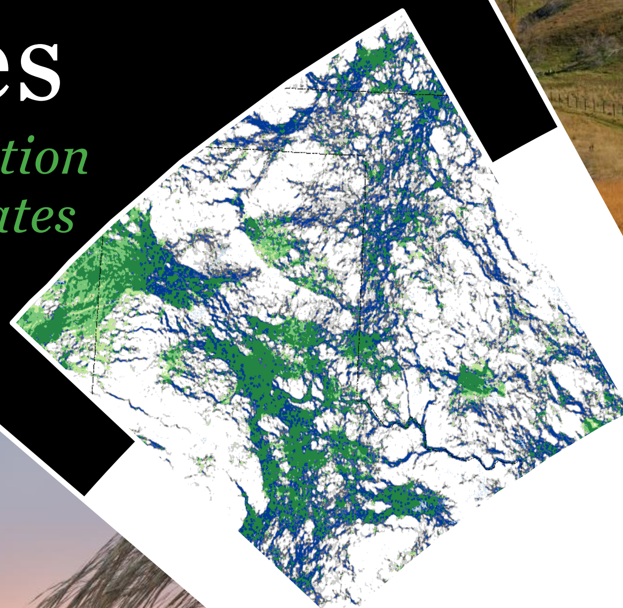
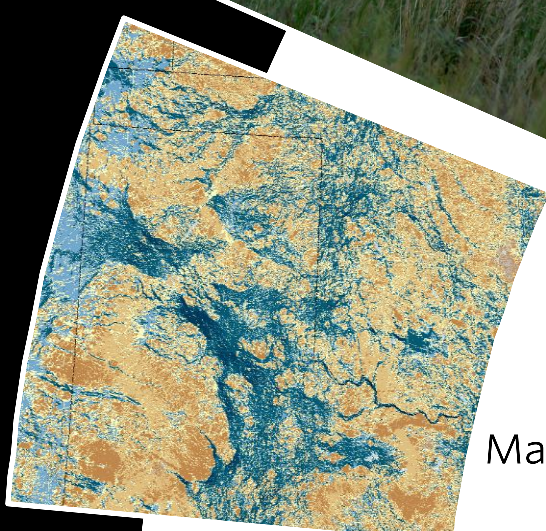
Resilient *and* Connected Landscapes

For Terrestrial Conservation in the Central United States





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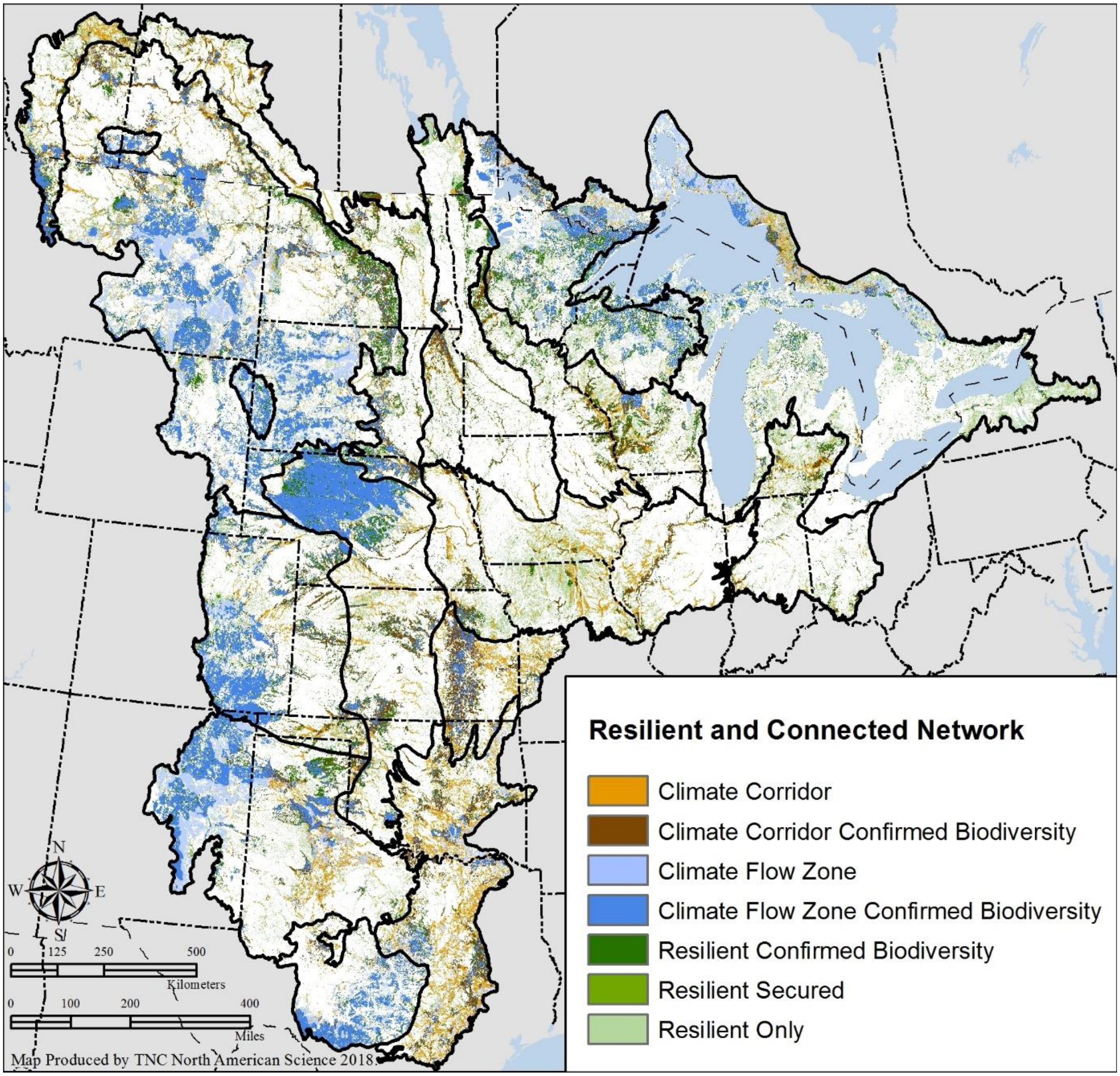
The Nature Conservancy

NOTE TO STEERING COMMITTEE MEMBERS AND OTHER REVIEWERS:

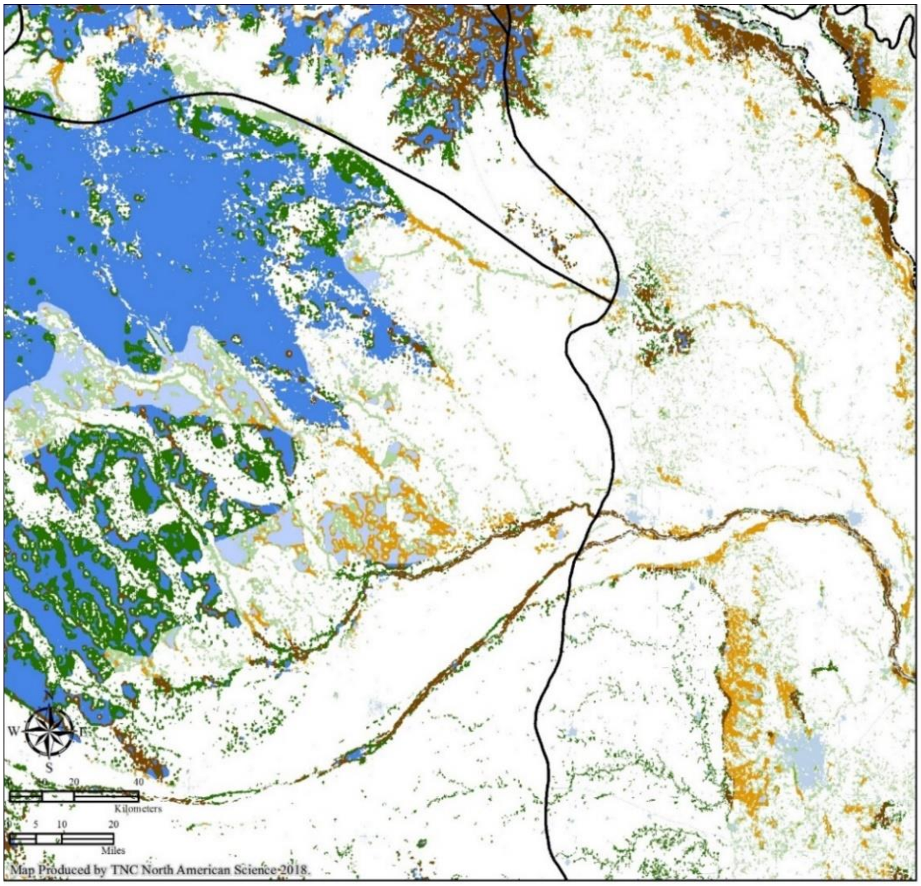
Once again, thanks for your help in developing these analyses and maps!

This is a review draft that includes the introduction and background, methods, and results. Importantly, it does not yet include key components that we will add following reviewer feedback on the core products – these added sections will include an executive summary, and a discussion/conclusions/"guide to applications" section. If you have thoughts on how to distill this information for the executive summary, or early adapter case study examples that we can include in the guidance section, please include those in your review comments. Thanks!

REVIEW DRAFT – January 14, 2019



The Resilient and Connected Network for the Great Lakes & Tallgrass region, and the Great Plains.



Resilient and connected landscape definitions (example above is a zoom-in of Zoom-in of north-eastern Nebraska).

Resilient Area: a place buffered from climate change because it contains many connected micro-climates that create climate options for species.

Resilient Area with Confirmed Diversity: a resilient area that contains known locations of rare species or unique communities based on ground inventory. Unconfirmed areas may contain the same species.

Climate Corridor: a narrow conduit in which movement of plants and animals becomes highly concentrated, often a riparian channel or linear ridgeline.

Climate Corridor with Confirmed Diversity: a climate corridor that contains known locations of rare species or unique communities based on ground inventory. Unconfirmed areas may contain the same species.

Climate Flow Zone: areas with high levels of plant and animal movement that is less concentrated than in a corridor, typically an intact forested or grassland region. Flow refers to the movement of species populations over time in response to the climate.

Climate Flow Zones with Confirmed Diversity: a climate flow zone that contains known locations of rare species or unique communities based on ground inventory. Unconfirmed areas may contain the same species.

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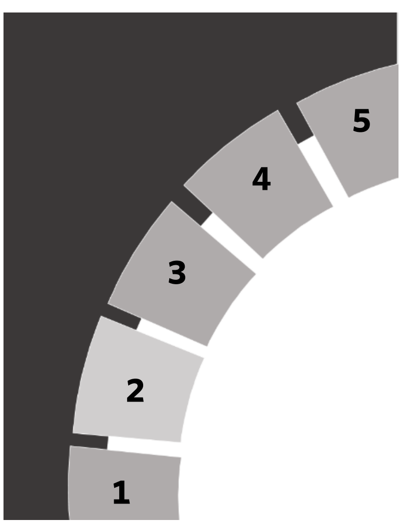
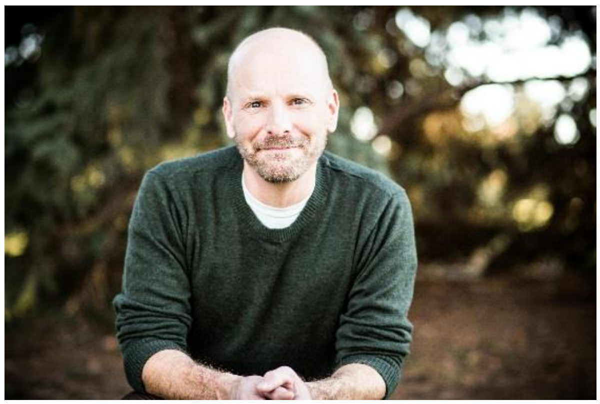
About the Cover:



1. © Harold E. Malde.
2. Map of Climate Flow. Zoom-in in Northern Texas.
3. © Jason Whalen/Big Foot Media. Kankakee Sands, Indiana.
4. Map of Climate Flow Classified. Zoom-in in Northern Texas.
5. © Chris Helzer/TNC. Loess Hills, Nebraska.

