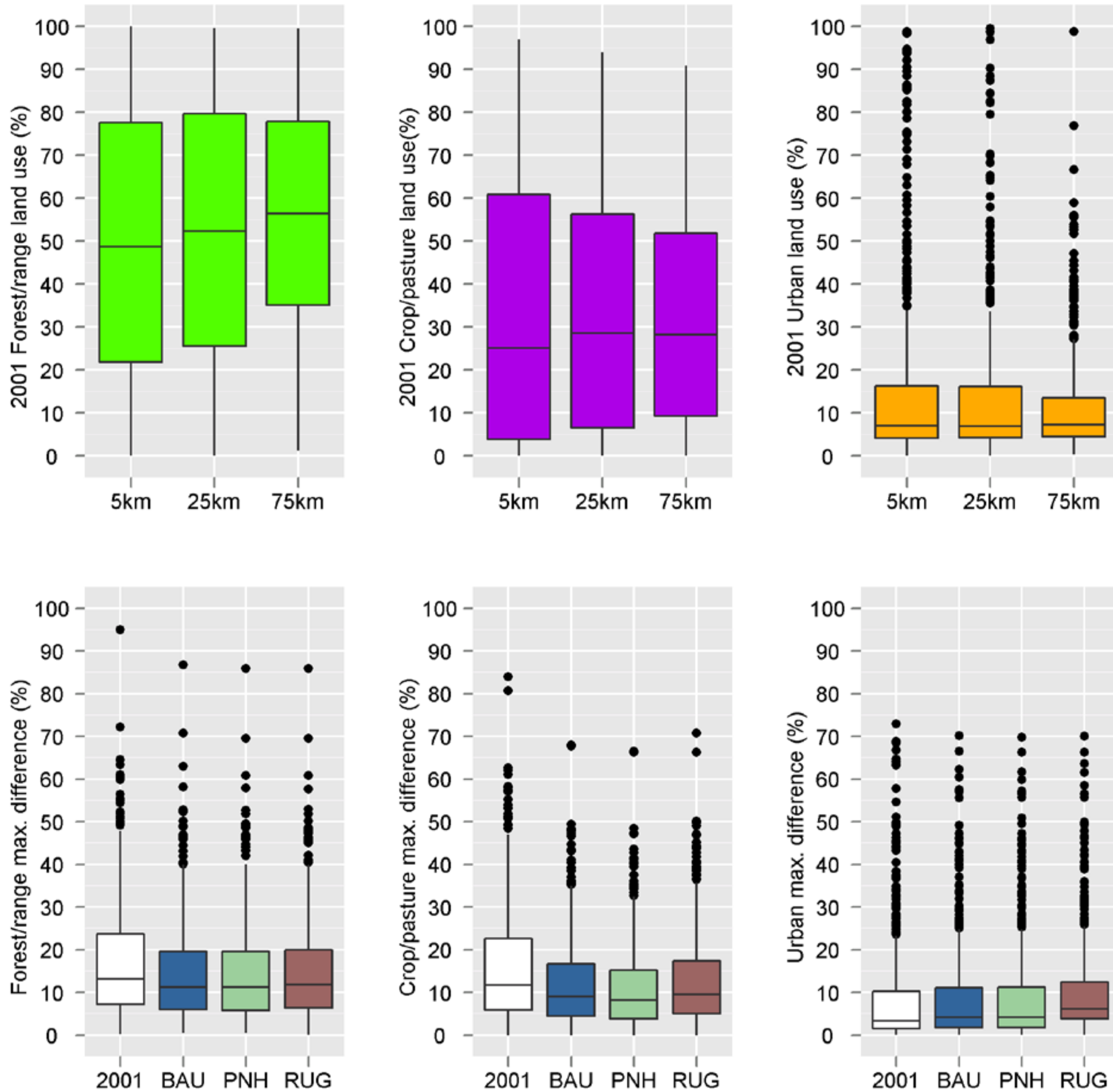

Figure 2. Box plots showing the variability in each land use across the scales of analysis for different land-use classes (row 1), and the maximum difference among scales in proportion of land in each use around the National Wildlife Refuges (row 2). Plots in row 2 compare conditions in 2001 (in white) with those in 2051 for each scenario (BAU=business-as-usual, PNH=preserve-natural-habitats, RUG=restricted-urban-growth).

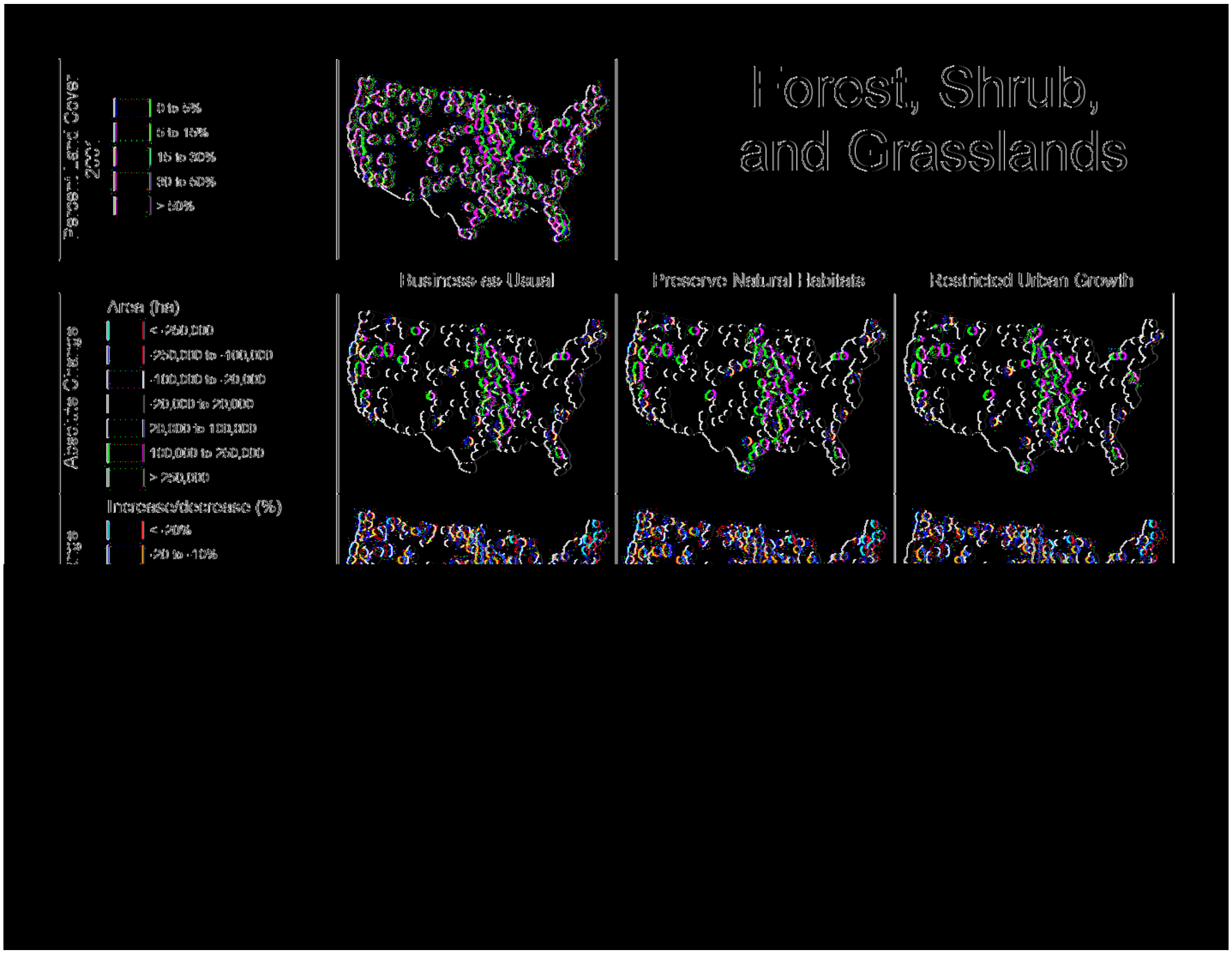

Figure 3. Initial land use and change in forest/range land use within 25 km of refuges under the different scenarios. Absolute change = change in area (ha), buffer change = percent of buffer that changes use, and rate of change = percent growth.

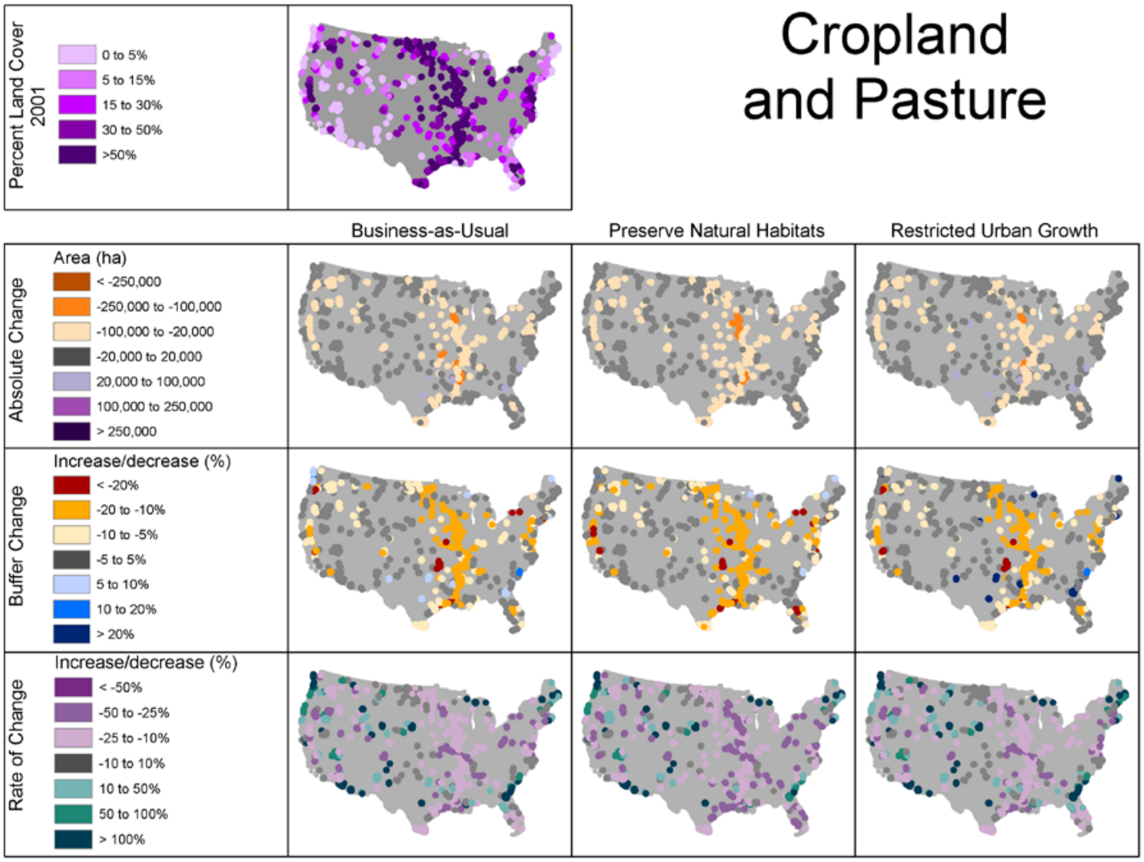

Figure 4. Initial land use and change in crop/pasture land use under the different scenarios.

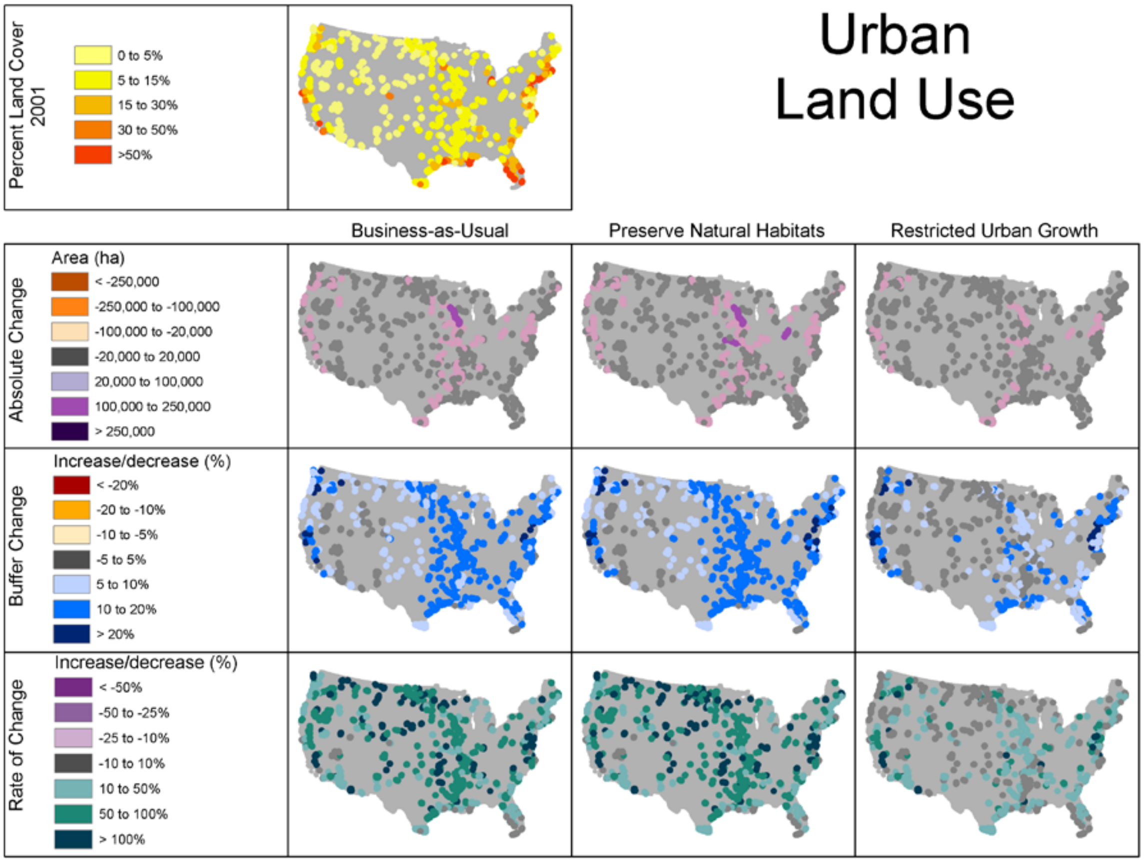

Figure 5. Initial land use and change in urban land use under the different scenarios.

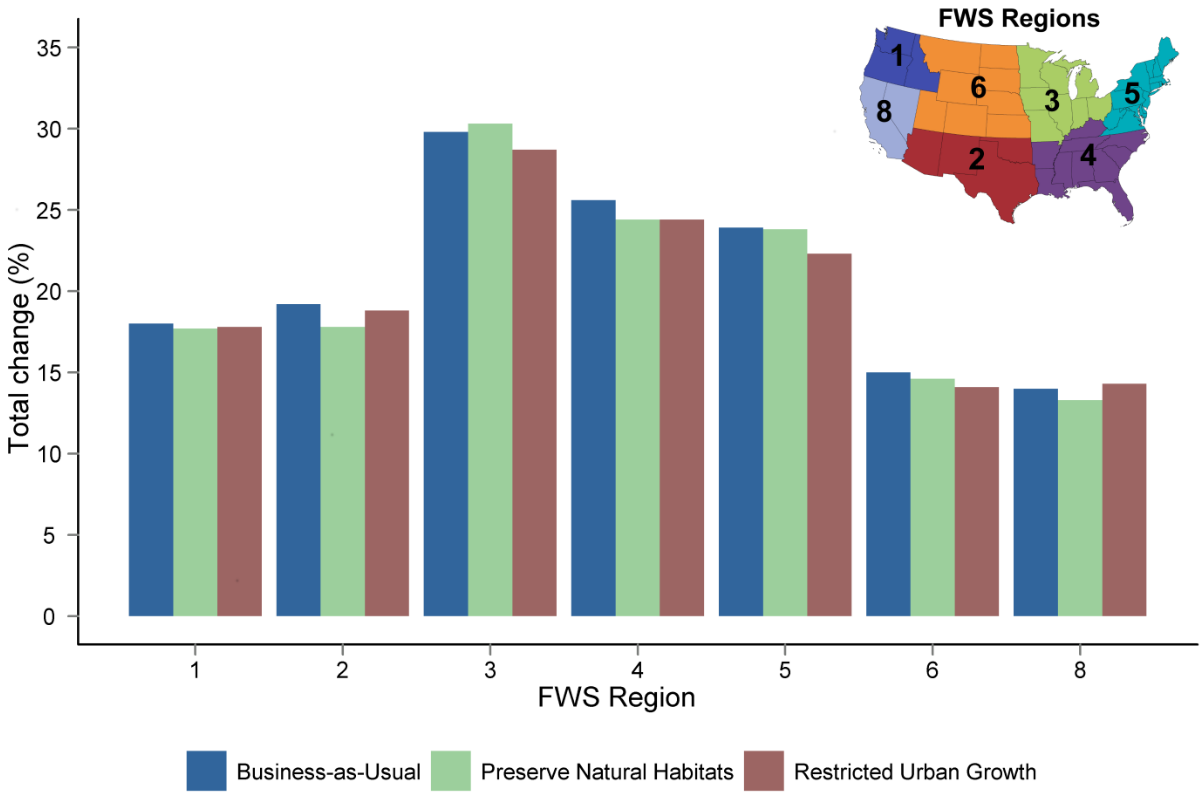

Figure 6. Regional predictions for the percentage of area within 25 km of refuges that will change under the different scenarios. Inset shows FWS administrative regions.

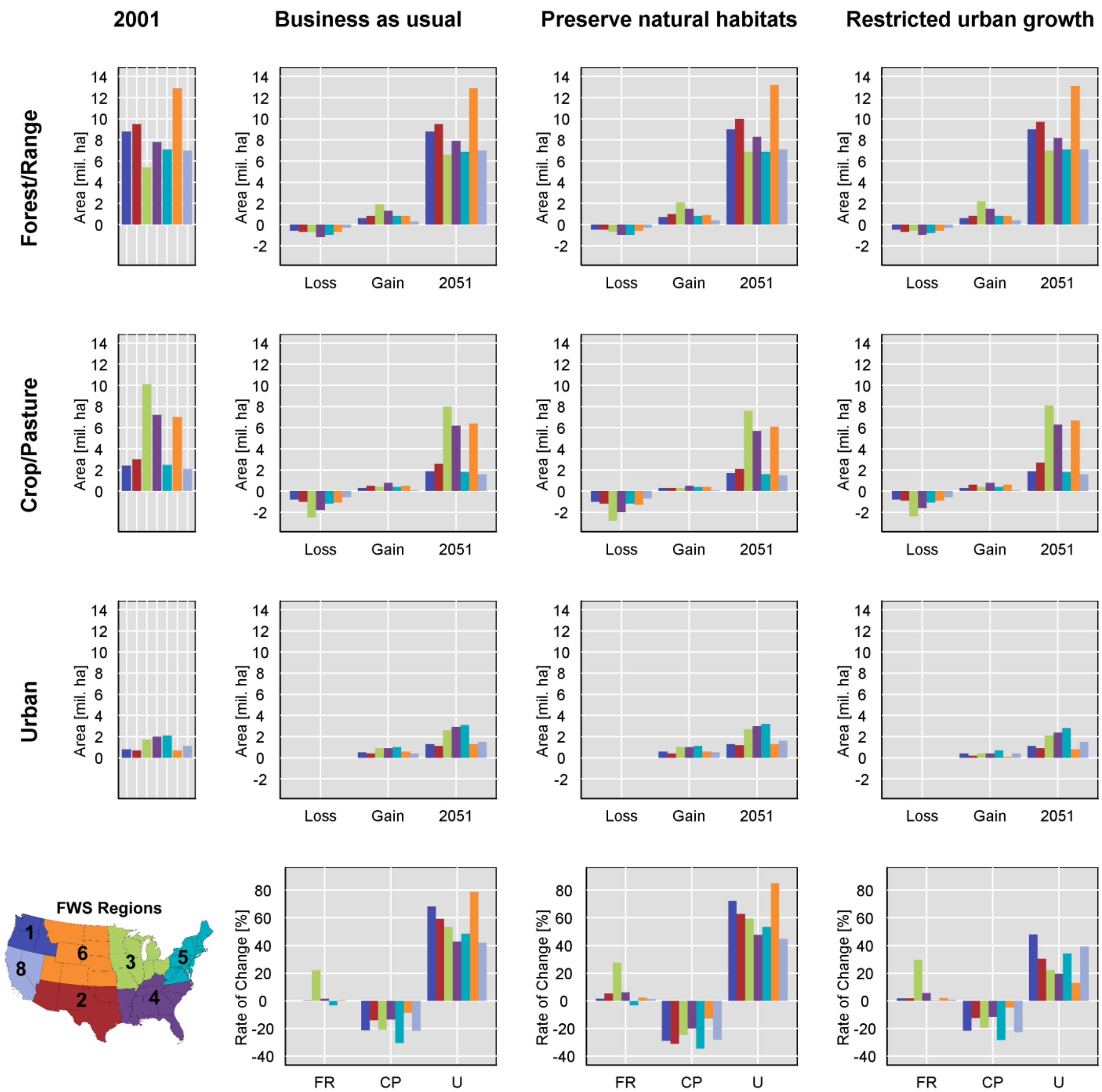

Figure 7. Change in area in different land uses and rates of change among the different scenarios for the FWS administrative regions. FR is forest/range, CP is crop/pasture, and U is urban land use.

Chapter 2: Past and predicted future effects of housing growth on open space pathways and habitat connectivity around National Wildlife Refuges

Abstract

Housing growth can alter the suitability of matrix habitats around protected areas, strongly affecting movements of organisms and, consequently, threatening the connectivity of protected area networks. Our goal was to quantify the distribution and growth of housing around the U.S. Fish and Wildlife Service (USFWS) National Wildlife Refuge System (NWRS). This is important information for conservation planning, particularly given the promotion of habitat connectivity as a climate change adaptation measure. We quantified housing growth from 1940 to 2000 and projected future growth to 2030 within three distances from refuges, and identified very low housing density open space "pathways" (contiguous areas with < 6.17 houses/km^2) both nationally and by USFWS administrative region. Additionally, we quantified the number and area of habitat corridors (contiguous blocks of habitat based on the 2006 National Land Cover Dataset) within the pathways in 2000. Our results indicated that the number and area of "pathways" generally decreased with increasing distance from refuges and with the passage of time. Furthermore, the total area in habitat corridors was much lower than in pathways. In addition, the number of corridors sometimes exceeded the number of pathways as a result of habitat fragmentation, indicating that corridors are likely vulnerable to land use change. Finally, regional differences were strong and indicated that some refuges may have experienced so much housing growth already that they are effectively too isolated to adapt to climate change, while others will require extensive habitat restoration work.

Introduction

Habitat connectivity maintains critical ecological flows and is a key method proposed to mitigate climate change and promote ecological resilience in the face of global change (Scheffer et al. 2001, Carpenter et al. 2006). Protected areas, our main tool for conserving biodiversity, must therefore be viewed in the larger landscape context in which they occur. The condition of matrix habitats, defined here as those areas outside of protected areas, strongly influences connectivity and, by extension, ecological flows to and from protected areas (Lindenmayer and Nix 1993, Fischer and Lindenmayer 2007).

Among land uses, housing growth is a significant threat to biodiversity in the United States (Flather et al. 1998, Hansen et al. 2005), especially because it is commonly associated with infrastructure development activities, which have their own environmental effects (Hawbaker and Radeloff 2004). Habitat changes related to housing affect individual species (Merenlender et al. 2009), community composition of many taxonomic groups (Miller et al. 2003, Pidgeon et al. 2007, Eigenbrod et al. 2008), predation rates (Wilcove 1985), species abundance and distribution (Fahrig and Rytwinski 2009), species invasions (Gavier-Pizarro et al. 2010), and ecological flows (Hawbaker et al. 2006, Patrick and Gibbs 2010). Once land is in residential development, it is unlikely to change to another use (Nusser and Goebel 1997). However, despite of the impacts of housing growth, our methods for identifying the location of housing at broad spatial extents are imperfect and residential development often remains undetected (Pidgeon et al. 2007).

Native species diversity and abundance tends to decrease with increased housing density along the rural-to-urban gradient (Blair 1996, Eigenbrod et al. 2008, Gagne and Fahrig 2010a). Low-density rural housing (densities ranging between 6 and 25 houses/km^2) has been a particularly fast-growing land use in the United States (Brown et al. 2005, Hansen et al. 2005). The area of influence of houses in low-density developments is proportionately larger than that of houses in suburban sprawl (Radeloff, Hammer, & Stewart, 2005). In addition, housing growth in recent decades has been notably high near the boundaries of protected areas (Hammer, Stewart, Hawbaker, & Radeloff, 2009; Radeloff et al., 2010; Wade & Theobald, 2010). This growth pattern is driven by the amenity-rich nature of protected areas and is problematic because protected areas are crucial for biodiversity conservation. Housing growth at the boundaries may thus reduce the conservation value of protected areas (Leinwand, Theobald, Mitchell, & Knight, 2010; Radeloff et al., 2010; Wade & Theobald, 2010).

Prior research has only reported average housing densities in the surroundings of protected areas, rather than the spatial distribution of housing at protected area boundaries (Gaston et al. 2008, Joppa et al. 2008). The spatial distribution of housing is important because comparable densities of housing in the surroundings of protected areas may vary in their configuration. Widely dispersed housing is much more likely to isolate refuges, while more clustered housing may still allow connectivity and the persistence of ecological flows critical to resilience of natural systems and wildlife populations. Given concerns that climate change will likely exacerbate other stressors that include urbanization, habitat loss, and habitat fragmentation, there is high interest in maintaining and/or restoring habitat connectivity. The USFWS is interested in maintaining, or through targeted restoration, improving connectivity for the NWRS as an adaptation measure for climate change (Griffith et al. 2009). Evaluating the current and future state of areas without housing and habitat corridors surrounding the National Wildlife Refuges is thus a necessary step in conservation planning aimed at improving resilience and climate adaptation (Griffith et al. 2009, Hamilton et al. 2013).

We evaluated the spatial distribution of housing around the NWRS in the conterminous United States. We posed four questions:

- How has the pattern of very low-density housing around National Wildlife Refuges changed over time?
- Does the current pattern of housing provide pathways through which species could migrate among National Wildlife Refuges across the United States?
- What is the current status of habitat corridors within existing very low-density housing pathways?
- How does the status of very low-density housing pathways and corridors vary among the administrative regions by which the NWRS is organized and managed?

Methods

Study area

The U.S. National Wildlife Refuge System (NWRS) is unique among federal lands in that its primary focus is on wildlife conservation in contrast with other federal lands (e.g. U.S. Forest Service, Bureau of Land Management, and National Park Service). Additionally, the NWRS has a stated goal of maintaining the biological integrity of the refuge system (Meretsky et al. 2006), which is complicated by the fact that many of the refuges occur in a matrix of intensive land uses such as agriculture (Scott et al. 2004). We evaluated housing growth around Refuges in the contiguous 48 United States. We only evaluated NWRS lands that were specifically designated as refuges in the USFWS cadastral database (http://www.fws.gov/GIS/data/CadastralDB/), and excluded lands that are not directly managed by USFWS (i.e., cooperatively managed lands). This resulted in a set of 455 refuges. We analyzed the NWRS as a whole, and each of the 7 administrative regions in the conterminous United States.