The authors dedicate this report, and our continuing work to highlight places where conservation actions are most needed to sustain the wild and wandering flow of nature, to our dear friend and colleague Dr. Brad McRae.



The power of imagination makes us infinite

– John Muir

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We also extend our thanks to Esri for making ArcGIS software freely available to The Nature Conservancy. The compelling maps in this report are a testament to Esri's ongoing generosity and support for protecting biodiversity.

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CHAPTER 1

INTRODUCTION

Objective and Background

The climate is changing. Insurance company records indicate that the last four decades have seen an increasing number of billion-dollar storms, droughts, floods, and fires. People pay these costs and adjust to the changes through a variety of approaches, from simple changes like shifting the way in which they heat their homes or irrigate crops, to collaborative efforts to prepare their communities for intense storms, droughts, or fires. In the face of increasing climate-related risks, some people may move to new locations, either by choice or by necessity. Plants, animals, and all the other species that comprise a region's biodiversity are also exposed to these changing conditions. The ability to find climatic refuge in a natural stronghold, or move to more suitable locations, are essential conditions that allow plants and animals to persist and thrive under rapid climate change.

In past eras of climate change, plants and animals shifted their distributions by gradually colonizing and establishing in new territory, finding suitable microclimates that allowed them to persist, and producing offspring that continued the process. The problem is that this takes time – generations - but the climate is changing faster than at any time in recorded history, and the landscape is fragmented by roads, intensive agriculture, dams, development, and other barriers to movement.

How do we ensure that the Great Plains and Great Lakes & Tallgrass Prairie regions will continue to support their vast botanical diversity and iconic wildlife? That nature will continue to provide ecosystem services such as pollinators for crops, productive grazing lands, forest products, and the clean water we depend on? And, that our grandchildren will experience places still directly linked to distinctive ecosystems like the prairie-pothole wetlands, northern forests, and vast expanses of native grasslands? The idea of conserving moving targets, and sustaining the capacity for adaptation in place, requires that we update our thinking about where to invest in land protection.

To address this challenge, The Nature Conservancy (TNC) engaged two Steering Committees of scientists and resource managers from across the Central US and Canada to identify the places where nature's own natural resilience is likely to be the highest (Anderson et al. 2018 a & b). Following a methodology first applied to the Northeastern US (Anderson et al. 2016) we identified "resilient sites" – sites that we expect to be more likely to maintain biological diversity and ecological function as the climate changes. These "biodiversity strongholds" are more variable in topography, and more locally connected by natural landcover, than other sites with similar soils/underlying bedrock. By identifying resilient sites across all types of bedrock and soil in a region, we hoped to create a blueprint for conserving ecosystem health over the long term, even as the specific character, species assemblages, and ecosystem structure at those sites changes over time. A map of **resilient** sites that **represent** the full range of geophysical settings can guide our investments in protection and management, and increase the odds that plants and wildlife will be able to find sites that meet their specific requirements as conditions change.

A resilient site offers multiple options to species, however, sustaining biological diversity and ecological processes across the region is more likely if the resilient sites are embedded in a larger network of connected natural areas that allow for dispersal and movement between sites. In this report, we examine the pattern of land use and barriers, and evaluate where dispersal and other movements are most likely across this highly variable section of the US and southern Canada. We recognize that the character of the landscape varies from the vast areas of grasslands in parts of the Great Plains to the agricultural corn belt of the Great Lakes region, to the northern forests of the upper Midwest, and that the options and character of movement corridors shift with different land use patterns and both anthropogenic and natural barriers. In our work to map connectivity across this landscape, we identify both broad areas of unrestricted flow zones, and more constrained areas where small corridors play essential roles in supporting species movements. Our assessment method also gives additional weight to connections that are likely to traverse climate gradients, such as northward trajectories, and movements toward cooler riparian areas.

In our integration of the resilient sites with the patterns of landscape connectivity, we identify resilient sites that also play a role in supporting either broad flow patterns or high rates of flow through narrow corridors. In this process, we maintain a focus on representation of different geophysical settings, as connectivity is only an advantage if it provides access to necessary site conditions. Our final step is to integrate known strongholds for biodiversity – if we know a place supports important biodiversity elements now, that increases our confidence that it will support important biodiversity in the future. We recognize that a site may be topographically diverse and in a relatively natural landscape, but the site may still have lost species diversity due to some stressor, such as competition from invasive species, or reduction in natural processes like fire or grazing. At the scale with which we are conducting these analyses, we are not able to obtain the data required to make site-by-site comparisons of current condition and diversity. However, we can incorporate known sites of biodiversity as mapped in other assessments. Our intent in incorporating these datasets is to identify resilient sites more likely to have long term biodiversity value the come both from their capacity to support adaptation in place (due to the site's diversity of microsites and local connectedness) and through acting as sources of dispersers moving to other sites.

This work to integrate site resilience, landscape connectivity, and biodiversity is described in the following chapters:

2. Site Resilience: This chapter briefly describes the counterpart reports *Resilient Sites for Terrestrial Conservation in the Great Lakes and Tallgrass Prairie* (Anderson et al. 2018a) and the parallel assessment for the Great Plains (Anderson et al. 2018b). These reports describe the concepts and metrics for estimating the relative resilience of a site and evaluate the status of protected lands in the region with respect to representation of geophysical settings and site resilience. We review the concepts to provide context for understanding how we integrate site resilience with landscape connectivity; readers familiar with these assessments can skip this chapter.

3. Landscape Permeability: This chapter describes our efforts to understand and map the permeability of the landscape and identify patterns of flow and connectivity across it. It begins with a review of the literature on species range shifts, highlighting key results and response patterns that guide our approach. The methods section describes our continuous ("wall-to-wall") method for quantifying and mapping the potential of areas across these landscapes to support species movement based on landcover in combination with anthropogenic and natural barriers. Next, we describe our methods for incorporating responses to climate change (i.e., favoring movement pathways that follow climate gradients) into the connectivity models.

4. Biodiversity: This section describes our methods for prioritizing resilient areas that contain rare species, or have been identified as a priority by ecoregional, regional, or state conservation planning efforts.

5. Resilient and Connected Conservation Networks: This section integrates resilience, flow, and diversity to develop a connected network of sites that both represents the full suite of geophysical settings and has the configuration and connections necessary to support the continued rearrangement of species in response to change.

CHAPTER

2

SITE RESILIENCE

Climate change is expected to alter species distributions, modify ecological processes, and exacerbate environmental degradation (Pachauri & Reisinger 2007). To offset these effects, the need is greater than ever for strategic land conservation. Conservationists have long prioritized land acquisitions based on rare species or natural community locations (Groves 2003). Now, they need a way to set priorities that will conserve biological diversity and maintain ecological functions, despite climate-driven changes in community composition and species locations (Pressey et al. 2007). We devised such an approach to identify potential conservation areas based on geophysical characteristics that influence a site's resilience to climate change.

Geophysical Settings

Geology defines the available environments and determines the location of specialist species. In the Central US, limestone supports Great Lakes coastal fen plants, rare snails, and cave fauna, whereas dry sand plains support species adapted to acidic soils and fire. Geophysical variables (geology, latitude, and elevation) explain 92% of the regional-scale variation in the species diversity of the eastern states and provinces, far more than climate variables do (Anderson & Ferree 2010). Because biodiversity is so strongly correlated with the variety of geophysical settings at the scale of states and ecoregions, conserving the full spectrum of geophysical settings offers a way to maintain both current and future biodiversity, providing an ecological stage for a different set of species, which turnover through time (Beier & Brost 2010).

Geophysical diversity as a surrogate for species diversity has a long history in conservation planning (e.g., Hunter et al. 1988, Faith & Walker 1996, review in Rodrigues and Brooks 2007), and recently it has been recognized for its potential role in conservation planning under climate change (Schloss et al. 2011, Lawler et al. 2015, Anderson et al. 2015). We used different aspects of geophysical diversity for different purposes: geological representation to capture species diversity, and topographic and elevation diversity to identify places that have the maximum resilience to climate change.

Characteristics that Impart Resilience

Our use of the term site resilience is distinguished from ecosystem or species resilience because it refers to the capacity of a geophysical site to maintain species diversity and ecological function as the climate changes (definition modified from Gunderson 2000). Because neither the site's species composition nor the range of variation of its processes are static under climate change, our working definition of a resilient site is a structurally intact geophysical setting that sustains a diversity of species and natural communities, maintains basic relationships among ecological features, and allows for adaptive change in composition and structure. Thus, if adequately conserved, resilient sites are expected to support species and communities appropriate to the geophysical setting for a longer time than less resilient sites.