Extent of analyses

We modeled housing and housing growth at different spatial and temporal scales around the refuges to quantify how the number and size of very low density housing pathways changed over the past 60 years and may change in the future. Housing was analyzed within 5, 25, and 75 km of each refuge. Some areas fell within the analyzed extents of multiple refuges due to their proximity (e.g., some housing was within 75 km of two or more refuges). These areas were only counted once for the refuge system as a whole and once within each region, but potentially more than once for different refuges or regions. In addition to spatial extent, we analyzed historical (1940, 1970, and 2000) and projected (2030) housing density at each distance (5, 25, 75 km) from refuges.

The spatial analysis extent was based on our previous work evaluating change around the NWRS (Hamilton et al. 2013) and allowed us to evaluate a range of distances given that body size and habit is known to generally affect dispersal distances of animals (Sutherland et al. 2000). In addition, the maximum distance reflected the distance from refuges within which most USFWS private land habitat restoration projects have been completed under the 25-year-old program called "Partners for Fish and Wildlife", which has restored over 1,000,000 acres of wetland as of 2010 (http://www.fws.gov/partners/).

Housing data

We obtained housing data from the 2000 U.S. Decennial Census at the partial block group level and used housing growth rates during the 1990s to project future housing growth out to 2030 (Radeloff et al. 2010). We summed the number of housing units for each decade and adjusted them using county-level housing projections based on the 2008 Woods and Poole county projections (http://www.woodsandpoole.com/). The Woods and Poole projections are based on an advanced demographic model and are considered the best available population forecasts. We then used county-specific household sizes to convert population growth to housing unit growth, an adjustment that accounts for high frequencies of vacant housing units in areas with high proportions of seasonal housing (Radeloff et al., 2010).

Housing summary and corridor analysis

We conducted the analysis using ArcGIS 10.1 (ESRI, Redlands, California). From the Census data, we extracted those areas that had fewer than 6.17 housing units/km^2 (i.e., 1 house/40 acres) across the United States. We designated these areas as very low-density housing in accordance with the wildland-urban interface definition (Radeloff et al. 2005a, USDA and USDI 2001). We then extracted areas of very low-density housing at each distance around the National Wildlife Refuges (5, 25, 75 km). Continuous areas of very low density housing that reached from a National Wildlife Refuge boundary to the outer boundary at a given distance (e.g., 5 km) were designated “open space pathways” (hereafter, pathways). Our reasoning was that very low-density housing may allow movement for some species that are sensitive to human activity but not particularly sensitive to a modified landscape or may present the opportunity to re-create or restore habitat for species with stricter habitat requirements (i.e., “opportunity areas”). We then summarized the number of pathways and the percent of the area within a certain distance from a refuge that was composed of pathway (pathway proportion = pathway area/buffer area) for each refuge and summarized the total number of pathways, the mean number of pathways, and the average proportion of buffer area comprised of pathways around refuges at all buffer extents and at each time step both nationally and regionally for the refuge system.

Finally, we used ArcGIS to identify habitat in all pathways at each distance for the year 2000. Within pathways, we identified habitat corridors that reached from the border of the wildlife refuge to the full extent of the specified buffer. We reclassified the 2006 National Land Cover Dataset (NLCD, 30-m resolution) to reflect only potential wildlife habitat, including open water (class 11), forest (classes 41, 42, 43), shrubland (classes 52), grassland (class 71), and wetlands (classes 90 and 95). We identified continuous pathways through habitat via GDAL (http://www.gdal.org/) using an 8-neighbor rule. Within the pathways, we summarized the number of corridors, the mean number of corridors, and the average proportion of buffer area comprised of corridor (corridor proportion = corridor area/buffer area) around refuges at all buffer extents both nationally and regionally. In our analyses, habitat corridors could only be a subset of pathways (i.e., in all cases, corridor area and proportion was by definition equal to, or less than pathway area and proportion).

Results

Pathways

The mean number of pathways per refuge declined with increasing distance from National Wildlife Refuges within each time-step, and it also declined with advancing decades (Table 3, Figure 8, Figure 9). However, there was one notable exception: the mean number of pathways increased slightly from 1940 to 2000 at the 5-km buffer extent, then decreased from 2000 to 2030. Variation in the mean number of pathways was very small among time steps (less than a 4% difference), compared to the level of variation among the different extents of analysis (up to a 30% difference).

The mean proportion of area around refuges that was composed of open space pathways decreased over time at each extent (Table 4). However, among spatial extents at a given time, the pattern differed. In 1940 and 1970, the maximum proportion of pathway occurred within 25 km (Table 4). In 2000 and 2030, the proportion of land in open space pathway decreased with increasing analysis extent. The highest mean proportions of area in pathway for the entire refuge system were all in 1940, with 0.86 at 25 km being the highest for any combinations of year and analysis extent, and approximately 0.60 at 75 km in 2030 being the lowest. Most NWRs retained at least one pathway in 2030 over the 75 km distance, but 23 were projected to have zero pathways by then (Figure 9).

Corridors

The number of habitat corridors in 2006 decreased with increasing extent of analysis, mirroring the pattern of pathways (Table 3, Figure 9). The mean number of corridors at 5 km was actually higher than the mean number of pathways, indicating instances of multiple corridors within a single pathway (Table 3). The mean number of corridors per refuge declined precipitously with increasing analysis extent, however, decreasing to 0.84 and 0.54 corridors per refuge at 25 km and 75 km, respectively (Table 4), a 40% greater decline than for pathways (Table 3, Figure 9). Additionally, the number of refuges with no habitat corridors increased substantially with increasing extent of analysis (Figure 9).

The mean proportion of buffer area composed of habitat corridor in 2006 was far lower than the mean buffer area composed of pathway (Table 4). In fact, the values were approximately half of the pathway values at 5 km, becoming much lower at 25 and 75 km. The mean corridor area was less than 25% of the comparable mean pathway area at 75 km.

Regional variation

Refuges with zero pathways were not distributed evenly across the nation or even within regions, and largely in the Northeast (Figure 8, Figure 9, Figure 10). Refuges with one pathway were widely distributed but those with more than one pathway were clustered in the Mississippi River region, Gulf Coast, and Florida, though there were widely scattered refuges with 2 to 3 pathways, particularly at the 5 km distance. Across all spatial extents, the number of pathways per refuge declined, with declines in the western and northeastern United States being the most notable.

Habitat corridors were also not distributed evenly and, once again, were far more numerous and widespread at the 5 km distance, decreasing with increasing extent of analysis (Figure 9, Figure 11). The pattern at 5 km was similar to the pathway patterns, where refuges with 1 to 2 corridors were relatively wide-spread, except in the northeast. However, at 25 and 75 km, the pattern became much different with almost no refuges with corridors found in the Mississippi River Valley, Great Plains, and Central Valley of California (Figure 9, Figure 10, Figure 11). These patterns had three distinct characteristics. First, there were very few pathways to a distance of 75 km east of the Mississippi River from the Mid-Atlantic region northward. Where pathways existed, they were relatively small and narrow (Figure 10, Figure 12). Second, the Mississippi and Ohio River valleys as well as the Northern Great Plains had a high number and proportional area of pathways but almost no habitat corridors beyond several small ones in the Lower Mississippi Valley (Figure 12). Third, nearly all of the habitat corridors that extended 75 km from refuges were found in the Western Great Plains, Rocky Mountains, and the Intermountain West, with a cluster of several corridors along the Columbia River and along the Pacific Northwest Coast. These three differences were exemplified in different USFWS administrative regions (Figure 10, Figure 11). USFWS Region 5 has very limited amounts of land in pathways or corridors (Figure 9, Figure 10, Figure 11). Region 4 has open pathway areas in Central and Southern Florida, as well as in the Lower Mississippi River Valley. There are also extensive areas within Region 3 and the eastern halves of Regions 2 and 6 that provide pathways but much of this is in use for agriculture or pasture and would likely require substantial restoration. The western halves of Regions 2 and 6, and large areas within Regions 1 and 8 have extensive corridor areas. In fact, the majority of the corridors in these areas occupied a very large percentage of the buffer areas. In addition, there are pathways in the Central Valley of California and in Eastern Washington, but very little area in corridor (Figure 10, Figure 11).

Discussion

We evaluated the past, current, and predicted future effects of housing growth on open space pathways around the National Wildlife Refuge System from 1940 to 2030, identified current habitat corridors, and identified regional variation in the patterns of opportunities and threats for the connectivity of wildlife refuges with habitat in their surroundings. The opportunities and threats are important to managers and policy makers because they highlight where the mitigation of climate change with habitat corridors need may be possible given strong regional and local variation. Our results highlight that we should be acting now, in order to protect connectivity since opportunities will become much more limited in the future.

Our results indicated that there are large regional differences in opportunities for restoring connectivity, but only few opportunities east of the Appalachian Mountains, even at relatively limited extents, because of the prevalence of residential land use. Many areas in the eastern United States already lack far-reaching corridors that could function as climate mitigation tools. Those refuges found in the Mississippi Valley and northern Great Plains have opportunities but will require significant restoration efforts because many of the open spaces in the agriculture-dominated Midwest contain very little habitat. In addition, many refuges in the western Great Plains, Intermountain West, and some areas of the Pacific Northwest are currently secure. Finally, our results show that opportunities and threats can vary widely even within a given administrative region. Our findings concur with other studies that have found housing growth to be a significant threat to protected areas, leading to isolation and disruption of ecological flows (Hansen & DeFries, 2007; Radeloff et al., 2010; Wade & Theobald, 2010).

Our findings that pathways and corridors surrounding refuges will decrease in coming decades supports other findings suggesting that residential development has, and will continue to, spread at low density throughout rural areas and will limit the effectiveness of protected areas (Brown et al. 2005, Wade and Theobald 2010). However, it appears that the predicted rate of open space in the vicinity of refuges loss to development is not as rapid as some projections have suggested (Wade and Theobald 2010). Nevertheless, the amount of habitat composing corridors was significantly lower than the amount of open pathway present on the landscape. In places where there is very little habitat in corridor, there may be opportunities to recreate or restore additional corridors and to expand the size of existing corridors, but doing so would require concerted management efforts.

The within-administrative region variability was also high in some cases. For example, the NWRs in the eastern halves of Regions 2 and 6 often had pathways but no corridors, in contrast to NWRs in the western halves of the regions which largely had corridors. We were not surprised to find that changes were strongly regional in nature. Other work on land use and housing change has demonstrated that total changes and rates and patterns of changes vary widely across the U.S. (Hamilton et al., 2013; Radeloff et al., 2010). Land use changes are typically strongly tied to socioeconomic processes within ecoregions (Radeloff et al., 2012; Sohl, Loveland, Sleeter, Sayler, & Barnes, 2010), highlighting the need for integrating social and ecological sciences in order to improve the effectiveness of conservation efforts (Dale et al. 2005, Liu et al. 2007).

Perhaps most alarming among our results were the extremely limited opportunities to restore habitat corridors in the northeastern U.S. The majority of corridors and pathways found in that region were associated with coastal waters, river channels, or large water bodies (e.g. the Finger Lakes in New York State, Figure 12). There was very little terrestrial buffer area that met our definition of pathways. These results indicate that there are likely to be many areas in which the window of opportunity to restore and secure corridors is rapidly disappearing or where habitat corridors are not a feasible mitigation strategy for climate change adaptation. Our results indicate that unassisted migration may not be possible in many instances for species with poor dispersal capability, or for those species who cannot disperse in water. In addition, the small proportion of area around refuges composed of corridors should be concerning. Such low proportions of the landscape in a contiguous corridor are likely to have very high edge densities which reduced the suitability of habitat and is susceptible to invasion by exotic species (Friesen et al. 1995, Fischer and Lindenmayer 2007, Predick and Turner 2008).

While our results had some worrying implications, the worst may be related to climate change itself. Even in areas where our results indicated that corridors or opportunities to restore corridors exist, those opportunities may not have the capacity to address shifting climatic condition for species migration. The velocity of climate change (i.e., the rate at which suitable environmental conditions are shifting across the landscape) may outpace our capacity to connect remaining habitat (Veloz et al. 2011, Williams et al. 2012).

There are several limitations and concerns related to our analyses. First, we selected one housing density threshold to identify pathways, but the most appropriate threshold may differ among species. The low value we used was conservative, since even very low densities of residential development can affect habitat quality and biodiversity (Pidgeon et al. 2007, Gagne and Fahrig 2010a, 2010b). Second, our estimation of corridors and connectivity evaluates structural connectivity (landscape configuration only) while ignoring functional connectivity (a species' response to a landscape; (Tischendorf and Fahrig 2000)). For instance, many species vary in their ability to move across features such as roads (Carr and Fahrig 2001, Fahrig and Rytwinski 2009). While we excluded roads from our definition of habitat, conversion of linear features such as roads into a raster such as we used in our analyses is likely to result in "cracks" in linear features (Rothley 2005). We did not address this in our analyses, and that may have led sometimes to an overestimate of structural connectivity. Finally, there were instances where some refuges showed an increase in the number of pathways. This result is potentially confusing, and occurred when a previously larger pathway was fragmented into two or more smaller pathways, with an overall loss of open space.

Conclusions

In terms of management implications, our results indicate that addressing climate change impacts to wildlife with habitat corridors will vary in difficulty and effectiveness. Some regions appear to be well-situated for the use of habitat corridors to mitigate the effects of climate change, as has been proposed (Griffith et al. 2009). However, habitat loss in all forms, not just to housing growth, is still the main driver of biodiversity loss (Sala et al. 2000, van Vuuren et al. 2006) and has affected the presence of corridors on the landscape. Policy makers will need to account for regional and local variation to maximize the effectiveness of climate change mitigation with a variety of techniques. While some areas appear to have limited capacity to address large range shifts for species with limited vagility, there are still many opportunities to improve habitat connectivity and quality at localized scales even in areas where corridors do not exist or do not reach great distances. Our results demonstrate the need to work close with private landowners and other private and public land managers to promote wildlife friendly landscape-scale planning. Working with local partners and neighboring land owners can still do much to improve the quality and effectiveness of many protected areas.

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Table 3. Mean number of pathways per refuge at each time step and spatial extent of analysis and the mean number of corridors in 2000.

Distance	1940	1970	2000	2030	In Corridor
5	1.36	1.38	1.4	1.38	1.78
25	1.05	1.05	1.02	1	0.84
75	1	1	0.97	0.96	0.54

Table 4. Mean proportion of landscape area per refuge composed of pathway at each time step and spatial extent of analysis with the mean proportion in corridors in 2000.

Distance	1940	1970	2000	2030	In Corridor
5	1.36	1.38	1.4	1.38	1.78
25	1.05	1.05	1.02	1	0.84
75	1	1	0.97	0.96	0.54

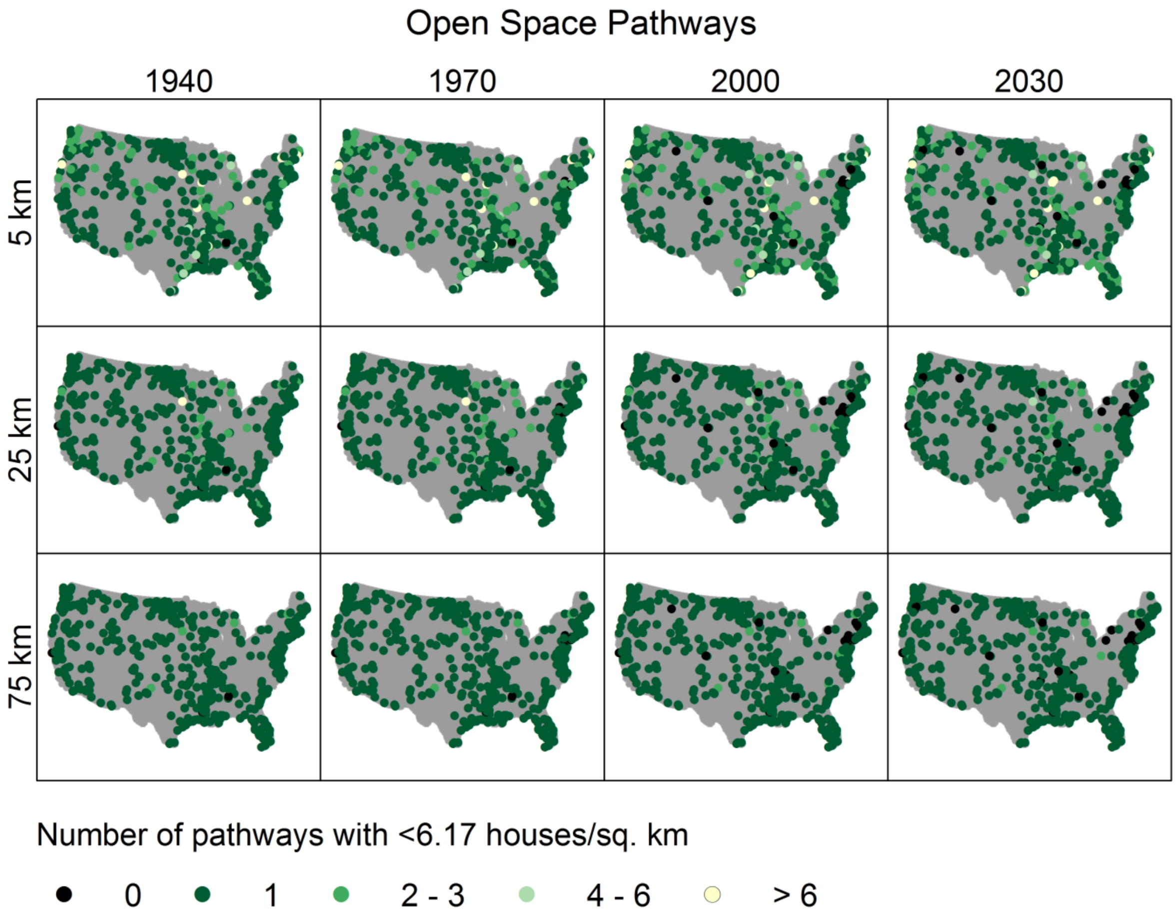

Figure 8. The number of open space pathways around each refuges at all spatial extents of analysis and all time steps.

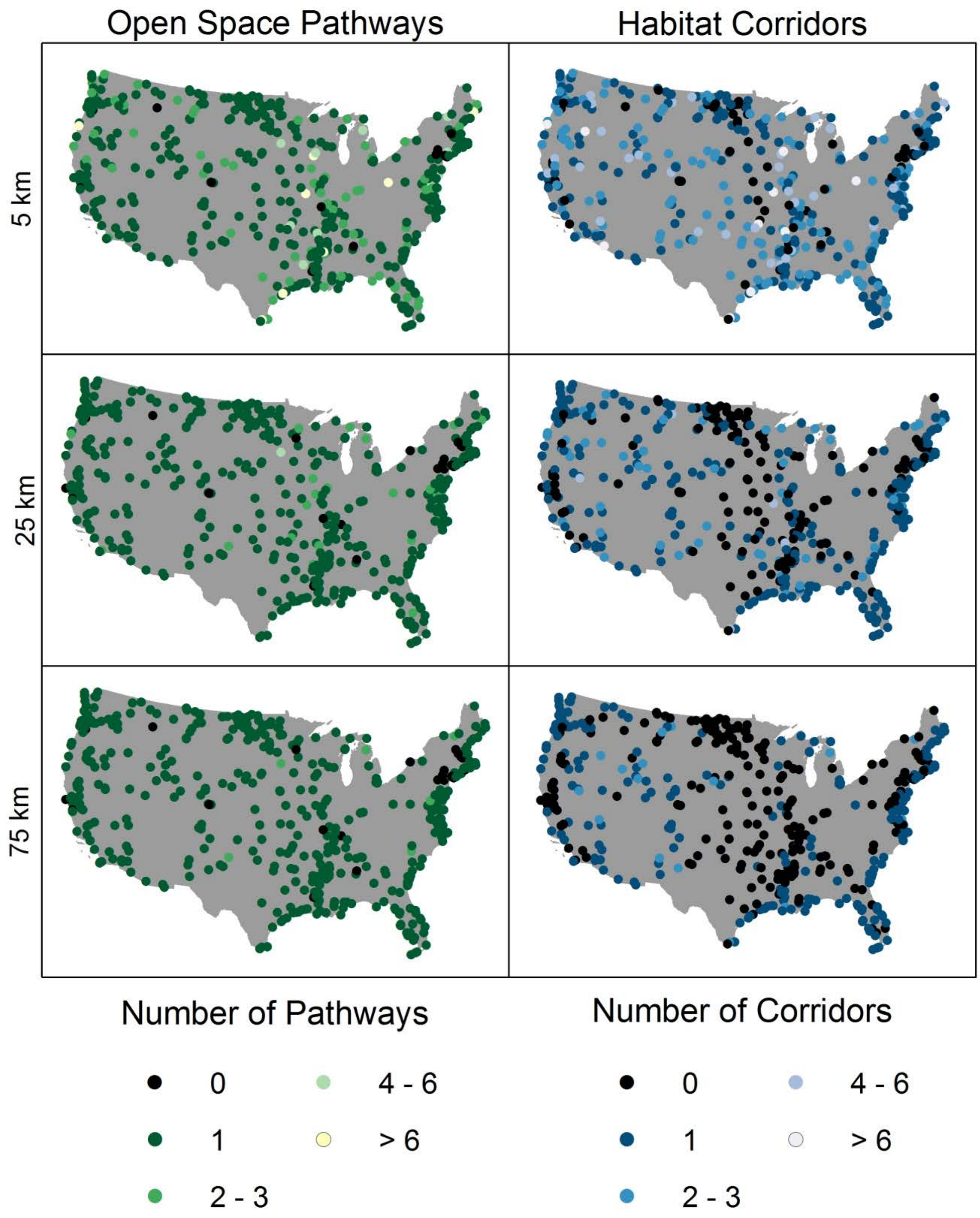

Figure 9. The number of open space pathways around each refuge in 2000 and the number of habitat corridors around each refuge based on 2006 National Land Cover Data.

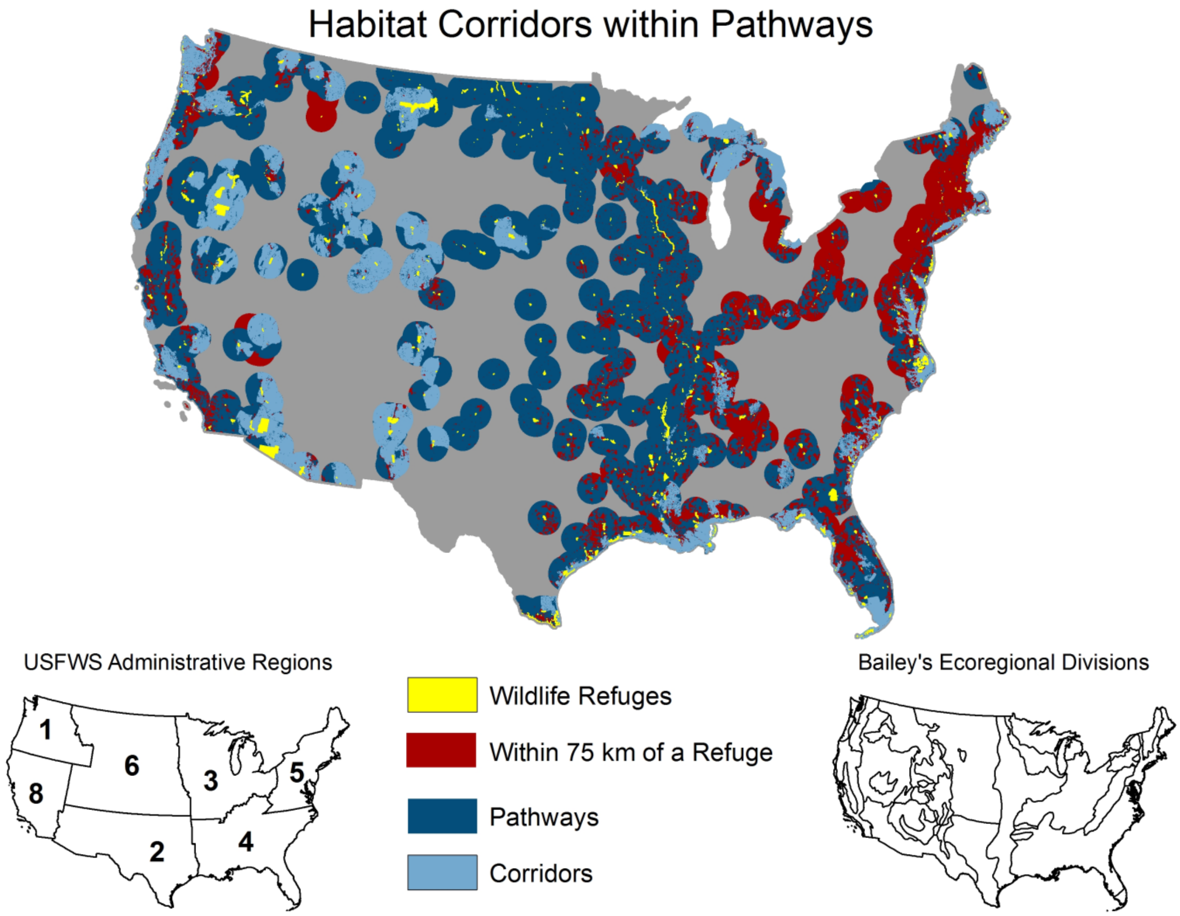

Figure 10. Visualization of conditions at 75 km around each refuge in 2000. Buffer zones, open space pathways, and habitat corridors at 75km are shown for all refuges.

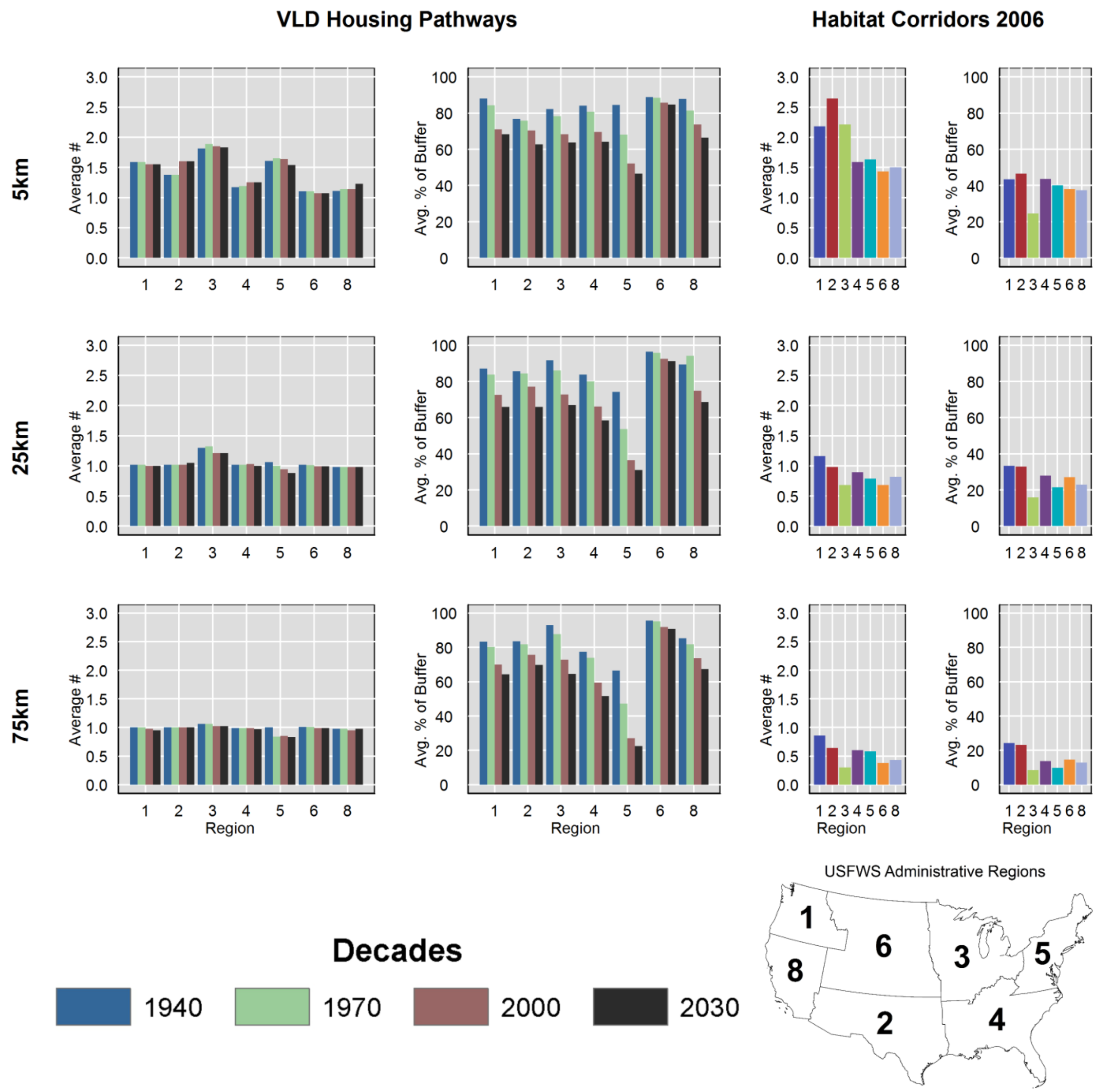

Figure 11. Regional change in the average number of pathways and proportion of buffer in open space pathway across time steps and regional variation in the average number of corridors and proportion of buffer in corridor in 2006.