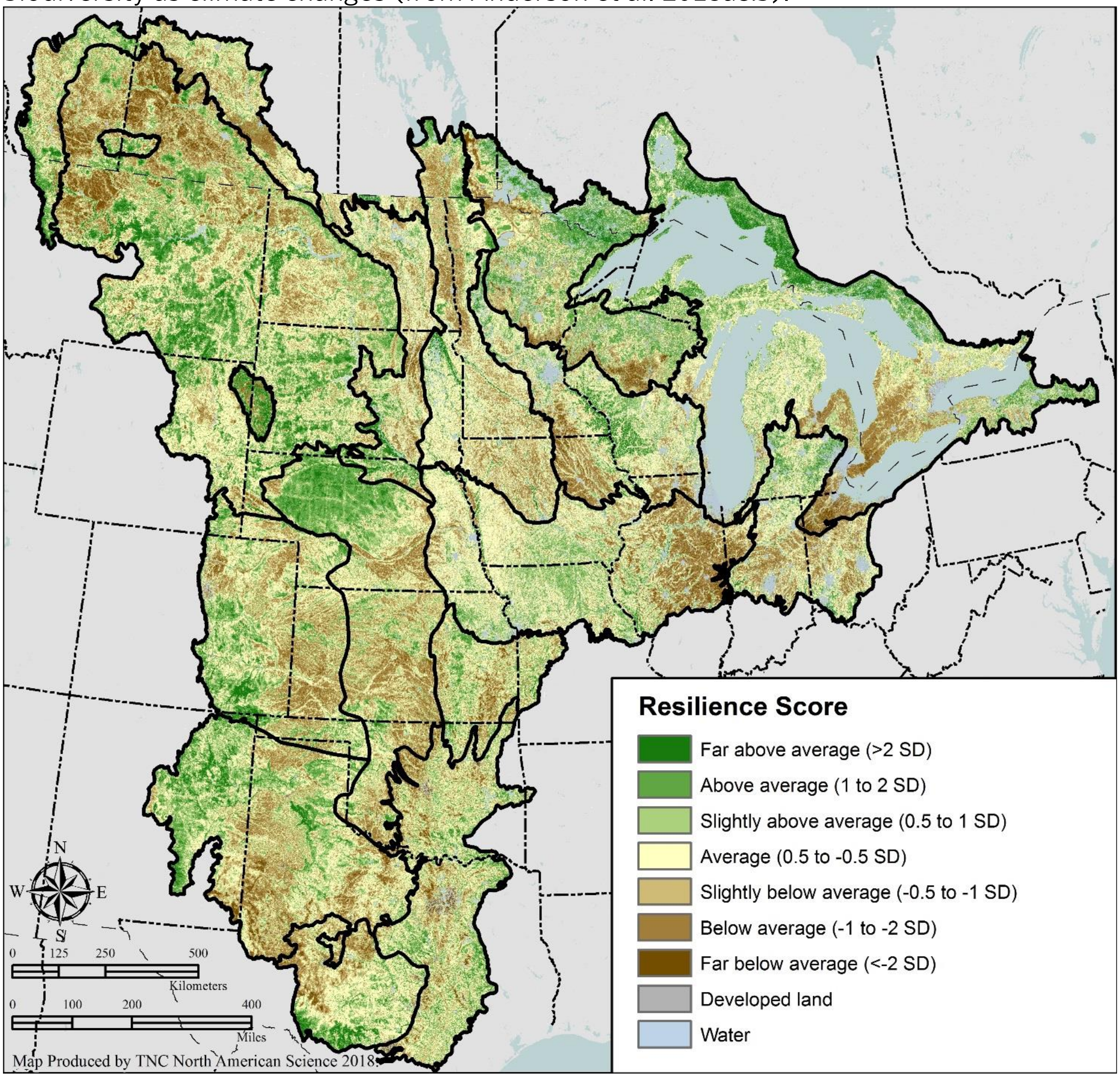
We developed a method to estimate site resilience as the sum of two metrics: landscape diversity (i.e., diversity of topography and range of elevation in a site and its surrounding neighborhood) and local connectedness (i.e., permeability of a site's surrounding land cover). Using a geographic information system (GIS) we calculated these metrics for every 30-m cell in the Northeast United States and Atlantic Canada and used the results to estimate the site resilience of specific places.

Landscape diversity, the variety of landforms created by an area's topography, together with the range of its elevation gradients, increases a site's resilience by offering micro-topographic thermal climate options to resident species, buffering them from changes in the regional climate (Willis & Bhagwat 2009, Dobrowski 2010, Ackerly et al. 2010) and slowing down the velocity of change in location needed to track changes in climate (Loarie et al. 2009). Under variable climatic conditions, areas of high landscape diversity are important for the long-term population persistence of plants, invertebrates, and other species (Weiss et al. 1988, Randin et al. 2008). Because species shift locations to take advantage of microclimate variation, extinction rates predicted from coarse-scale climate models that fail to account for topographic and elevation diversity have been disputed (Luoto & Heikkinen 2008, Wiens & Bachelet 2010).

Local connectedness is a measure of the permeability of an organism's local surroundings, defined as the degree to which the surroundings are conducive to movement, dispersal, and the natural flow of ecological processes (definition modified from Meiklejohn et al. 2010). A highly permeable landscape promotes resilience by facilitating local movements, range shifts, and the reorganization of communities (Krosby et al. 2010). Accordingly, measures of permeability such as local connectedness are based on landscape structure: the hardness of barriers, the connectedness of natural cover, and the arrangement of land uses. In this work we describe a generalized form of terrestrial permeability that will vary in terms of appropriateness for any given species, depending on specific habitat requirements, movement potential, and sensitivity to human disturbance.

A climate-resilient conservation portfolio includes sites representative of all geophysical settings selected for their landscape diversity and local connectedness. We developed a method to identify such a portfolio. First, we mapped geophysical settings across the entire study area. Second, within each geophysical setting we located sites with diverse topography that were highly connected by natural cover. Using this information, we identified places that could serve as strongholds for diversity both now and into the future (Figure 2.1, from Anderson et al. 2018a&b).

Figure 2.1. Site resilience for the Central US. Areas in yellow are comprised of cells with an "average" estimated resilience score based on their landscape diversity and local connectedness as compared to others on the same geophysical setting and in the same ecoregion. Areas in green score above average, or "more resilient." Areas in brown had below average scores, and are expected to be less able to support biodiversity as climate changes (from Anderson et al. 2018a&b).



CHAPTER
3

LANDSCAPE PERMEABILITY

Maintaining a landscape that facilitates range shifts for terrestrial species

Objective and Background

Maintaining a connected landscape is the most widely cited strategy in the scientific literature for building climate change resilience (Heller & Zavaleta 2009). While it makes intuitive sense that species must have the ability to move in order to adjust to a changing climate, it is less clear how we design a network that facilitates change and adaptation over time while conserving the full range of biodiversity. The interplay between range shifts, local persistence, changing habitat suitability, and evolving populations remain poorly understood despite a rapid increase in research on these topics.

The goal of this section is to describe several mechanisms by which climate change leads to species range shifts, and to illustrate how those shifts can be influenced by the condition of the landscape through which species must move. This information underlies our spatially-explicit assessment of relative permeability across the Central US America. Our intent is to produce a map of connectivity "assets" that we expect will facilitate range shifts for terrestrial species so that this essential process can be incorporated into strategies for land protection and management.

Introduction

The history of the Earth has been characterized by dramatic shifts in climate leading to radical shifts in the range of species. At the dawn of the Eocene 55 million years ago, as global temperatures rose 5-6^0 C, cypress trees and alligators had moved as far as the high Arctic (Krosby et al. 2010). More recently, much of North America and Eurasia were repeatedly ice-covered during more than 2 million years of glacial cycles, causing species to continually shift their ranges. While they did so at different rates and in different directions, all the species that currently occur in formerly glaciated areas like the northern Great Lakes region expanded their ranges north to occupy their current ranges in the last 12,000 years. Despite these dramatic changes during the last glacial period, there were remarkably few known extinctions (Botkin et al. 2007).

We are now facing a period of even more rapid climate change where temperatures are changing at roughly ten times the average rate seen during recovery from historical ice ages. We assume many species will again respond by shifting their distributions to respond to changing conditions. Indeed, in response to present climate change, species' ranges are already shifting northward at rates of 10-20 km per decade and upslope at rates of 11 m per decade (Chen et al. 2011). However, our world is very different than it was 10,000 years ago. Human development has radically altered the landscape, causing fragmentation of natural land and creating obstacles to dispersal (Fischer & Lindenmayer 2007, Haddad et al. 2015). ***How do conservationists ensure that the landscape remains permeable enough to allow such large-scale movements, particularly by species that disperse slowly or may be hindered by a variety of factors?*** In this report, we address this question for terrestrial landscapes in the Central US.

Climate Change and Range Shifts

Species respond to changes in climatic conditions in several ways: 1*) individuals actively or passively adapt* their behaviors or habitat niches while staying in the same location, perhaps showing a change in phenology (timing) of seasonal activities such as budburst or migration, choosing shadier nesting sites, spending more time in cooler riparian areas, or shifting some activities to cooler times of the day; 2) *populations evolve* new climate tolerances as a result of natural selection favoring individuals with traits that provide an advantage under changing conditions. We often think of evolution as happening very slowly, but as was demonstrated by studies of the Galapagos Island finches (Weiner 1995, Visser 2008), traits can shift rapidly in response to dramatic changes in climatic patterns. Many species, from trees to corals, are known to have genetic differences in their populations related to differences in climate experienced across the species range (Davis and Shaw 2001). Such genetic differences at the population level may facilitate rapid adaptation as a way of responding to climate changes.

Range Shifts

One of the most well-studied way that species may respond to climate changes is by 3) *populations and species shifting their distributions*. Shifts in location can occur when climate change leads to previously unsuitable habitat becoming suitable for population persistence, which allows colonization of new habitat patches outside of the current range of a species. Distributional shifts can also result from differential survival of individuals within the current range, for instance individual propagules surviving preferentially in shadier or moister areas, causing a local population to shift in elevation or to a more shaded aspect. Shifts in location may be essential for species with narrow climatic tolerances experiencing rapid and extreme climatic changes in their current ranges, or for species that depend on naturally patchy landscape features with little variety in microclimate, such as isolated wetlands.

The term "range shift" refers to the permanent colonization and subsequent spread into a new geography by a species through dispersing juveniles, propagules, seeds, eggs, adults, or other life history stage. The "pressure" of dispersal is driven by the number of source populations and the abundance of reproducing individuals within them. The probability of reaching the new habitat is partially a function of dispersal pressure and partially of the permeability of the landscape through which the species must disperse. Additionally, a successful colonization requires that enough propagules arrive, establish, and reproduce in a suitable new area to persist for more than one generation. Thus, range shifts are population processes that occur over generations, and these shifts are sensitive to variation in three factors: dispersal pressure and vagility of dispersers, the permeability of the landscape, and the suitability of the receiving habitat for the species in question.

A range shift, for example a northward range expansion, may be accompanied by permanent extirpation in some other parts of the range, with the resulting range retraction reflecting locally failed recruitment due to unsuitable habitat or other factors. If extirpations occur, but new and climatically suitable areas are not reachable by potential dispersers due to the loss and fragmentation of habitats, and/or the low dispersal capacity of a species, then the concern is that species will fail to colonize suitable habitats, ultimately resulting in increased extinction rates (Walther et al. 2002). This has been found to be the case globally for some bumblebee species no longer found in the southern part of their historic ranges but not yet expanding their ranges northward (Kerr et al. 2015). Indeed, the modeled dispersal ability of a range of taxa including North American trees (Loarie et al. 2009 quoted in Iverson and McKenzie. 2013) and mammals (Schloss et al. 2012) suggests that many species are unlikely to be able to keep pace with predicted rates of shifts in the distribution of suitable climate. However, to date, few examples of this extinction phenomenon have been documented and some evidence suggests that, at least in the short term, communities are tolerating climatic variation and/or incorporating new species without necessarily losing their current species (Roth et al. 2014). For example, Swiss alpine areas which are demonstrably sensitive to climate change (Walter 2016) have yet to show any local extinctions apparently due to the abundance of local microclimates (Roth et al. 2014).

Dispersal and Dispersal Pressure

Whether species arrive in a new location that may be suitable for colonization depends on the population size and the build-up of dispersal pressure, the ability of individuals to disperse, and the proximity, relative abundance, and size of patches of suitable habitat (Primack & Miao, 2002). Research has shown that dispersal limitation is often more important than recruitment limitations for sustaining populations of forest plant species (Honnay et al. 2002). Some animals are capable of long-distance dispersal in a single generation such as birds and large mammals. Smaller mammals and herptiles are more likely to be restricted to shorter dispersal distances and therefore dependent on adjacent suitable habitats. However, smaller-bodied animals tend to reach sexual maturity earlier and often have higher fecundity. Assuming dispersing individuals can successfully establish in new habitat patches, these attributes allow the population to rapidly produce the next generation of dispersers for further expansion. Plants have evolved a host of mechanisms for dispersing their propagules: wind and water, hooks that hitchhike on feathers and fur, or seeds consumed by birds, ants, and small mammals. Bryophytes, ferns, and orchids, have tiny wind-dispersed propagules that can effectively disperse over long distances and thus make up a greater proportion of the non-endemic flora in remote locations such as New Zealand (Meurk et al. 1995). Some species are particularly dependent on rare and inherently stochastic events for long-distance dispersal, whether by natural vectors, or inadvertently assisted by ubiquitous and constant human movement - in the mud of car tires or dust on freight trains or the cargo of ships (Higgins et al. 2003). Snails, for instance, are normally very short-distance dispersers, but can extend their ranges great distances when their larvae are caught in the tarsi of birds.