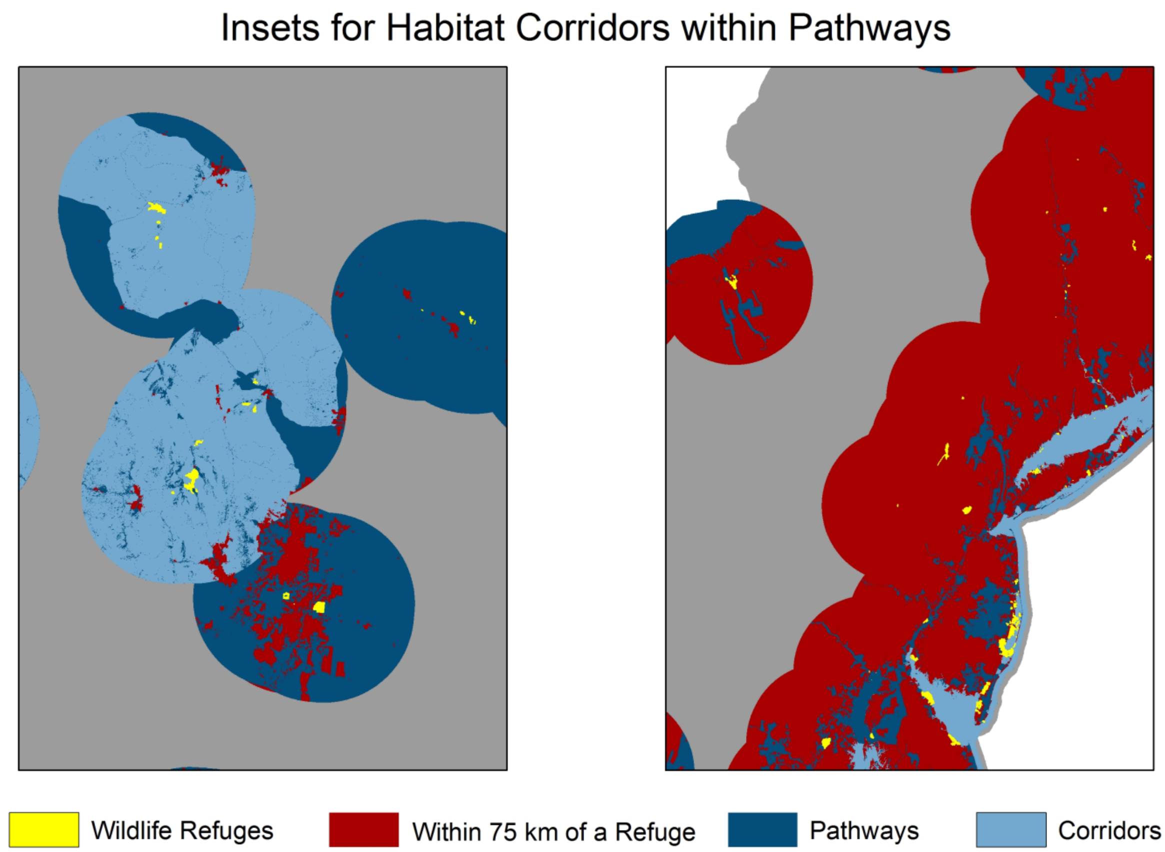

Figure 12. Example of the variability in amount and configuration of open space pathways and habitat corridors around refuges in the western Great Plains/foothills of the Rocky Mountains (left) and the northeastern United States (right). The left map is centered near Denver, CO and the right is centered near New York, NY.

Chapter 3: Current and future connectivity and changes in protected area suitability for Blanding's turtle (*Emydoidia blandingii*) in Wisconsin

Abstract

Climate change is forcing shifts in species distributions as portions of current ranges become less suitable and species seek new areas with suitable climate conditions. Improving landscape connectivity to facilitate species movements is thus one of the primary approaches to mitigate the effects of climate change on biodiversity. However, it is not well understood how continuing land use and climate change affect the existing connectivity of landscapes. We used species distribution modeling in combination with different future scenarios of both land use change and climate change to evaluate shifts in habitat suitability and habitat connectivity for the Blanding's turtle (*Emydoidia blandingii*) in Wisconsin. We found very little difference in outcomes of different economic scenarios for future protected area habitat suitability and landscape connectivity. However, climate change had significant effects on both habitat suitability and connectivity, and it differed considerable among scenarios. Under both our low and high emissions scenarios, suitable habitat shifted to northern Wisconsin. In the high emissions scenario almost no suitable habitat remained for Blanding's turtle in Wisconsin by the 2050s and there was a large increase in landscape resistance to turtle movement. The effects were exponentially greater for connections in southern versus northern Wisconsin, indicating a strong trailing edge effect on habitat suitability wherein populations at the southern edge of the range are likely to "fall behind" their projected distribution faster than populations in the north. Blanding's turtle is likely to lose suitable habitat at a rate far faster than its ability to adjust to changing conditions.

Introduction

In response to climate change, many species will need to move large distances when their current range becomes unsuitable and newly suitable areas need to be colonized in order to persist (Chen et al. 2011), and land use change may limit opportunities for species to do so due to landscape fragmentation. Protected areas are a key conservation tool to maintain biodiversity (Rodrigues et al. 2004; Joppa et al. 2008). It is not clear though how future changes in land use and climate will influence the effectiveness of protected areas (Fleishman et al. 2011). A commonly proposed solution is to establish habitat corridors and habitat patches that can function as stepping stones to improve connectivity among protected areas (Heller and Zavaleta 2009; Krosby et al. 2010). The assumption is that a network of protected areas and a well-connected landscape will reduce impediments to species dispersal and facilitate movement among resource patches (Griffith et al. 2009, Beier and Brost 2010). With limited funding available for conservation, it is critical though that such conservation investments account for current and future threats to maximize conservation gains (Merenlender et al. 2009; Mairota et al. 2013).

Humans have extensively altered the surface of the planet and the majority of the land area is either used by humans or altered by them (Vitousek and Mooney 1997; Sanderson et al. 2002; Foley et al. 2005). Landscapes can be viewed as a mosaic of patches representing habitat and non-habitat and, in human-dominated landscapes, many of the non-habitat patches result from human use (Lindenmayer et al. 2008; Franklin and Lindenmayer 2009). Land outside of protected areas, i.e., in the matrix, still includes some natural or semi-natural elements, with use varying from natural to urban. These lands are typically in non-conservation use and the type of use strongly affects potential movement of species through the landscape (Hamilton et al. 2013;

Baum et al. 2014). The distribution and arrangement of both natural elements and area of land use within this matrix affects its ecological function and, therefore, the condition of the matrix must be considered in any planning for habitat connectivity (Lindenmayer et al. 2008; Franklin and Lindenmayer 2009; Mairota et al. 2013).

Adaptation, the process of adjusting management practices to mitigate their negative impacts, is the strategy proposed to address the consequences of human-induced global change and emphasizes adjustments to socio-economic and land use practices (Smith et al. 2000a). Improving habitat connectivity is one of the primary adaptation strategies to enhance resilience (i.e., the ability of a system to recover from perturbations) within biological systems (Griffith et al. 2009; Mori et al. 2013). Connectivity reflects the degree to which a landscape facilitates or impedes movements among habitat patches (Taylor et al. 1993). It is an important component of the resilience of ecological systems because connectivity is associated with maintenance of species movements among habitat patches (DeFries et al. 2007; Hansen and DeFries 2007). Connectivity is affected by both habitat loss (i.e., overall reduction in the amount and quality of habitat) and habitat fragmentation (i.e., the breaking apart of habitat). Habitat loss has consistent negative impacts to biodiversity, while habitat fragmentation effects are weaker and more variable (Fahrig 2003). Connectivity depends on the spatial patterns of habitat, which his affected by land use, and therefore adjustments to land use are the primary method to improve connectivity.

The establishment of habitat corridors and of habitat patches that can function as stepping stones are the two main management actions to improve connectivity and dispersal opportunities for species (Krosby et al. 2010; Kramer-Schadt et al. 2011). Corridors and stepping stones are, by definition, embedded in the matrix (Beier and Noss 1998; Baum et al. 2014). Habitat corridors are linear habitat patches that connect two or more larger blocks of habitat (Beier and Noss 1998). Stepping stones, on the other hand, are a series of small habitat patches that connect otherwise isolated habitat blocks (Baum et al. 2014). While there has been debate about the effectiveness of corridors, both literature reviews and empirical studies have demonstrated their conservation value (Damschen et al. 2006, Noss 1987, Simberloff et al. 1992, Beier and Noss 1998, Gilbert-Norton et al. 2010, Haddad et al. 2003, Haddad and Tewksbury 2005). Stepping stones tend to have weaker effects but are still useful in many situations (Leidner and Haddad 2011; Baum et al. 2014), and in some cases may be critical for improving landscape connectivity (Krosby et al. 2010; Saura et al. 2013). Regardless, improving connectivity is a primary conservation goal given that range shifts driven by climate change have already been documented for a number of species and in the future large changes in species distribution and community compositions are anticipated (Thuiller 2004; Heller and Zavaleta 2009; Chen et al. 2011).

Connectivity has two components: structural and functional connectivity (Tischendorf and Fahrig 2000a). Structural connectivity assesses only the amount and spatial arrangement of habitat. Functional connectivity incorporates also species' behavioral response to the spatial patterns of habitat, recognizing that the same landscape will have different connectivity for different species based on their habitat use and movement capabilities (Tischendorf and Fahrig 2000a, b). Functional connectivity, can also be assessed either as potential or actual connectivity. Potential functional connectivity is an indirect, or hypothesized, measure of functional connectivity (i.e., based on a model), while actual functional connectivity is quantified based on actual species movements (Crooks and Sanjayan 2006).

In order for connectivity assessments to be most valuable for conservation decisions, it is crucial to examine both current connectivity and likely future changes, including potential threats to, and shifts in, connectivity (Smith et al. 2000b; Mori et al. 2013). Incorporating threat into conservation decisions is crucial to maximizing conservation outcomes from the investment of limited conservation funding (Merenlender et al. 2009b). Identification of future threats is recognized as a priority by the U.S. Fish and Wildlife Service National Wildlife Refuge System (Griffith et al. 2009) and understanding the potential future effects of matrix land use and climate change on protected areas is essential for guiding conservation policy (Fleishman et al. 2011). Assessing the effects of future change on connectivity among protected areas should thus be an important aspect of conservation planning, yet this has rarely been done (Piquer-Rodríguez et al. 2012). When analyzing connectivity among protected areas, the protected areas are typically assessed based on current landscape conditions (Rouget et al. 2003). Quantifying future connectivity is difficult because it is difficult to predict future habitat patterns, which is necessary given the importance of spatial arrangement of habitat patches to connectivity (Goodwin and Fahrig 2002; Fahrig 2003). Projecting future conditions can be relatively accurate at estimating proportions across broad areas but is difficult to do in a spatially explicit manner, owing to problems identifying which specific parcels of land are likely to undergo changes (Radeloff et al. 2012). In general though, when projecting future conditions, the combination of exploring potential scenarios and constructing predictive models is useful to increase the value of ecological research for management application (Coreau et al. 2009). The comparison of scenarios can provide important insights about the effects of potential alternate futures on biodiversity and other ecological resources (Gude et al. 2007, White et al. 1997).

Our goal here was to evaluate current and future potential functional connectivity among protected areas in Wisconsin for Blanding's turtle, a widely-distributed but declining species. We asked the following four questions:

- Which protected areas are currently important refugia for Blanding's turtle in Wisconsin?
- What is the current pattern of functional connectivity among those protected areas?
- How might climate and land use change affect the importance those protected areas in the future under different emissions and land use scenarios?
- What is the relative effect of different combinations of economic policy and emissions scenarios on connectivity?

Methods

We modeled habitat connectivity for the Blanding's turtle, a semi-aquatic species with a center of distribution around the Great Lakes, ranging from Nebraska to Maine and north to Ontario and Nova Scotia. The species is listed as threatened or endangered in many states within its range (Mockford et al. 2006). The species' range was pushed southward during the Wisconsin glaciation and that the species moved north- and eastward from several potential points of refugia to occupy its current range (Schmidt 1938; Mockford et al. 2006; Rödder et al. 2013).

Study area and current habitat suitability

Our study area was the state of Wisconsin. We used Maxent software version 3.3.3 for species habitat modeling (Phillips et al. 2006) to create a habitat suitability map for Blanding's turtle over its entire U.S. range based on 229 known occurrences since 1993 from the Global Biodiversity Information Facility (GBIF; http://www.gbif.org/) and 115 locations provided by co-authors. Maxent is a machine learning program that can use presence-only species records to model distributions and is widely applied because it normally outperforms other algorithms in its predictive power (Elith et al. 2006; Hijmans and Graham 2006; Elith and Graham 2009). We used default Maxent settings (Phillips and Dudík 2008) with the exception of the removal of threshold and hinge features to provide more ecologically realistic response curves and more general predictions (Bateman et al. 2012). We developed a rangewide model by randomly generating 10,000 pseudoabsence locations within 100 km of the 334 known occurrence locations and comparing environmental conditions between pseudoabsences and occurrences. We created a rangewide model to ensure that we captured the full range of variability of Blanding's turtle habitat. Our environmental layers included one climate layer (historic mean annual temperature) and eight land use classes based on a reclassification of the 2006 National Land Cover Dataset (NLCD, 2006). The land use classes we used were: open water (NLCD class 11), crop (class 82), pasture (class 81), forest (classes 41, 42 and 43), urban (classes 21, 22, 23 and 24), rangeland (classes 52 and 71), woody wetlands (class 90), and emergent herbaceous wetlands (class 95). We resampled all environmental layers to 500-m resolution for our analyses. We then projected a model of current suitability for the entire state of Wisconsin based on the parameters from the range wide model.

We used the suitability output from the Wisconsin-wide projected model to identify what are, under current conditions, the 250 most important protected areas for Blanding's turtle from among all class 1 and 2 protected areas in the U.S. protected area database for Wisconsin (http://gapanalysis.usgs.gov/data/padus-data/). Class 1 and class 2 protected areas provide the highest degree of protection and are typically managed for biodiversity, whereas other classes include resource extraction or high degrees of human use. We determined protected area rank based on the total amount of habitat area with probability of occurrence values greater than 0.9 (based on the Maxent logistic probability of occurrence scale, estimated between 0 and 1). Finally, we used the “maximum training sensitivity plus specificity” threshold in Maxent to determine our cut-off for suitable vs. unsuitable habitat. This threshold is relatively conservative (higher omission rate) and we selected a threshold of 0.34 below which we deemed sites as unsuitable. Above this threshold, we divided the suitable range into two classes: moderately suitable (probability of occurrence values between 0.34 and 0.66) and (highly suitable above 0.66 probability of occurrence). We totaled the amount of unsuitable, moderately suitable, and highly suitable habitat for each of the 250 protected areas as well as for the entire state of Wisconsin. We evaluated model performance based on the AUC from Maxent for this model and all subsequent Maxent models.

Future habitat suitability

We projected our models to quantify future habitat suitability using output from a previously published econometric model (Radeloff et al. 2012; Hamilton et al. 2013) and two different climate change emissions scenarios. We used the Maxent “fade-by-clamping” option, which removes heavily clamped pixels from the final model predictions (Phillips et al. 2006). The econometric model is based on observed land-use changes between 1992 and 1997 from the National Resources Inventory, county-level net economic returns, and soil productivity and provides estimated land-use transition probabilities for crop, pasture, forest, urban, and rangeland from 2001 to 2051. The inputs to the model can be adjusted to represent different economic policies and generate alternate maps of future land-use change patterns. We used two economic policy scenarios to evaluate future changes in connectivity. The first scenario was our “baseline” scenario, which reflects a continuation of the land-use change patterns between 1992 and 1997.

The second scenario was a "pro-agriculture" scenario, where the net economic return for agricultural land-use increases by 10% every 10 years. We chose these scenarios because they exhibited notable differences in terms of future conditions in previous analyses, and because the increasing economic returns in the pro-agriculture scenario reflects recent economic conditions (Hamilton et al.; in review). The land use classes in the scenarios were identical to those we used in the "current suitability" map. Since pixel-specific changes are difficult to predict, we generated 10 replicates of each of the economic policy scenarios (see below).

For our future climate data, we used "low" and "high" emissions based climate change scenarios. We used climate data from the Research Program on Climate Change, Agriculture and Food Security (CCAFS) data portal. We analyzed 2050s output from the MIROC 3.2 hires General Circulation Model (GCM) under the SRES A1B scenario model for our high emissions climate change scenario, and the MRI CGCM 2.3.2a GCM under the SRES B1 model for our low emissions climate change scenario. We selected the models based on information provided at the CCAFS portal, and selected the models with the strongest and weakest effects on climate change that covered our study region at 30 second resolution.

Finally, we modeled future habitat suitability for each possible combination of our climate and land use scenarios to generate habitat suitability maps for Blanding's turtle. This resulted in 40 future habitat suitability maps for Blanding's turtle in Wisconsin (2 economic policy scenarios x 10 replicates of each economic policy scenario x 2 emissions scenarios). We summed the amount of unsuitable, moderately suitable, and highly suitable habitat within the 250 protected areas as well as for the entire state of Wisconsin using the mean values of the 10 economic policy scenario replicate/emission scenario ensembles for each of the 4 economic policy/emissions scenario combinations.

Connectivity

We quantified connectivity among protected areas based on connections from a triangulated irregular network, a standard GIS data structure that can be used to identify nearest relevant neighbors, and used a subset of those connections for comparison among the scenario combinations (Longley et al. 2005; Figure 13). Thus we evaluated only 195 connections rather than the over 62,000 possible connections. We used Circuitscape (McRae & Shah, 2009), a software package that employs circuit theory to quantify landscape connectivity, to determine the functional distances for each of the 195 connections. Circuitscape is distinctive among habitat connectivity measurement tools in that it allows for the possibility of more than one path connecting two habitat patches. This is more realistic than least-cost paths which identify connections as a single path, when there may in fact be many paths connecting two habitat patches (McRae et al. 2008). The distances generated in Circuitscape are "resistance distances" based on the difficulty of traversing the landscape. Resistance distances do not equate to geographic distance, but they do scale linearly (McRae et al. 2008), meaning that estimated distances are relative (e.g., a resistance distance of 2 is twice as "far" as a resistance distance of 1) and, that the relative difficulty of traversing a network of habitat patches can be compared among networks and over time. We used the habitat suitability surface maps generated from Maxent as "conductance" (i.e., ease of movement) inputs in Circuitscape, with higher suitability equating to higher conductance. The output from Circuitscape was a table of resistance distances between patches within our protected area network. As we did with the habitat suitability maps, we generated mean change in resistance distance among the 10 replicates of each of the 4 economic policy-emission scenario combinations.

We tested whether changes in the resistance distances were larger among economic or policy scenarios and whether the changes varied by geographic location. We accomplished this by first identifying the mid-point of all connections from the TIN surface and including the "northing" of each of those points as a value in subsequent analyses (Figure 13). We regressed mean proportional change in resistance distance for the connections against their northing, resulting in 4 curves, each of which represented the effect of geography under a different scenario.

Results

Current habitat suitability

The highest priority protected areas (based on the 0.9 probability of occurrence criterion) were distributed across the state, with the majority found in northern Wisconsin (Figure 14). Interestingly, 31 of the 250 protected areas containing the most habitat with probability of occurrence values greater than 0.9 (i.e., highest priority refugia) for Blanding's turtle were located within counties with no history of Blanding's turtle occurrence as of 2012 (Figure 14). Emergent herbaceous wetland (land use class 95), urban land use (class 4), open water (class 0), and mean annual temperature were the most important variables predicting Blanding's turtle occurrence (AUC = 0.898) with 29, 17, 15, and 13% relative contribution, respectively. Most of Wisconsin is currently unsuitable for the Blanding's turtle (14.2 million ha), but there are approximately 2.4 million ha of moderately suitable habitat (probability of occurrence between 0.34 and 0.66), and 0.3 million ha of highly suitable habitat (> 0.66) (Figure 15, Figure 16). The 250 priority protected areas for Blanding's turtle included 70,000 hectares of highly suitable habitat under current conditions (Figure 17). The amount of highly suitable habitat within priority protected areas ranged from 0 to 11,600 ha (mean 269 ha), 0 to 24,800 ha (mean 1021 ha) of moderately suitable habitat, and 0 to 126,900 (mean 3,200 ha) of unsuitable habitat). The proportion of land area within protected areas that provided highly suitable habitat (0.06) and moderately suitable habitat (0.23) were both higher than these proportions within the state of Wisconsin as a whole (0.02 and 0.14, respectively).

Future habitat suitability

Changes in habitat suitability were largely driven by climate change. Suitable habitat shifted northward under both the low and high emissions scenarios, with relatively widespread suitability in the southern 2/3 of the state under the low emissions scenario and with suitable habitat remaining only in northern Wisconsin under the high emissions scenario (Figure 14, Figure 15). The shift in habitat suitability was so extreme that only 158 and 160 of the priority protected areas for Blanding's turtle retained any suitable habitat under the low-emissions/baseline and low-emissions/pro-agriculture scenario combinations, respectively. The changes were even stronger under the high-emissions/baseline and high-emissions/pro-agriculture scenarios with only 35 and 39 protected areas retaining any suitable habitat, respectively. Across Wisconsin, for both economic policy scenarios, the low emissions scenario exhibited nearly identical and minor increases in available habitat with small increases in moderately suitable habitat offsetting even smaller decreases in highly suitable habitat (Figure 15, Figure 16). Under the high emissions scenario, however, there was a complete loss of highly suitable habitat and large decreases in moderately suitable habitat, regardless of economic policy scenario, and moderately suitable habitat became restricted to a small region within northern Wisconsin (Figure 15, Figure 16).

Under the low emissions climate scenario and within priority protected areas, the pro-agriculture economic policy scenario resulted in slightly more moderately suitable habitat than the baseline scenario (494,150 ha and 488,500 ha, respectively) and slightly more highly suitable habitat as well (39,000 ha and 30,025 ha, respectively; Table 5, Table 6). Once again, within priority protected areas the proportion of moderately suitable habitat under the baseline and pro-agriculture economic policy scenarios (0.44 in both cases) and the proportion of highly suitable habitat (0.03 in both cases) was higher than the proportion of moderately suitable habitat and highly suitable habitat in Wisconsin as a whole (0.16 and 0.006, respectively).

Under the high emissions scenario, the pattern of habitat suitability between the economic scenarios was similar, with the pro-agriculture policy scenario again providing more moderately suitable habitat (72,475 ha) than the than the baseline economic scenario (60,925 ha; Table 5). However, under the high emissions scenario there was no highly suitable habitat within all of Wisconsin regardless of the economic scenario (Figure 15, Figure 17, Table 6). In addition, the areas with suitable habitat were largely located in Wisconsin counties where Blanding's turtle is not known to occur currently (Figure 14, Figure 15). Once again, priority protected areas retained suitable habitat in higher proportions under the baseline (0.05) and pro-agriculture scenarios (0.06) than the remainder of Wisconsin (0.006 and 0.01, respectively). As in all other cases, the pro-agriculture economic policy scenario retained slightly more suitable habitat.

Connectivity resistance distances

Relative changes in resistance distance between protected area pairs increased more quickly in southern Wisconsin than in northern Wisconsin under all future scenarios, reflecting large decreases in connectivity among protected areas, especially in the south. The differences in connectivity among the scenario combinations were largely due to climate change, with the high emissions scenarios resulting in increases in resistance distance that were orders of magnitude greater than the low emissions climate scenarios in the southern portion of the Blanding's turtle's range (Figure 17). For a given emissions scenario, differences among economic policy scenarios were close to zero in all cases, and they were highly correlated ($r > 0.99$), making the economic policy scenarios indistinguishable from one another from the perspective of landscape connectivity for Blandings turtles (Figure 18). In contrast, in northern Wisconsin, habitat connectivity improved under the low emissions climate scenario, and this was also the case for the high emissions climate scenario, but improvements were smaller (Figure 15, Figure 18). Changes in landscape resistance to turtle movements were essentially zero at approximately 300 km north (low emissions climate scenarios) and 400 km north (high emissions climate scenario) within Wisconsin, with differences between the emissions scenarios nearly zero at the northern limits of Wisconsin (Figure 18). The centers of zero change in resistance distance essentially track the changes in habitat suitability (Figure 15, Figure 18). Finally, while protected area connectivity improved in northern Wisconsin, the absolute value of improvements was minor compared to the substantial decrease in connectivity in southern Wisconsin (Figure 18).

Discussion

We predicted substantial future changes in the habitat suitability and connectivity of Wisconsin's protected areas for Blanding's turtle by the 2050s and our results showed substantial changes unequivocally. The changes in protected area importance, habitat suitability, and protected area connectivity were largely driven by climate change, as indicated by the notable differences between the high and low emissions scenarios that we evaluated. The two economic policy scenarios that we evaluated were nearly identical in their effects on protected areas and habitat connectivity, probably because the effects of climate change were so much greater and essentially swamped effects of differences in land use. Under all scenarios, our habitat models predicted significant northward shifts in habitat suitability and, therefore, protected area importance for Blanding's turtle. In addition, changes in habitat suitability were predicted to occur at a higher rate in southern Wisconsin, where landscape resistance to movement among protected areas was projected to become orders of magnitude greater. Our findings are unique in the demonstration of relative changes in landscape resistance and expand on other research showing a poleward shift in habitat suitability as well as substantial changes in protected area suitability and connectivity (Parmesan and Yohe 2003; Thuiller 2004; Piquer-Rodríguez et al. 2012).

Our results indicated that there are substantial areas of suitable habitat in portions of Wisconsin where Blanding's turtle is not currently found. This is not entirely surprising. Blanding's turtle's range contracted southward and westward during the Pleistocene and expanded northward since the retreat of the glaciers (Schmidt 1938; Stephens and Wiens 2009). As climate changes, this northward expansion will have to accelerate, but there are several fortunate artifacts of the Wisconsin protected area network that may make it easier for Blanding's turtle to adapt to changing conditions. Blanding's turtle uses complexes composed of multiple wetlands throughout the year (Beaudry et al. 2009) and our results reflect their preference for forested wetland habitat. The largest protected areas in Wisconsin are found in northern Wisconsin where most of the unoccupied areas currently occur. This may be good news for Blanding's turtle given that their suitable habitat is predicted to shift northward. In addition to their large size, those protected areas are also likely to harbor disproportionate amounts of wetland habitat since wetlands are well represented within Wisconsin's protected area network (Carter et al. 2014), a fact reflected in our results where habitat suitability is higher within protected areas than outside.