The greater the number of propagules, and the greater the number of vectors (in the case of chance long-distance dispersal), then the greater the likelihood of *some* successful dispersals leading to successful colonization (Rouget & Richardson 2003). High levels of dispersal pressure facilitate geographic spread regardless of biological traits, although the latter play a role in establishment and colonization (Pysek et al. 2009). Because the abundance of propagules is typically dependent upon the number, size, and demographic characteristics (such as density, age structure, and fecundity) of local source populations, these attributes are essential ingredients influencing successful dispersal and ultimate range shifts. Populations not producing surplus juveniles are unlikely to move, and thus, facilitating range shifts is directly tied to traditional conservation practices aimed at maintaining robust populations and source areas of breeding habitat with adequate resources for successful population growth.

<u>Landscape Permeability: The Influence of the Medium through which the Organism is Dispersing</u>

Successful dispersal and colonization is a numbers game, a question of enough dispersers beating the odds to get to new habitat. Thus for terrestrial dispersers, a key factor in determining the likelihood of a range shift to an unoccupied territory is the nature of the intervening landscape. To maintain genetic connectivity among populations through dispersal, a few individuals occasionally reaching a new area might be enough, as even a few new genes can make a difference in an isolated population (Soule & Simberloff 1986). However, for dispersal to promote range shifts to places not yet occupied by the species is likely to require a higher frequency of successful dispersal events, with sufficient individuals dispersing to initially establish a population, followed by continued arrivals of new dispersers over time to prevent stochastic extinction. Under these circumstances, the extent to which the intervening landscape facilitates or impedes successful dispersal can be critical in determining whether a range shift occurs.

The relationship between specific landscape characteristics (e.g., land use, land cover, elevation, or landform) and the likelihood of dispersal is often quantified on a species-specific or taxa-specific basis through the concept of *resistance*. Resistance refers to the degree to which specific landscape features facilitate or impede the movement of a species. It can be thought of as the willingness of an organism to cross the habitat type combined with the likelihood of surviving such a crossing.

The resistance of a landscape to successful dispersal may be due to anthropogenic changes in land use. Satellite images of the Atlantic Seaboard or California's Central Valley make it obvious that human land use changes have created "islands" of native habitat, similar to forests in the East now surrounded by development, or patches of grassland in the Midwest surrounded by intensive agriculture. It seems intuitive that species in these native habitat patches may have difficulty successfully crossing a landscape of development or agriculture, or be reluctant to cross due to increased exposure to risk or higher mortality from predators or traffic collisions. Indeed, many studies have confirmed that movements among patches of habitat are influenced by, or dependent on, the characteristics of the intervening matrix (Ricketts 2001, Hokit et al. 1999, Haddad et al. 2015). For instance, Richard and Armstrong (2010) tracked radio-tagged forest passerines (*Petroica longipes*, in New Zealand) in a fragmented agricultural landscape and found that juveniles move preferentially through native forest, followed by plantation forest, then shrubland, then pasture, with a marked hesitancy to cross the latter. Observations such as these have given rise to a plethora of "landscape resistance" models that simulate species movement through a landscape based on the degree of resistance expected from different land use/land cover types relative to the preferred type. In these GIS models, resistance values are assigned to individual cells in a raster layer based on the cell's land cover type and the expected degree of resistance. Such a GIS resistance model, discussed later in this document, forms the basis of the continuous permeability models we used to model potential range shifts.

The resistance of a landscape to successful dispersal may also be ecological, i.e. a function of natural discontinuities in the landscape. The most obvious is dispersals of terrestrial species across ocean. The emergence of the Beringia Land Bridge during the Ice Age allowed dispersal of species (including *Homo sapiens*) to the Americas. The emergence of the Panamanian Isthmus allowed North American species to expand their ranges to South America. Large-scale landscape features that are highly contrasting habitat with surrounding land, such as deserts surrounding mountains, can also create "sky islands." This phenomenon has led to marked diversification of species on the mountains of the Basin and Range country of America's West (McCormack et al. 2009). On a smaller scale, some species dependent on moist conditions such as prairie potholes or riparian areas are likely find the surrounding dry prairie landscape resistant to dispersal; species that prefer dry prairie may experience resistance when the prairie is invaded by shrubs and trees. On the other hand, the pattern of high genetic variation in red maple, even in northern parts of its range, suggests that the northern Appalachian Mountains were not a significant barrier in the most recent post-glacial climate warming. Rather, it is likely that the contemporary range of red maple is the result of a combination of frequent long-distance dispersal events, only minor topographic obstacles, and diffuse northern refugia near the ice sheet (Gugger et al. 2008). Of course, some features of the landscape may facilitate more frequent successful dispersals, both ecological, such as river valleys or long mountain ridges, and anthropogenic, such as roadside verges. For example, purple loosestrife dispersed north along ditches of the I-95 corridor (Stuckey 1980), and New England cottontail populations in Maine remain connected via roadside verges and power line right-of-ways.

Any feature that facilitates or impedes movement is likely to have different impacts on different species; however, long-term studies on the effect of anthropogenic fragmentation have shown remarkably consistent negative effects across many taxonomic groups. Haddad et al. (2015) synthesized the results of fragmentation experiments spanning multiple biomes, multiple scales, five continents, and 35 years, and demonstrated that habitat fragmentation reduces biodiversity by 13% to 75% and impairs key ecosystem functions. Across all studies, they found generally consistent decreases in the abundance of birds, mammals, insects and plants, and reduced species richness of arthropods, birds, butterflies and plants and this accumulated over time as a fragment became more ecologically isolated (i.e., there was marked resistance to species movement between fragments resulting in both local extinctions and immigration lags). This overall pattern emerged despite complex patterns of increases or declines in abundance of individual species with various proximate causes such as release from competition or predation, shifts in disturbance regimes, or alteration of abiotic factors. Haddad et al. (2015) conclude that although the effects of fragmentation are mediated by variation in traits across species (e.g., rarity, trophic level, dispersal mode, reproductive mode, movement behavior), this primarily helped to interpret variation around the overarching pattern of consistent reductions in richness and abundances across many species. If there is a positive side to these findings it is that the effects of fragmentation can be reversed by restoring the appropriate natural cover and adding a corridor which can produce up to 50% more movement (Gilber-Norton et al. 2005).

<u>Establishment and Colonization</u>
Successful range shifts also depend on the conditions found in the new patches of suitable habitat available for colonization. In addition to the factors influencing the number of dispersers arriving, whether species successfully colonize a new location depends on the breadth of their habitat tolerances, the rapidity with which they can reproduce, their success in competing with or escaping predation by native fauna or flora, and the amount of available habitat. In general, successful establishment is more likely for rapidly reproducing habitat generalists (including many of our "weedy" species) that can quickly establish and are more tolerant of spatial and temporal variation in the environment.

The more specific, uncommon, and distant the appropriate habitat is for any given species, the lower the frequency of chance dispersal into such habitats. It is easier to imagine that the arctic flora and fauna of dispersed mountaintops is a relic of a glacial period when such habitats were much more widespread than of long-distance dispersals since deglaciation. Furthermore, some specialist species have evolved lower dispersal abilities, thus stacking the odds against being stranded or landing in inhospitable habitat. The evolution of flightlessness in island-inhabiting birds is a familiar but not unique example. Likewise, although aerial ballooning is a common means of passive dispersal for many spiders, habitat specialist spiders in fragmented landscapes are much less likely to balloon (Bonte et al. 2003). Nevertheless, decades of inventory by botanists, have shown a remarkable consistency of flora on apparently isolated small-patch habitats like alkaline fens, shale slopes, serpentine outcrops, and limestone cliffs that, because of the discontinuousness of the underlying geology, are difficult to explain as remnants of once widespread populations.

The Evidence for Range Shifts in Response to Climate Change

For a range shift to be attributed to climate change it must occur when dispersing species gain access to suitable habitat that had previously been unavailable due to climatic conditions. This can happen directly through changes in mean temperature or short-term climate extremes that allow a population to expand northward, or through climate-mediated interactions with other species that remove competitive barriers. However, understanding and predicting climate-driven range shifts is complex, in part because species tolerances are not fixed. Davis and Shaw (2001) reviewed tree taxa shifts in latitude or elevation in response to changes in Quaternary climate and stressed the complexity of climate changes. Summer and winter temperature, seasonality, and the distribution and amount of precipitation, all changed in different ways that produced new combinations of climate, not simply geographic displacements of the same climate. Although range shifts clearly occur, they questioned the assumption that taxa are likely to disperse seed and establish in new regions more readily than they evolve a new range of climate tolerances, or even that the tolerance range for a species remains temporally stable given wide intraspecific variation. This is important because it is not clear how rapidly plant populations can track climatic changes (Corlett and Westcott 2013).

The evidence is clear that rapid periods of climate change in the Quaternary saw many shifts in species distributions. As the climate cooled, the distribution of tree species such as red spruce in North America and Scots pine in Europe shifted south, and as the ice sheet receded they moved north again 150 km/century (Davis & Shaw 2001). Considering that much of the northern third of the US was covered by ice miles thick for millennia multiple times, every species that now lives in this region had to arrive in the last 12,000 years by shifting their ranges northward. The fact that there were so few extinctions associated with all these massive displacements of species over broad areas of North America has been dubbed the Quaternary conundrum. A hypothesis put forward to explain this for North America is that the landscape remained highly connected by natural cover allowing species distributions to track the climate (Botkin et al. 2007). It may also be that the north-south trending mountain ranges and lack of major landscape impedances to northward movement facilitated these shifts, which is consistent with the assumed mechanism of differential extinction and colonization rates at northern versus southern range edges (Honnay et al. 2002). There is some evidence that northern Europe has been slower to recover its former species diversity in part because of the obstacles posed by east-west mountain ranges such as the Pyrenees and the Alps (Adams & Woodward 1989).

Evidence for contemporary range shifts in response to climate has now been documented for over 1000 species as populations shift their geographic distributions in one of four ways: 1) upslope toward higher elevations, 2) northward toward cooler latitudes, 3) downslope towards moist riparian areas or valley bottoms, and 4) locally toward suitable microclimates associated with changes in aspect or vegetation cover. The evidence for upslope and northward movements is strong and consistent across many taxa groups and across several continents (Table 3.1, Walther 2002, Chen et al. 2011) and there are increasing indications of the other responses as well. As we review the evidence for these four responses, it is helpful to remember that a variety of ecological factors may create variation in a species response to climate: competitive release, habitat modification, or changes in amounts and patterns of precipitation, snow cover duration, water balance, or seasonality (Groffman et al. 2012). Any of these may cause range shifts to differ substantially from straightforward poleward or upslope movement largely driven by temperature (Garcia et al. 2014). These factors, coupled with relatively gradual rates of temperature change with latitude in the tropics, mean that detecting and predicting range shift patterns in the tropics will be much more difficult. In this report we focus on temperate regions.