The strong northward shift in habitat suitability even under the low climate scenario is startling but not unprecedented. Shifts in habitat suitability from climate change is already outpacing the capability of many species to adapt *in situ* or to disperse to areas with suitable environmental conditions (Thuiller 2004; Williams and Jackson 2007; Loarie et al. 2009; Veloz et al. 2011). The changes in distribution suggested by our model, and the consequences to Blanding's turtle, are similar to eastern massassauga rattlesnake (*Sistrurus catenatus catenatus*) range changes, which are also largely due to climate change (Pomara et al. 2013). Biogeography and habitat preferences of Blanding's turtle and eastern massassauga rattlesnake are similar and both followed a similar historical change in distribution following the Pleistocene glacial retreat (Schmidt 1938). One main finding of our analysis is the nearly complete loss of suitable environmental conditions for Blanding's turtle from Wisconsin in the future. This is particularly sobering given that climate impacts will continue to be felt for centuries.

The effects of future change on habitat suitability have serious consequences for Blanding's turtle corridors and stepping stones. Our results indicate that there will not be any suitable habitat remaining in the southern 1/3 of Wisconsin under the low climate scenario and none in the southern 3/4 of Wisconsin under the high climate scenario, thus essentially removing the possibility of using habitat corridors and natural dispersal as a strategy to ensure dispersal into northern suitable habitat for Blanding's turtle. Furthermore, the effects of climate on habitat suitability were projected to be so strong that even the retention of stepping stones is precluded, which would typically be the default alternative when land use is intense enough that corridors are not an option (Kramer-Schadt et al. 2011; Saura et al. 2013; Baum et al. 2014). Unfortunately, Blanding's turtle is not a vagile species and has taken a long time to reach those areas which it currently occupies. Even under the low emissions scenario, habitat suitability is decreasing faster than the turtle would be able to disperse.

In addition, our results clearly demonstrate an alarming “trailing edge” effect. Previous studies have indicated that the leading and trailing edges of suitable environmental conditions move at different speeds because they are driven by slightly different mechanisms (Anderson et al. 2009; Loarie et al. 2009). While the extent of our analysis did not allow us to model change at the leading edge of the Blanding’s turtle’s suitable environmental conditions, our results indicated different rates of change across the projected distribution of Blanding’s turtle, with the decrease in habitat suitability at the trailing edge occurring at an exponentially faster rate than in the core of the projected distribution. In general, species respond more slowly at the trailing edge of a shifting climate space (Anderson et al. 2009). This compounds an already bleak outlook for a species with limited dispersal capability, such as Blanding’s turtle. Furthermore, we did not include biotic interactions in our model (Bateman et al. 2012). It is possible that the suitability of Blanding’s turtle might be limited to the south of its range by competition from other turtle species. However, it seems unlikely given that Blanding’s turtle is in the taxonomic family Emydidae, a group whose distribution appears to be restricted by temperature rather than competition (Stephens and Wiens 2009).

While we emphasize the strong impact of climate in our models of future distribution of suitable habitat, we do not imply that land use change is not an important factor. First, the lower importance of land use in our models may be more of an indication that land use conditions as they currently stand are already problematic. Indeed, the fact that Blanding’s turtle is of conservation concern in many states in which is occurs is directly attributable to land use and habitat fragmentation (Attum et al. 2008; Beaudry et al. 2008). Second, and perhaps more importantly, we modeled future landscapes for a species whose distribution appears to be strongly limited by climate (Rödder et al. 2013). The relative effects of climate versus land use on habitat suitability and future landscape connectivity may be very different for a species whose distribution is limited by habitat availability more than it is by climate.

Finally, we would like to touch on several limitations of our analyses. First, there is significant temporal variation in wetland area both seasonally and inter-annually, which could further affect habitat suitability for Blanding's turtle given that the turtles typically use a mosaic of wetlands throughout their active season (Beaudry et al. 2009; Niemuth et al. 2010). In fact, our approach disregards the seasonally and inter-annually dynamic nature of wetlands and the impacts of extreme drought on wildlife species (Albright et al. 2009; Niemuth et al. 2010). Given that wetlands were the most important predictor of Blanding's turtle occurrence in our models, alterations of wetland temporal and spatial extent would likely further change habitat suitability and protected area connectivity for Blanding's turtle. Second, the land use change model we used does not predict changes to wetlands because the data used to generate the econometric models of land use change found almost no change in wetlands, reflecting that wetland area has largely remained constant in recent decades (Nusser and Goebel 1997; Dahl 2011). Thus, we treated wetlands as a static element in the environment, keeping their area and extent constant over the 50-year timeframe of our analysis, because it is unlikely that wetlands will change in their land use, but we recognize that changes in hydrology may affect them. A third limitation is the turtle's preference for urban lands reflected in our model. This may reflect the impacts of reporting bias since turtles near roads are more likely to be reported than turtles far from roads (Kadmon et al. 2004). In addition, although turtles can be attracted to urban areas such as roads and residential lawns because they provide attractive nesting sites, these areas are also ecological sinks that actually are associated with increased turtle mortality (Grgurovic and Sievert 2005; Steen et al. 2006; Beaudry et al. 2008). Finally, the effect of temperature on Blanding's turtle is uncertain. The projected temperature increases within the timeframe of our study are not likely to exceed the physiological tolerance of adult turtles but they may be significant enough to exceed the range of temperatures under which eggs can successfully incubate (Mockford et al. 2006).

Our study reaffirmed what has been demonstrated in prior research, in that future land use and climate changes will only exacerbate what are already challenging landscape level conditions (Pomara et al., 2013; Hamilton et al., in review). The strategy of restoring habitat corridors, while intuitively appealing and relatively feasible given the tools available to land managers, may be limited given that land use change has already isolated many protected areas. Substantial investments would be necessary to significantly improve connectivity even under static climatic conditions (Hamilton et al.; in review). Our results indicate that the velocity of climate change is too high to mitigate climate change effects solely by improving habitat connectivity.

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Table 5. Amount of moderately suitable habitat for Blanding's turtle in priority protected areas under the combinations of high/low emissions climate and baseline/pro-agriculture (Proag) economic policy scenario.

	Moderately Suitable			
	Low climate		High climate	
Area (ha)	Baseline	Proag	Baseline	Proag
Upper range	48,150	50,150	22,425	24,875
Lower range	0	0	0	0
Total	488,500	494,150	60,925	72,475
Mean	1,954	1,976	243.7	289.9

Table 6. Amount of highly suitable habitat for Blanding's turtle in priority protected areas under the combinations of high/low emissions and baseline/pro-agriculture (Proag) economic policy scenario.

	Highly suitable			
	Low climate		High climate	
Area (ha)	Baseline	Proag	Baseline	Proag
Upper range	6,000	7,100	0	0
Lower range	0	0	0	0
Total	30,025	39,000	0	0
Mean	120.1	156	0	0

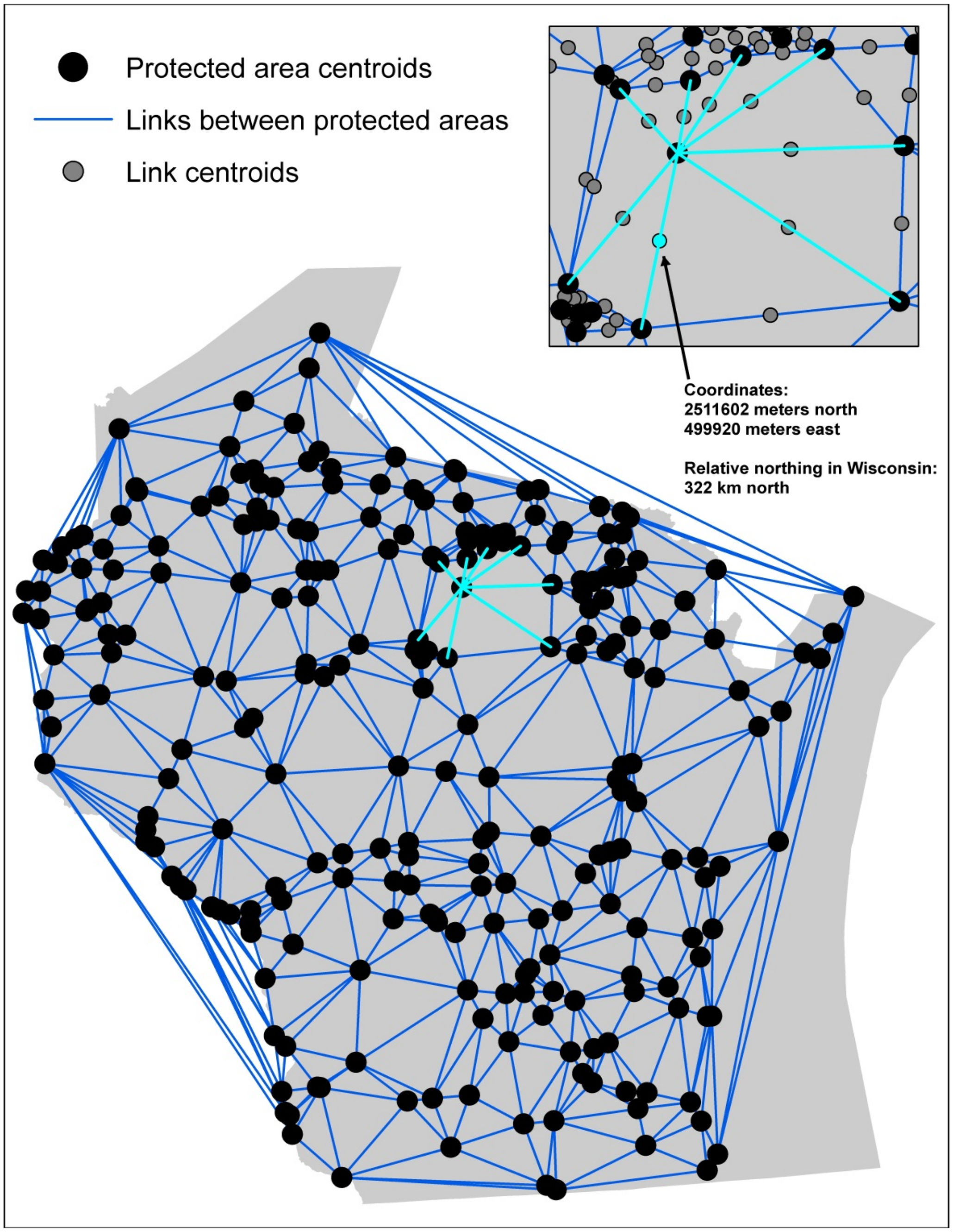

Figure 13. Triangulated irregular network representing priority protected areas for Blanding's turtle in Wisconsin. The inset shows the connections to relevant neighbors for one protected area. The centroid for one link is highlighted and the northing and relative northing within Wisconsin for that centroid are provided.

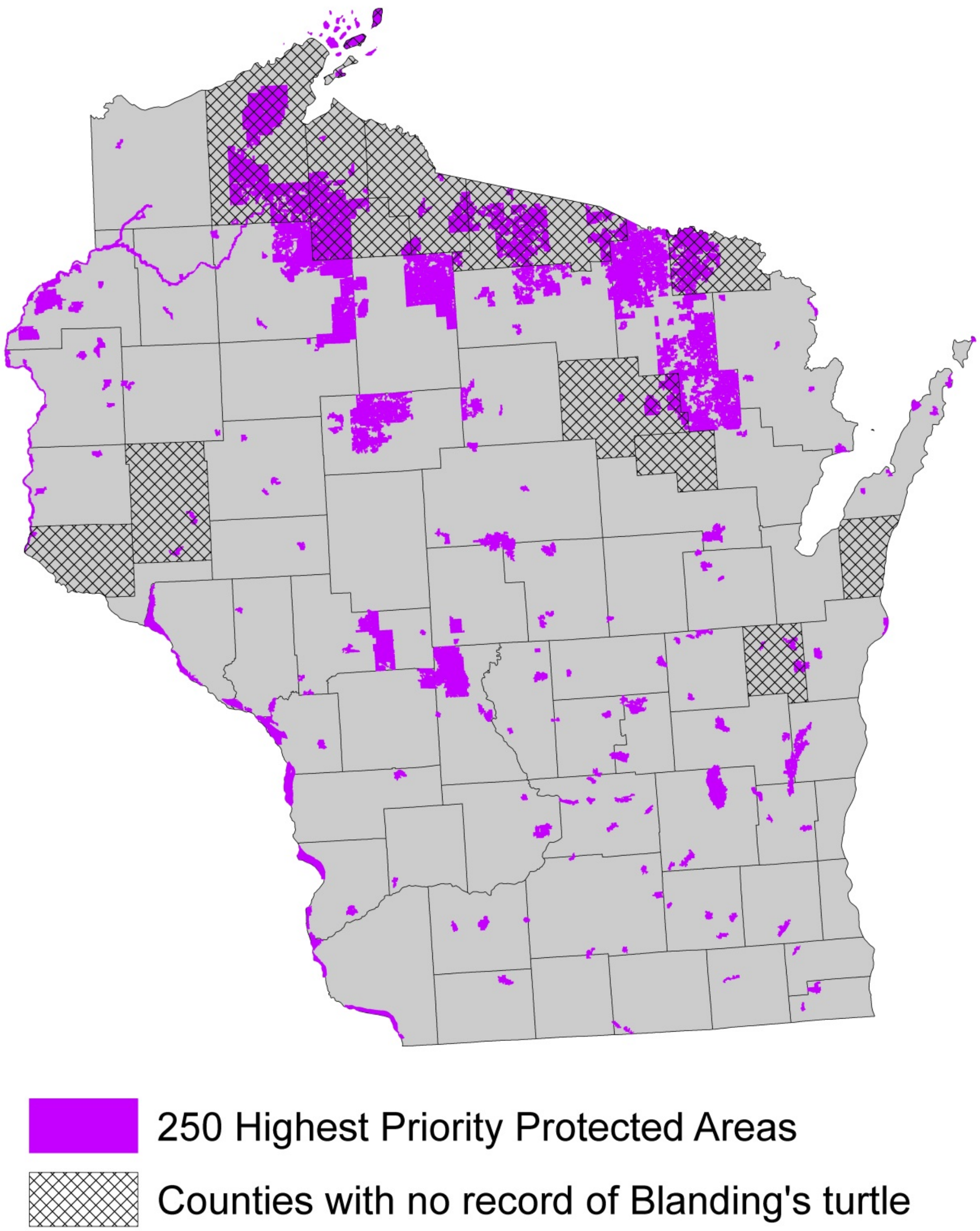

Figure 14. Map showing the distribution of the 250 highest priority current protected areas for the Blanding's turtle and those counties with no recorded occurrence of the species.