Table 3.1. Summary of elevational and latitudinal observed range shifts from 30 studies (modified from Chen et al. 2011). ORS = observed range shift, SE = standard error. "Margin" refers to whether the studies focused on changes in the upper leading margin or average distribution. The list of sources for Chen et al. 2011 is located at http://www.sciencemag.org/content/333/6045/1024/suppl/DC1

Observed Elevational Range Shifts

Taxa group	# of Species	Margin (Upper / Avg.)	Duration (yrs.)	Mean ORS (m)	Min ORS (m)	Max ORS (m)	SE of ORS (m)	Temp change (C)	# Studies
Invertebrate	554	U/A	20-42	37.7	7.4	108.6	12.3	0.62	5
Fish	15	U	25	32.7	32.7	32.7	12.7	0.65	1
Herptiles	30	A	10	65.3	65.3	65.3	24	0.24	1
Birds	326	A/U	11-25	-4.75	-19.3	7.6	9.3	0.795	4
Mammals	37	U/A	25-88	50	31	69	71.6	3.05	2
Plants	495	U/A	22-94	62.4	21	89	16.2	0.97	7

Observed Latitudinal Range Shifts

Taxa group	# of Species	Margin	Duration (yrs.)	Mean ORS (m)	Min ORS (m)	Max ORS (m)	SE of ORS (m)	Temp change (C)	# Studies
Invertebrate	332	U	8-25	59.1	7.9	104.2	15.9	0.6	3
Fish	15	U	25	47.2	47.2	47.2	15.4	0.65	1
Birds	361	U/A	12-31	24.2	3.6	46	19	0.49	4
Mammals	9	U	25	22.4	22.4	22.4	38.4	0.45	1
Algae	37	A	50	61.4	61.4	61.4	31.6	0.74	1

Upslope Movement: Recent studies have detected upslope elevational range shifts for five taxonomic groups with magnitudes ranging from 6.1 m to 11.0 m per decade (Chen et al. 2011, Parmesan & Yohe 2003, Lenoir et al. 2008). Upslope movement appears to be greatest among plants and herptiles, followed by mammals, invertebrates, and fish (Table 3.1). Responses by birds have been inconsistent (Tingley et al. 2012) although an eight-year monitoring study in Switzerland found significant upslope shifts in communities of birds (42 m), butterflies (38 m) and vascular plants (8 m), with rates of community changes decreasing with altitude in plants and butterflies (Roth et al. 2014). For immediate climate relief, moving upslope is more efficient than moving latitudinally.

Although evidence for upslope movement seems overwhelming (Lenoir et al. 2010) and it may be the dominant way in which many species are accommodating climate change in the short term, there are obvious limitations to it as a long-term strategy for all species. First, it only works for species where upslope movement of suitable habitat is an option – some species require a lowland physiographic setting, such as wetland-associated species or plants that need deep, moist, nutrient-rich soils. Second, the extent of available upslope habitat is limited in many regions where the slopes are either so gentle or so distant that they offer little practical climate relief to most species, or the hills are so small that their summits are rapidly reached as species shift upslope.

Northward Expansions: Chen et al's (2011) review demonstrates that northward movements are also well documented (754 species across five taxa), and they appear to be ubiquitous across the northern hemisphere (Table 3.1). Studies have found latitudinal range shifts averaging 6.1 km to 16.9 km northward per decade depending on the taxa and region (Chen et al. 2011, Parmesan & Yohe 2003, Lenoir et al. 2008). It is likely that latitudinal expansions will be the predominant long-term strategy of most species in response to climate change, and this is largely concordant with the evidence of historic range shifts in response to previous periods of rapid climatic change. Despite fears that the movements of some species will lag behind the rate of climate change, Chen et al. (2011) found that nearly as many studies of observed latitudinal changes fell above as below the expected rate suggesting that mean latitudinal shifts are not consistently lagging behind the climate.

Downslope Movements: Upslope and northward movements correlate with temperature change, but many species are more limited by moisture availability than temperature. Downslope regions collect moisture and feature microclimates that may be significantly cooler and more humid than immediately surrounding areas (Olsen et al. 2007). A recent study examining the response of eastern trees to climate change found changes in moisture availability had significantly stronger near-term impacts on vegetation dynamics than changes in temperature (Fei et al. 2018). Species seeking moisture tend to move downslope towards the water-collecting regions at the base of slopes or into moist riparian areas.

Species showing downslope shifts have been well documented (Archaux 2004, Popy et al. 2010). A survey of such range shift studies suggests that while roughly 65% of species have shifted their ranges upslope, 25% have shifted their ranges downslope, and 10% have not changed their mid-range positions (Lenoir et al. 2010). Similarly, a global review of the literature (Parmesan & Yohe 2003) suggests that about 20% of species have adjusted their ranges towards lower elevations. Long-term downhill shifts in the optimal elevations of plant species has been shown for California, apparently in response to decreased climatic water deficit (Crimmins et al. 2011). Our own spatially-explicit climate resilience analysis (Anderson et al. 2013, Anderson et al. 2018a&b) identifies many slope bases and riparian corridors as key landscape features ("resilient sites") because of the many climate options they provide, especially in relatively flat landscapes.

Moisture and temperature differences between riparian areas and their surrounding landscapes may be substantial, with riparian areas being 5-20^{0} C cooler and 10-15% higher in soil moisture (Yeakley et al. 2008, Bennie et al. 2008). Thus, riparian areas are expected to provide microclimatic refugia from warming and drought for many species, particularly those that tolerate wet conditions (Seavy et al. 2009). Additionally, riparian areas naturally connect many landscape features, and this unique attribute make them logical and perhaps vital elements in any conservation network designed to maintain landscape resilience and facilitate range shifts. It is not surprising that the use of riverine corridors in a connectivity network has been proposed as a strategy for maintaining climate resilience (Fremier et al. 2015). Although they comprise a minor proportion of the landscape, riparian areas are structurally diverse and more productive in plant and animal biomass than adjacent upland areas, supplying food, cover, and water for a large diversity of animals. Riparian areas serve as migration routes and connectors between habitats for a variety of wildlife (Manci 1989), particularly within highly modified landscapes (Hilty & Merenlender 2004).

Riparian areas that span climatic gradients might provide natural corridors that species could use to track shifting areas of climatic suitability and have been called riparian climate corridors (Krosby et al. 2014). In the Northeast; however, the temperature gradients *within* most riparian or floodplain corridors was found to be very small (Anderson et al. 2015), averaging 0.14^0 C on the Coastal Plain to a high of 1.3^0 C in the Central Appalachians. This suggests that although there is ample incentive for species to move into downslope or riparian areas, there may be less of a climatic benefit from moving directionally along the corridor.

The numerous studies documenting preferential use of naturally vegetated riparian zones by a wide range of species of terrestrial wildlife (e.g., Hilty & Merenlender 2004) do not necessarily demonstrate the use of such areas for long-distance dispersal. For example, a study of riparian zones as dispersal corridors for herptiles found that for many species dispersal along the riparian zone was likely impeded by species-specific habitat needs such as inundation patterns, appropriate adjacent upland habitats, or fishless pools (Burbrink et al. 1998). However, riparian habitat tends to include a higher density of wetlands in comparison to upland areas and thus on average will provide suitable breeding sites in closer proximity to one another, leading to an increased probability of successful dispersal of wetland fauna in riparian areas over time. Additionally, the rivers, themselves, clearly play a role in dispersal of fish and other aquatic species, and in the passive dispersal of plants in riparian zones whose propagules survive inundation (Jansson et al. 2005). Such dispersal is, of course, driven by the movement of the water downhill so could not be expected to contribute much if any to dispersal upslope or poleward in response to increasing temperatures, except on rivers that flow north.

Where intact riparian areas or bottomland floodplains occur in developed or converted landscapes it may be difficult to separate questions of the preferential use of riparian zones for movement from the use of strips of natural landscapes. In the Southeast Coastal Plain, for example, extensive, intact, large river floodplains contrast strikingly with the surrounding landscape providing both habitat and natural movement corridors. Radio-tracking studies have documented the use of these riparian areas for movement of large mammals in Georgia (Cook 2007) and it seems likely that many wildlife species would use a riparian corridor for dispersal if that is the only safe natural cover in the wider landscape (Fremier et al. 2015). Such corridors may allow multi-generational dispersal to occur between larger heterogeneous areas of protected habitat if the corridors include appropriate breeding habitat, and this may be particularly important for species with limited dispersal abilities. Further, it is postulated that ensuring riparian corridors right up to headwaters can provide critical over-the-ridge links for dispersal across watersheds (Olson & Burnett 2013). It is less clear in a landscape were the riparian areas occur within intact natural land cover whether upland terrestrial species would preferentially disperse along a river valley rather than along ridge lines or contour lines that have their preferred cover or food sources.

Microclimates and Rates of Change: The fourth and perhaps most common alternative for species is to find suitable habitat nearby, moving a small distance to take advantage of a local microclimate. Species experience climate at extremely local scales (centimeters to meters) and the available moisture and temperature in the near-ground "boundary layer" can differ greatly from the local average (Geiger et al. 2009). Thus, a topographically diverse landscape is experienced by its resident species as a heterogeneous mix of microclimates many of which might be suitable for persistence even where the average background climate appears unsuitable. Landscape-based climatic variation can be substantial, on par with or greater than the 1.5°C warming expected for the future. Studies where climate data loggers are placed across gradients of slope, aspect and elevation have found maximum temperature differences over 20^0 C (Surgett et al. 2010, Dobkin et al. 1987) and 15-20% fractional soil moisture differences (Yeakley et al. 1998, Bennie et al. 2008). In Southern Appalachian watersheds, topography explains 40% to 72% of the variation in near-surface soil moisture (Yeakley et al. 1998). Even microscale patches of suitable climate may allow persistence of species over long time scales and serve as a source for recolonization or further dispersal. For example, Roth et al. (2012) found that although lowland plants in Switzerland were moving upslope, alpine plants were persisting in place, finding suitable habitat within a few meters due to the highly varied surface of the landscape. It is probable that both lowland and alpine plants were taking advantage of all suitable microclimates, and that the apparent difference in response was due to the difference in availability of upslope microclimates.

The examples above support the idea that stable refugia, effectively decoupled from the regional climate, may offer longer-term respite in a climatically variable regional landscape. Proximity to such refugia seems to have helped some species survive the last glaciers and then served as dispersal points for populations post glaciation (Provan & Bennett 2008). Besides the better studied refugia of southern and eastern Europe, it now appears there were also cryptic refugia in northern Europe in areas of sheltered topography with stable microclimates (Steward & Lister 2001). Mapping the distribution of topographically-derived microclimates is key to our work identifying climate resilient sites (Chapter 2).

Some types of cool climate refuges occur at scales larger than the topographic microclimate, such as orogenic rain shadows, lake effects, cold air pooling, or maritime cooling. In the short term, ephemeral climate refuges that offer the coolest maximum temperatures when regional temperatures are relatively high may provide relief to transient species or even populations (Gollan et al. 2014). In eastern North America there is evidence of a refugium along the coast of Maine where the maritime influence allowed spruce to survive even when the relatively dry and warm climate of the hypsithermal prevented spruce survival inland (Schauffler & Jacobson 2002). These populations were likely the source of the rapid expansion and dominance of spruce through the rest of the state about 1000 years ago during a region-wide shift to cooler and moister conditions.