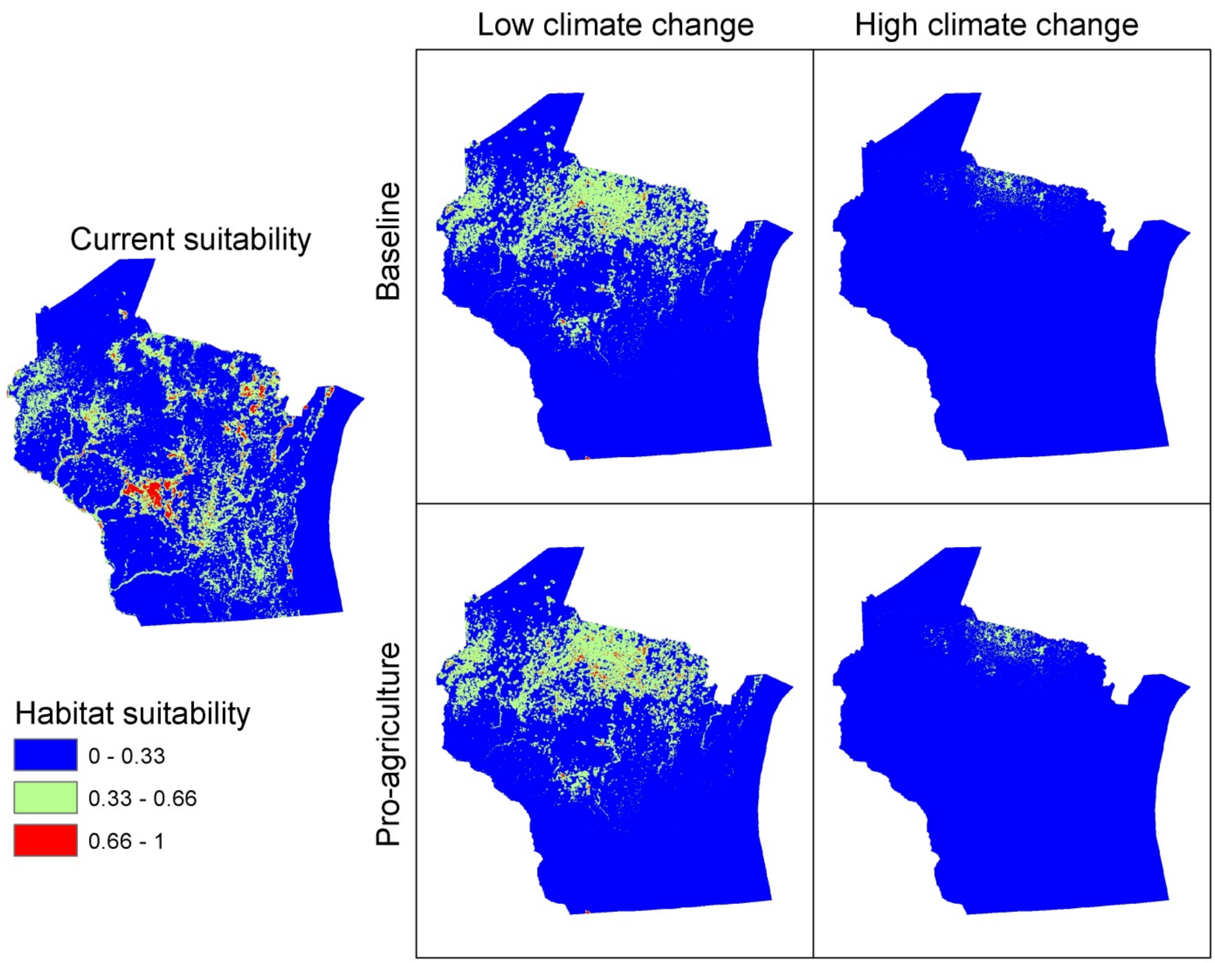

Figure 15. Habitat suitability maps for Blanding's turtle under current conditions and 4 combinations of future land-use and climate scenarios projected for the 2050's.

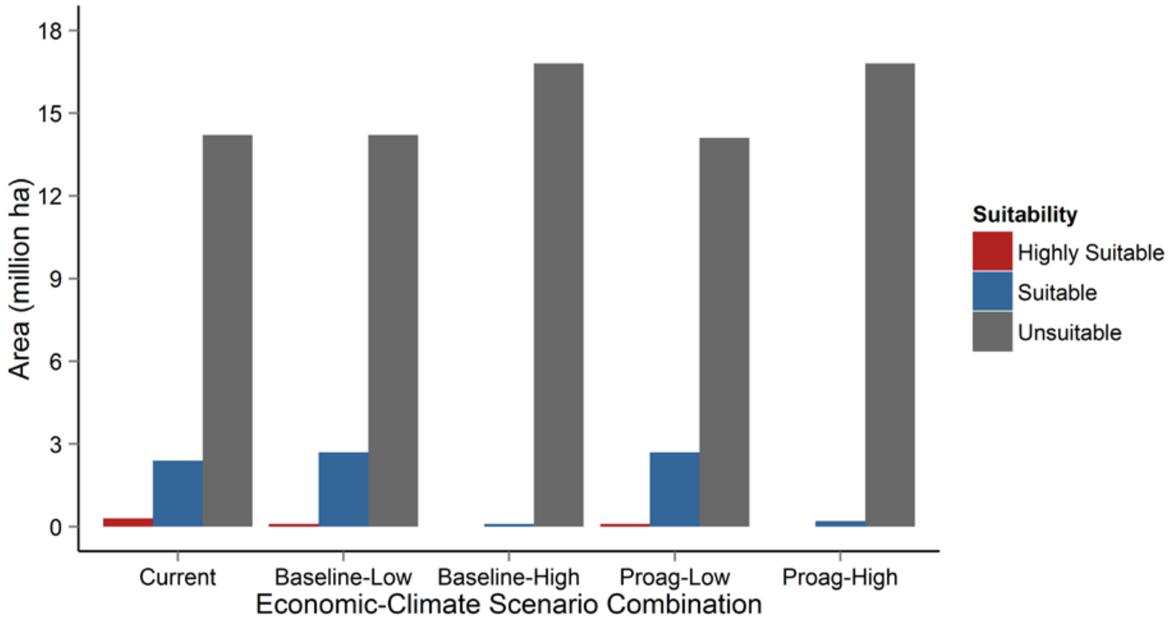

Figure 16. Areal distribution of habitat suitability for highly suitable, suitable, and unsuitable habitat within the entire state of Wisconsin.

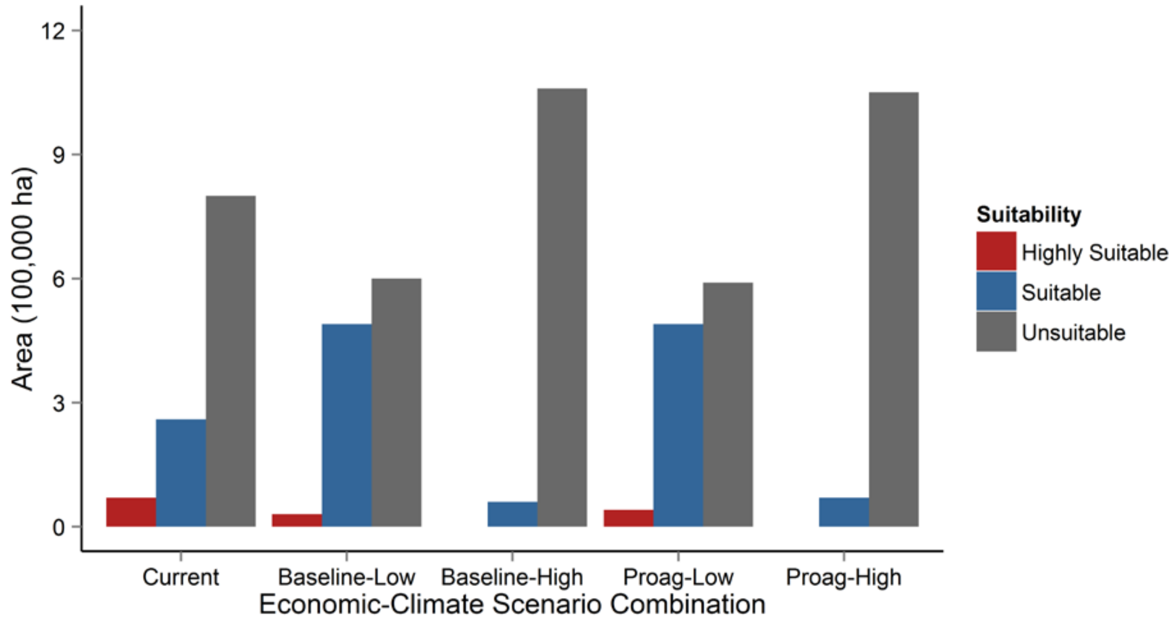

Figure 17. Areal distribution of habitat suitability for highly suitable, suitable, and unsuitable habitat within the 250 most important protected areas for Blanding's turtle in Wisconsin.

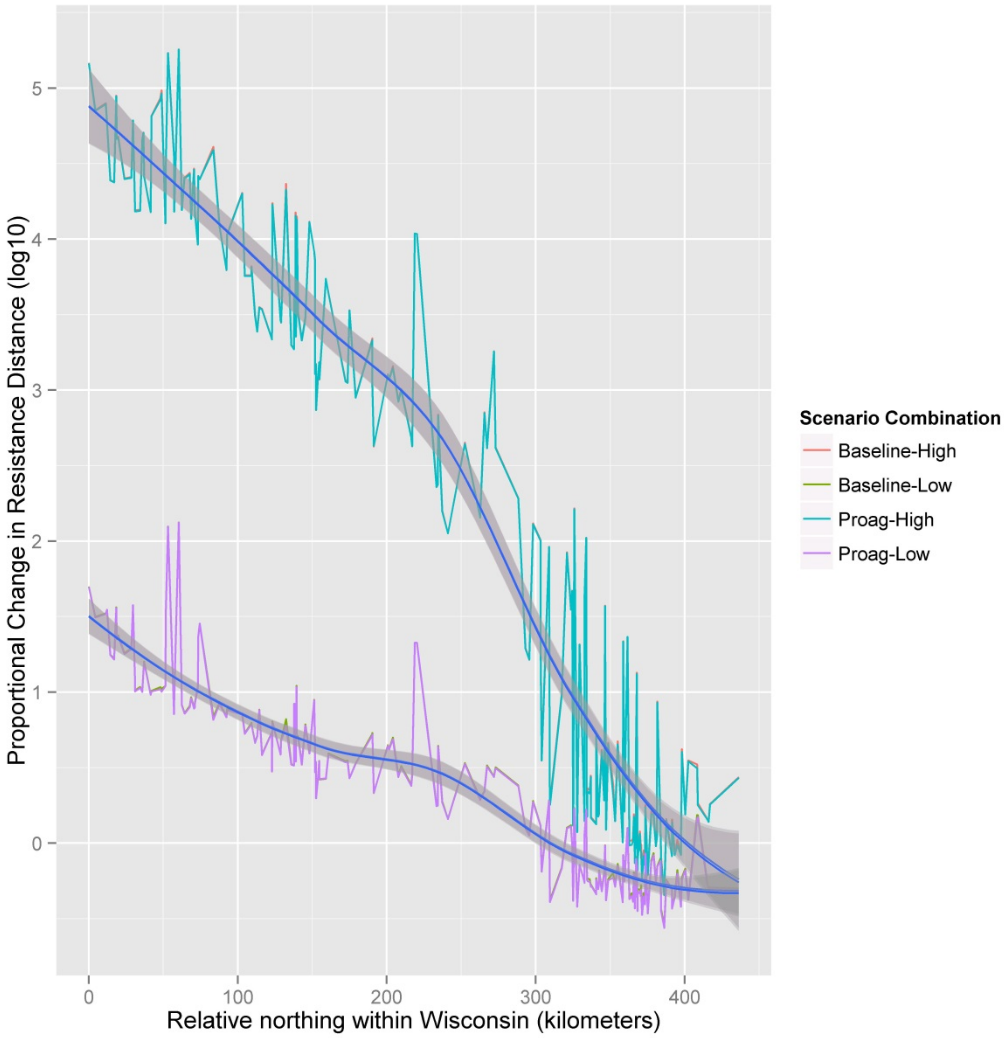

Figure 18. Comparison of the proportional change (log base 10) in resistance distance among scenario combinations. The x-axis represents the northings of the centroids for connections between protected areas ranging from south to north in Wisconsin. The values on the y-axis reflect the proportional change in resistance distances between the protected area pairs. The values on the axis are the power to which 10 is raised (i.e.; 3 = 10^3,or indicates a 1,000-fold increase in landscape resistance to movement) for the proportional changes in resistance distance. Given the log scale, the rate of change in resistance distance is exponentially higher for the more southerly connections.