The localized movement of populations to utilize microclimates is so restricted that it probably does not qualify as a range shift unless accumulated small movements add up to a directional change (i.e., upslope). However, utilization of microclimates may explain how poor dispersers can track the changing climate within larger-scale range expansions. Chen et al. (2014) hypothesized that the real and apparent lags in species response to climate may reflect the topographic and microclimatic complexity of mountainous terrain, and they emphasized the need for finer-resolution analyses with additional topographic and geological detail if we are to understand the actual climates that species are tracking. Loarie et al. (2009) noted that owing to topographic effects, the velocity of temperature change varies spatially, and is lowest in mountainous areas, which may effectively shelter many species into the next century. Coarse-scale climate models are mapping something distinctly different from very local climates experienced by species on the ground, and this can lead to erroneous conclusions about extinction rates or the rates of dispersal needed to track climate change (Willis and Bhagwat 2009). This is good news because the rates of change in species distributions documented in recent decades as well as in the last post-glacial period do not match the estimated rates necessary to keep up with predicted climate changes at a coarse scale (e.g., 300-500 km/century as per Anderson and Shaw 2001, or one to two orders of magnitude faster as per Honnay et al. 2002). There are probably limits to the buffering effect of microclimates as the only precisely dated extinction of a tree species, *Picea critchfieldii*, during the Quaternary coincided with the exceptionally rapid warming during the transition from the Last Glacial maximum to the Holocene about 15,000 years ago.

Conclusion: The evidence for contemporary range shifts provide support for the four types of responses discussed above, but the studies are unavoidably focused on cumulative short distance dispersals and leave many unanswered questions about long distance jumps to suitable habitat, or responses to broad-scale episodic extreme disturbances. It is likely that we simply do not understand enough about the actual dispersal of most species, particularly the low frequency but long-distance dispersals that could explain dispersal rates during the last post-glacial period (possibly aided by hurricanes or large migrating herbivores) being much higher than what is being observed or modeled currently. In plants especially, observed average seed dispersal distances cannot account for the rapid northward migration that occurred in many species (Reid's Paradox; Clark et al. 1998). In fact, Cain et al. (1998), modeling the seed dispersal curve for *Asarum canadense*, a woodland herb dispersed by ants, concluded that an empirically calibrated diffusion model would show that since glaciation *A. canadense* should only have traveled 10-11 km from its glacial refugia, but in fact it moved hundreds of kilometers during this time. They conclude that most woodland herbs and many other plant species have such limited dispersal capabilities that occasional extreme dispersal events and mechanisms are the only explanation for their documented migration. Griffin and Barret (2004) concurred after using a genetic analysis to study the range expansion of the woodland herb *Trillium grandiflorum*, finding that it likely survived in two refugia in the southeastern US during the last glaciation and that post-glacial recolonization of northern areas was characterized by long-distance dispersal beyond what the plant appears capable. Higgins et al. (2003) suggest that long-distance dispersal events in plants are usually caused by non-standard means of dispersal, that is, a plant seed adapted to wind dissemination may get lodged in the feathers of a bird and transported much farther than wind would take it. Although such infrequent long-distance dispersal events are likely to allow some species to move much further and faster than evidenced by their typical form of dispersal, it is important to recognize that for many taxa, especially specialist species, for such events to result in locating and establishing on a patch of uncommon habitat is highly improbable without animal or human intervention.

Habitat Fragmentation and Climate Change

Current species' responses to climate change may differ from historic responses because humans have modified the landscape, fragmenting habitats and disrupting natural movements. Fragmentation of the landscape has been shown to slow dispersal and hamper the successful colonization of new habitat by creating resistance to population movement through the intervening matrix. Above, we reviewed the 35-year synthesis by Haddad et al. (2014) of the world's largest and longest running fragmentation experiments, which clearly demonstrate a resistance to movement, and/or high mortality rates, for all major taxa groups when crossing contrasting or unfamiliar land cover. Further, colonization and radio-tagged movement studies reinforce these observations with respect to tree species (Honnay et al. 2002), forest passerines (Richard & Armstrong 2010), and many other taxa. Climate change does not appear to fundamentally alter the effects of fragmentation other than to intensify the need for species to move in response to directional changes in climate and to concentrate those movements on upslope or northward gradients, or downslope into local riparian areas. We assume that the responses to fragmentation are equally applicable to these features, and that even the dispersal of species to nearby suitable microclimates is facilitated by a connected landscape through which organisms can move easily.

Implications for Conservation

This review of the mechanisms for range shifts in response to climate change highlights several points. Range shifts are a well-documented species response to past episodes of climate change and there is abundant evidence that they are already occurring in response to current climate change. Range shifts are detectable as expansions upslope and northward, as downslope movement into riparian areas, or as very local movements to take advantage of proximate microclimates. The magnitude and pattern of the current response is likely to differ from historic responses because humans have modified the landscape, fragmenting habitats and disrupting natural movements. These modifications create resistance that may prevent species from colonizing new habitat, instead creating range constrictions.

The conservation implications of this review guide the work presented in the rest of this report. Some of the findings reinforce well-known conservation design principles while others call for new mapping and integration methods to identify the spatial implications of climate-driven range shifts. These are organized below as ten key points with the first three focused on facilitating dispersal, and the next seven on facilitating dispersal under climate change. When appropriate, we link the points directly to the resilience analysis (Anderson et al. 2016, 2018 a & b).

1. It all starts with dispersal pressure. It is essential that there are <u>source areas</u> for all species to produce enough propagules to ensure a high probability of successful dispersal. To function well as source areas, sites need to have the requisite size and optimal breeding conditions for that species. For many species, we believe sites that

are above-average in local connectedness and landscape condition as defined by the resilience analysis (Anderson et al. 2016) are likely to correspond with source areas.

2. The quality of the landscape through which species disperse can impede the movement of species, and there is strong and consistent evidence for this across all taxa. There is good justification for using resistance-based models to identify potentially important flow zones, linkages and pinch points and solid evidence to support conservation efforts aimed at facilitating movement by maintaining or restoring suitable natural cover. This can often be accomplished through compatible land management over broad areas in conjunction with high natural cover in specific areas.

3. All species, especially habitat specialists, need sufficient suitable habitat to meet their specialized needs both now and in the future. This argues for the importance of the representation of all geophysical settings in a variety of climate zones as part of the resilient portfolio concept. For specialists, the uncertainties of occasional long-distance range expansions make the need for refugia even more important.

4. Upslope range shifts in response to climate are already widespread and are likely important for short-term reprieve, particularly in landscapes with low topographic relief. Mapping, prioritizing, and conserving connections to available upslope features are important when designing a local landscape for climate resilience.

5. Northward range extensions have been detected in over 500 species. Mapping permeability across north-south gradients should highlight areas for explicit conservation focus. This may include pinch-points that play a disproportionally important role in facilitating range shifts, diffuse areas that offer many options for movement, or low-flow areas that could be improved through restoration.

6. Downslope areas and riparian corridors are unique in that they offer cool, moist microclimates and also connect many features on the landscape. Wherever possible they should be used to connect resilient sites or already conserved land. Prioritizing downslope regions based on their degree of permeability and flow should identify areas that likely play an essential role in facilitating range shifts because they are cooler, wetter and more intact.

7. Microclimate refugia can play a role in promoting long-term persistence and slowing the velocity of climate change. In the short term, a species may find refuge by moving upslope or to another aspect of a hillside or valley or to a rock and soil type that holds more or less moisture. Such opportunities are more likely in areas with higher landscape diversity, as defined by an analysis of resilience.

8. Over the longer term, some places are likely to play key roles as longer-term refugia. Some of these can be predicted based on microtopography or attributes that make their climates intrinsically more stable. Others may be harder to predict in advance, but this argues for ensuring a portfolio of conservation sites that includes geographic distribution, stratification by ecoregion, and geophysical representation.

9. Absolute contiguity of appropriate habitats may not be necessary and is in many cases impossible for most species, but proximity helps increase the odds of successful dispersal. The stepping stone concept makes sense. Even if we do not know and cannot

model how occasional long-term dispersal events occur, the evidence shows that after glaciation many specialist species with poor dispersal prospects somehow relocated to pockets of suitable substrate and climate.

10. Given the apparent importance of infrequent long-distance dispersal in accounting for the pace of past range shifts, we should not discount the importance of sites that are distant and seemingly disconnected from additional habitat if they are robust source areas for multiple species, especially for uncommon habitat specialists. Integrating known sites with confirmed rare taxa or high-quality examples of unique communities should provide the best starting point for the latter.

Regional Flow: Mapping Landscape Permeability

The Nature Conservancy's analysis of resilient sites in the Great Lakes, Tallgrass Prairie and Great Plains (Anderson et al. 2018 a & b) addresses many of the recommendations summarized in the previous section. This includes recommendations to: 1) identify potential intact habitat for species; 2) represent all geophysical settings in a variety of climate zones; 3) identify microclimate refugia in areas with higher landscape diversity; and 4) ensure a portfolio of conservation sites includes representation and geographic distribution of all geophysical settings within ecoregions. The previous studies stop short, however, of identifying a connected network of sites that includes the linkages and confirmed biodiversity features needed to facilitate range shifts. This report addresses those issues. Specifically, we develop methods to map the permeability of the landscape in relation to anthropogenic uses and barriers, we examine where needed latitudinal or slope movements are likely to concentrate, and we locate sites with confirmed biodiversity elements such as rare species or exemplary communities. Finally, we integrate these components into a single connected network designed to sustain diversity under climate change.

Introduction

The permeability of a landscape is a function of the resistance of its major elements and their spatial arrangement: the types and penetrability of barriers, the connectedness of natural cover, and the configuration of land uses. It is defined as the degree to which a landscape, encompassing a variety of natural, semi-natural, and developed land cover types, will sustain ecological processes and be conducive to the movement of many types of organisms (Meiklejohn et al. 2010). Our goal in understanding landscape permeability was to map it as a continuous surface, not as a set of discrete cores and linkages as might be used to map an individual species' movement between areas of suitable habitat (Fischer & Lindenmayer 2006, Beier et al. 2011).

Several approaches have been developed to create a continuous model of landscape permeability including: moving window (McRae et al. 2016), centrality (Theobald et al. 2012), resistant kernel (Compton et al. 2007), and wall-to-wall (Clark in Anderson et al. 2012 and Pelletier et al. 2014). The wall-to-wall approach is particularly suitable for modeling potential range shifts because it allows for the creation of multidirectional and omnidirectional connectivity maps illustrating flow paths and variations in the ease of movement across large regions. The results provide a continuous view of connectivity across a study area at the full original resolution and highlight pinch points, blockages, essential corridors and broad flow zones (Pelletier et al. 2014).

The mapping of permeability as a wall-to-wall surface is possible through the use of the software Circuitscape (McRae & Shah 2009), an innovative program that models species and population movements as if they were electric current flowing through a landscape of variable resistance. Circuit modeling is conceptually aligned with the concept of landscape permeability because it recognizes that movement through a landscape is affected by a variety of impediments, and it quantifies the degree and the directional outcomes of the compounding effects. One output is a “flow” map that shows the behavior of directional flows and highlights concentration areas and pinch-points. The results identify locally and regionally significant places where species range shifts are likely to be impeded by anthropogenic resistance, and that may warrant conservation.

“Flow” in an ecological sense refers to the gradual movement of plant and animal populations across the landscape over time. Populations expand when they produce a surplus of juveniles which disperse and colonize new habitat at a distance from their source point. Juvenile animals can walk, climb, fly, float, swim, glide, crawl or burrow their way to new locations, and plants have evolved a host of mechanisms for dispersing their propagules by taking advantage of many dispersal vectors such as wind, water, animals, and people. If the current habitat becomes unsuitable, but available suitable habitat exists nearby, a constant flow of dispersers helps ensure that the new habitat will be discovered and colonized.

Population responses to current climate change differ from historic responses because humans have modified the landscape, fragmenting habitats, and disrupting natural movements. Such modifications can create barriers that prevent species from colonizing new habitat, and may result in range constrictions in areas where range expansions were historically possible. Alternatively, the configuration of land uses can serve to channel population flow through a narrow corridor, increasing the importance of that corridor to maintaining flow. The goal of our mapping was to detect and quantify these patterns. By modeling how species populations in North America will likely migrate and disperse through the heavily modified landscape, we could identify where critical pinch points, blockages, or flow concentrations occur.

In a previous study (Anderson et al. 2016b), we compared the results of regional scale connectivity modeling in Eastern North America with results from 58 smaller scale studies. The results can be found in the section of that report called “Comparisons and Confirmation” and more completely in the report’s Appendix 1. We found that in spite of the scale and methological differences, our “wall-to-wall” methods produced similar results, particularly in modified landscapes where there were fewer available choices for movement through natural cover. Results were most similar between the regional flow models and species based movement studies, giving us confidence that species were likely to utilize the flow concentration areas identified by our methods. Results were least similar between studies that connected predeterminded habitat blocks, particularly when the spatial location of the blocks did not fall along any natural flow pattern. This suggested that prioritizing habitat blocks that are located within the natural flow patterns might be an effective way of maintaining movement between blocks. We will come back to this point in the later section on integration of flow, diversity and resilience.

Initially we modeled flow based solely on anthropogenic resistance, the product of which we refer to as ‘regional flow.” This model estimates population movement patterns of a generalized species based on the arrangment of human-modified barriers such as roads and development and the resistance they create. Our next step was to incorporate the influence and response to climate change directly into the model. This is presented in the susequent section entiled “Climate Flow.” Using evidence on how species are already repsonding to climate change, the climate flow model is simply the regional flow model with more weight given to flow pathways that provided cooler temperatures (upslope and northward) or higher moisture (downslope, riparian).

Circuitscape Model

All modeling of landscape permeability and regional flow was done using Circuitscape (McRae & Shah 2009). Circuit modeling recognizes that movement through a landscape is affected by a variety of impediments (resistances) and quantifies the degree to which these impediments will affect movement and the directional outcomes of the compounding effects.

The Circuitscape program calculates the amount of "current" moving directionally across a landscape based on an input grid of cells with values indicating their degree of "resistance." One output of the program, a current map, shows the behavior of directional flows, analogous to electric current flowing across a surface with varying levels of resistance. Like water moving across an uneven watershed, the flow of current over the resistance surface results in patterns of high and low concentrations very similar to the streams, gullies, eddies, and braided channels associated with flowing water. The program's ability to highlight flow concentration areas and pinch-points makes it particularly useful for identifying key linkages for permeability. Concentration areas are easily recognized in the Circuitscape output by their high current density.

In the Circuitscape program, the landscape is converted into a graph, with every cell in the landscape represented by a node (or a vertex) in the graph and connections between cells represented as edges in the graph with edge weights based on the average resistance of the two cells being connected (Shah & McRae 2008). The program performs a series of combinatorial and numerical operations to compute resistance-based connectivity metrics, calculating net passage probabilities for random walkers passing through nodes or across edges. Unlike a least cost path approach, Circuitscape incorporates effects of multiple pathways, which can be helpful in identifying critical linkages where alternative pathways do not exist (McRae & Beier 2007). More detail about the model, its parameterization, and potential applications in ecology, evolution, and conservation planning can be found in McRae and Beier (2007) and McRae and Shah (2009).

Anthropogenic Resistance Grid

In a Circuitscape analysis, the current flows across the landscape through a resistance grid, with lower resistance being more permeable and higher resistance less permeable. The base grid we used for anthropogenic resistance was land cover, but in theory resistance can be any factor that impedes movement (in climate flow models we use slope and land position as well). When based on land cover, obstructions to species movement are assigned high resistance scores based on the degree to which they impede species population movements.

Our assumption was that the resistance between cells increases with their contrast to natural land. Elements that contrast strongly with natural land, such as high or low intensity development, were considered less permeable because of differences in structure, surface texture, chemistry, temperature, or exposure. In this model dispersing wildlife and plant propagules can cross any landscape elements, but sharp contrasts such as forest adjacent to development disrupts or decreases movement because an animal may prefer to avoid the risk inherent in crossing the more exposed habitat or a plant may fail to establish in the new environment. Our three basic landscape elements were as follows:

Natural lands: landscape elements where natural processes are unconstrained and unmodified by human intervention such as forest, wetlands, or natural grasslands. Human influences are common, but are mostly indirect, unintentional, and not the dominant process.

Agricultural or modified lands: landscape elements where natural processes are modified by direct, sustained, and intentional human intervention. This usually involves modifications to both the structure (e.g., clearing and mowing), and ecological processes (e.g., flood and fire suppression, predator regulation, nutrient enrichment).

Developed lands: landscape elements dominated by the direct conversion of physical habitat to buildings, roads, parking lots, or other infrastructure associated with human habitation and commerce. Natural processes are highly disrupted, channeled or suppressed. Vegetation is highly tended and controlled.

To create the anthropogenic resistance grid, we combined several datasets representing land cover, land use, roads, railroads and agriculture. We started with the land cover/land use datasets as our base grids but made several modifications to improve its performance as a resistance grid. These modifications included adjustments or addition related to:

1) Roads and Railroads,
2) Barrens and Mines
3) Prairies and Grasslands
4) Industrial Agriculture
5) Industrial Forests
5) Oil and Gas
6) Wind Energy
7) Transmission Lines, Pipelines and other Energy Infrastructure
8) Water and Waterbodies

To make these improvements, we worked with our two Steering Committees for the combined geography, and in some cases the same land cover/land use category was treated in a different way, or given a different resistance score, based on the Committee members expert opinions/local knowledge. These variations are described in each of the sections below. All improvements to the land cover grid were performed on the 30-m grid cells and integrated with the NLCD, Provincial Canadian datasets, and other source data into one dataset (Figure 3.2). For the Circuitscape analysis, processing limitations required us to coarsen the data to 180-m cell resolution which we did using the “aggregate” function by mean in ArcGIS. their performance as resistance grids.

Landcover

For the U.S., the source data for the resistance grid were the 30-m 2011 NLCD, which identifies each grid cell as belonging to one of 16 classes of land cover (Homer et al. 2015). For Canada, we used provincial land use and agriculture datasets for Ontario and Manitoba (Ontario Natural Resources and Forestry 2016, Manitoba Conservation and Water Stewardship 2005 - 2006). Although both Alberta and Saskatchewan have provincial land use datasets, after examination we found that the scale and attributes varied too far from the US 2011 NLCD to be usable in combination with this source. For Alberta and Saskatchewan we used Agriculture and Agri-food Canada Annual Crop inventory (AAFC 2015, Fisette et al. 2014). AAFC data was a much closer match to the NLCD, as it is a 30-m, satellite derived dataset that includes information in categories that are like the NLCD, including water, barrens, shrublands, wetlands, and forests. Waterbodies were obtained from Canada's National Hydrology Network (NHN) (Natural Resources Canada 2016) and were merged with the land use data.

We created a look-up table to crosswalk the detailed Canadian classifications to our more generalized NLCD classification as the Canadian datasets had different schema and land use categories. After crosswalking the data, categories were assigned resistance scores based on the US landcover equivalents (Table 3.2). We visually compared provincial datasets with current aerial photos and older land use data to confirm their accuracy, and that we had correctly matched the resistance weights.

Roads

The 2011 NLCD landcover data set (Homer et al. 2015) contains an embedded roads data set from the Bureau of Transportation Statistics that does not align with the newer and more accurate 2016 Tiger Road dataset (US Census Bureau 2017). To correct this issue, we removed the older roads from the NLCD and replaced them with roads from the Tiger 2016 dataset. To do this, cells in the 2011 NLCD's "developed open space" class were shrunk by one pixel to remove linear road pixels but not the larger developed areas. Values for these cells were replaced with the majority value of the surrounding pixels. Next, the 2016 Tiger roads were "burned in" on top of the 2011 NLCD replacing the older road data with the more recent data. Similarly, we burned road data from the National Road Network (National Road Network 2017) into the compiled Canadian land use data, which did not contain information on roads except for major highways. For railroads, we used the Bureau of Transportation Statistics active railroad lines dataset (BTS 2016).

<u>Dirt/unpaved roads:</u> Dirt roads or unpaved forest management roads are unevenly mapped in both the US and Canadian land use datasets, even though they may create substantial road networks in some parts of the region. To map unpaved roads, we used data from OpenStreet Map (2017) which is an opensource global dataset built by a community of mappers that contribute and maintain data about roads and trails. We extracted roads tagged as "track" which includes roads used primarily for agriculture and forest logging (i.e., two-track roads). This class of roads is usually unpaved but may include paved roads. Trails and paths that are not wide enough for a two-track vehicle are excluded from this class. Although the quality and consistency of this dataset is not known, visual inspection suggested that it was more comprehensive than any other available dataset for mapping unpaved roads.

Table 3.2. Land cover types and assigned resistance values. This table shows the available attributes and the resistance score assigned to the land cover category. Resistance scores range from "1," no resistance, to "20," very high resistance.

Land Cover Code (NLCD)	Land Cover Description	Resistance Score	Source
21	Developed, Open Space	8	NLCD 2011
22	Developed, Low Intensity	8	NLCD 2011
23	Developed Medium Intensity	9	NLCD 2011
24	Developed, High Intensity	20	NLCD 2011
31	Barren Land, Non-Natural	9	NLCD 2011
32	Barren Land, Natural	1	NLCD 2011
41	Deciduous Forest	1	NLCD 2011
42	Evergreen Forest	1	NLCD 2011
43	Mixed Forest	1	NLCD 2011
52	Shrub/Scrub	1	NLCD 2011
71	Grassland/Herbaceous	1	NLCD 2011
81	Hay/Pasture in the Great Lakes/Tallgrass Prairie	3	NLCD 2011
81	Hay/Pasture in the Great Plains	1	NLCD 2011
82	Cultivated Crops	7	NLCD 2011
90	Woody Wetland	1	NLCD 2011
95	Emergent Herbaceous Wetlands	1	NLCD 2011

We assigned major roads (e.g., multi-lane interstate highways, MTFCC code S1100) a resistance score of 20 and secondary roads a resistance score of 10 (e.g. two-lane county highways) (MTFCC codes S1200, S1630, SS1780). Residential roads were assigned a score of a resistance score of a 7 (MTFCC code S1400, S1640). Cells were assigned an additional resistance point if they contained one or more dirt/unpaved roads. For example, the resistance of agriculture cells with unpaved roads increased from a "7" to a "8" (Table 3.3). All active railroads were given a score of a 9.

Barrens and Mine Lands

In the land cover datasets, the category "barrens" often mixes developed lands such as oil and gas wellheads with natural barrens such as blowout areas, mudflats, and summits.

For both the Great Plains and the Great Lakes and Tallgrass Prairie sub-regions, we manually inspected all polygons over a specified size threshold (180 acres in the Great

Lakes and Tallgrass Prairie, 50 acres in the Great Plains). For areas under this threshold, we used a set of decision rules (for example, cell is touching water, cell is mostly natural in crop data, or cell is surrounded by a high percentage of development) to classify the barrens into natural and non-natural barrens. After these rules were applied, some areas that were not able to be classified; in the Great Lakes & Tallgrass Prairie these were assign to "unclassified" and in the Great Plains these we assigned to "natural" based on the statistics of the classified barrens and visual study of a sample of these barrens in the two regions.

In the Great Plains, some mining operations were identified using USGS's significant topographic changes in the United States Dataset (https://topochange.cr.usgs.gov/), which captures areas of topographic changes from surface mining, urban development, and landfills. Areas identified in this dataset were given a score same as "developed barrens." In addition, for Ohio, we used a GIS dataset of Ohio Surface Industrial Minerals (IM) Mine Operations from the Ohio DNR to classify non-natural surface mines (ODNR 2017).

Natural barrens were given a resistance score that was the same as natural ("1"). Developed barrens are usually highly developed and disruptive of the landscape. They received a resistance score of "9". Unclassified barrens in the Great Lakes received a score in the middle, a "7", as they were more likely to be developed than natural.

Industrial Forestry

In the northern Great Lakes region, industrial forestry represents a significant component of land use on the landscape. In the US, industrial forests a common in sections of Michigan's Upper Peninsula and the Great Lakes shoreline region but are not distinguished from natural forest in the NLCD 2011 (Homer et al. 2015). In some Canadian landcover datasets, industrial forest ownership is specified, but the area is mapped in the forest land use category. To distinguish industrial forests from unmanaged forests, we did not use the ownership information but instead identified forest lands that had been recently been cut using the Global Forest Change dataset (Hansen et al 2013) as the measure of use. The Hansen et al. (2013) is a 30-m dataset developed from satellite imagery analyzed across 15 years to detect areas of forest loss or gain. We assigned any recently cut (between 1997 and 2012) forest cell a resistance score of "3" to reflect a likely logging history and potential forest road development or other anthropogenic disturbances.

An exception to the above rule was when the forest cutting was on known conservation land (e.g. land permanently secured against conversion, GAP Status 1 – 3). Cutting on these lands were assigned a score of "1.5" because, by definition, they are being managed for natural values. For the conservation land boundaries, we created a secured lands dataset based on the U.S. Protected Areas database (PAD-US, U.S. Geological Survey, Gap Analysis Program (GAP) 2016) augmented with Conservation and Recreation Lands (CARL), a dataset that contains information on conservation lands in the Great Lakes region (Ducks Unlimited 2016), and the National Conservation Easement Database (Ducks Unlimited and Trust for Public Land 2017).

The Great Plains region is a grassland dominated landscape and does not have industrial forestry. We visually examined the satellite imagery in areas of forests in this region using the Global Forest Change dataset and found that areas of change (like the Black Hills), appeared to be largely from natural causes such as fire and not due to industrial forestry.

Grassland, Pasture, and Cultivated Crops
The grassland class, pasture class, and the cultivated crop classes are often intermixed in the landcover datasets, because they are hard to differentiate using remote sensing which is sensitive to time of year, planting timing, and green-up. To identify and map industrial agriculture we used the Cropscape dataset (USDA National Agricultural Statistics Service Cropland Data Layer 2016), a USDA dataset that inventories and maps the type of agricultural crop grown nationwide

In the Great Lakes and Tallgrass Prairie, we augmented the grassland/pasture data in the NLCD (Homer et al. 2015) with information on native grasslands and cultivated crops. Historically native prairie covered most of the non-forested portion of the Great Lakes and Tallgrass Prairie study area. Native prairie habitat has been destroyed and degraded through many factors such as agricultural conversion, urban sprawl, energy development, loss of major grazers, and fire suppression, so that today, only a tiny fraction of the original prairie remains. Many of these remnants are managed closely to try to mimic natural processes that support biodiversity. These remnants are important for conservation but are not always consistently mapped – and are difficult to detect on satellite imagery due to the difficulty of distinguishing them from other grasslands, and their typically small size. As a result, they are often misclassified in landcover datasets. To create a dataset of native prairie remnants we compiled several sources of data identifying areas of current prairie habitat. These included:

- Natural Heritage Program natural community data (see end of Chapter 4);
- Remnant Prairies in Iowa dataset (Iowa Department of Natural Resources 2012);
- Prairie datasets from Mississippi River Basin/Gulf Hypoxia Initiative (The Conservation Fund 2016);
- Northern Tallgrass prairie restorations projects with boundaries in the TNC secured lands dataset. These included: Glacial Ridge National Wildlife Refuge (NWR), Midewin National Tallgrass Prairie, Kankakee Sands, Emiquon Preserve, Neal Smith NWR and Nachusa Grasslands (Gerla et al. 2012).

Areas of confirmed native grasslands or prairies in the Great Lakes and Tallgrass Prairie were classified as natural cover and given the lowest possible resistance score of a “1.” The “hay/pasture” and “grassland” categories in the landcover for this region is often a mix of native and introduced grasses. In the Great Lakes and Tallgrass Prairie Region we assigned this category a resistance score of a “3” which was higher than native prairie (“1”) but lower than cultivated cropland (“7”). The Cropscape dataset sometime disagreed with the NLCD and in these cases we overrode NLCD with Cropscape data, this include the occasional times when cells classified as agriculture in the NLCD dataset were identified as grassland/pasture in the Cropscape dataset for at least half the years assessed (2008-2016).

In the Great Plains, grasslands have undergone massive conversion and are at high risk, but are much more widespread than in the Tallgrass section of the Great Lakes and Tallgrass Prairie. Our Steering Committee members felt that data were not available to accurately identify native prairie (i.e., never plowed) from grassland that may be in use as pasture or rangeland, and could be native, non-native, or a mixture. We evaluated several additional datasets in addition to the NLCD and Cropscape dataset to see if there might be some way to make a consistent and meaningful distinction between these types, but in the end agreed with their sound advice. Because of the lack of information and classification errors, we classified all hay/pasture the same as natural grasslands in the Great Plains and gave them a score of a "1" (equal to natural).

High Intensity Agriculture

The Great Lakes and Tallgrass Prairie region has the largest production of corn and soy in the nation (see maps from USDA - https://www.nass.usda.gov/Charts_and_Maps/Crops_County/cr-pr.php 2017). High intensity industrial agriculture can have severe effects on the physical, ecological, and hydrological environment, and can create barriers to movement for many species. To identify and map industrial agriculture we used the US Cropscape dataset (2016).

If a grid cell was classified as corn or soy in the most recent year (2016) or was identified as corn or soy in majority of the years of the dataset (2008-2016), we classified the cell as high intensity agriculture. We gave industrial-scale corn and soy cell a resistance score of "9" because it degrades the natural environment more than most other cultivated crops which received a resistance score of a "7." In the Great Plains, where industrial agriculture is much less prominent we did not differentiate between corn/soy agriculture and other agriculture. All agriculture in the Great Plains got a resistance score of a "7". These effects were later normalized within each ecoregion so that regional differences did not influence the ecoregional scores.

Oil and Gas Development

With over 1,750,000 active and inactive wells, the Great Plains region is the heart of oil and gas development in the US. Oil and gas development results in both direct and indirect effects on species movement. Roads and well pads fragment the landscape and the noise associated with pumping and daily vehicle traffic amplify the effect of fragmentation discouraging the movement native species and favoring invasive species. Hydraulic fracking uses large amount of water, which can exacerbate water stress in this drought-prone region. In the Great Lakes and Tallgrass Prairie Region, oil and gas development does not dominate the landscape and it was not assessed as a contributor to landscape resistance.

To accurately map the spatial effects of oil and gas development, we collected oil and gas well data from all the states and provinces in the Great Plains (a full list and description of all sources in in Table 3.2 in Anderson et al. 2018b). In our resistance grid, we set the resistance weights to give the highest density oil and gas areas (>16 wells per square mile) a resistance effect like that associated with medium-density development. We used a two-pronged approach to accomplish this. First, using the well locations, we calculated a point density grid based on a kernel density function in

ArcGIS. To estimate the resistance of the well pads themselves, we created a 540-m x 540-m well pad area around each well point (540 m^2 is the size at which the highest density well pads (>16 wells per square mile) form a continuous coverage). We included both inactive wells and active wells in the density calculation, but inactive wells received 1/10 (0.01) the weight of active wells. Second, we estimated the indirect effects of oil and gas development using a point density grid based on the individual well points only (no well pads) and using a kernel density function in GIS. We used a graduated weighting so cells with a higher density of points had higher resistance. The calculation of kernel density is sensitive to, and often magnifies, small changes in the resistance score.

Well density weights were added to the score from the NLCD as follows: 0 – 1 wells per square mile = "0", 1-2 wells per square mile = "0.2", 2-4 wells per square mile = "0.4", 4-8 wells per square mile = "0.6", 8- 16 wells per square mile = "0.8", 16 or more wells per square mile = "1". For example, an area that was natural but had 6 wells per square mile got a resistance value of 1 (natural) plus 0.6 (well density) = 1.6. An agricultural area that has 6 wells per square mile got a resistance score of 7 (agriculture) plus 0.6 (well density) = 7.6.

Wind Energy

55% of the US's wind power capacity is in states that are in the Great Plains region (https://www.awea.org/windenergyfacts.aspx), with over 27,000 wind turbines in the Great Plains states. Although wind power is one of the cleanest and sustainable energy sources, there are a variety of environmental impacts associated with wind energy that may affect the connectedness of the area surrounding a turbine. The landcover at the base of the wind turbine is permanently disturbed, and a larger area is disturbed during construction. There are also impacts from the roads connecting the turbines. Research is ongoing on the effect of turbines on wildlife. The impact on birds and bats is well studied and the area of impact varies depending on the species. Wind energy development is not as common in the Great Lakes–Tallgrass Prairie region and following the guidance of our Steering Committee, we did not assess it there.

To represent wind energy development in our resistance dataset for the Great Plains, we combined the two key datasets for wind turbines in the United States:

- Federal Aviation Administration Digital Obstacle File (https://www.faa.gov/air_traffic/flight_info/aeronav/digital_products/dof/).
- U.S. Wind Turbine Database (https://eerscmap.usgs.gov/uswtdb/).

The latter was collected and compiled from various public and private data sources, and quality checked and position-verified from aerial imagery. The two datasets were combined, and duplicates were removed. We estimated the impact using a 1-mile kernel density with the same weights as oil and gas development. However, we did not inflate the area of the turbine base, as we had done with the oil and gas well heads, because of the lower impact of wind development.

Transmission Lines, Powerlines, and Pipelines

To account for the influence of energy infrastructure, we added the locations of pipelines and powerlines to the landcover datasets in both the Great Lakes and

Tallgrass Prairie, and the Great Plains geographies. To do this, we obtained power industry GIS data (Venti 2017, used with permission). We selected all transmission lines in service by voltage class, and all in-service natural gas pipelines. These were incorporated into the landcover dataset using power industry standard right-of-way widths: 30-m width for transmission lines 230 kilovolts. All pipelines were given a 30-m width (Duke Energy 2014). Underground powerlines are occasionally in the Ventyx data and where they are specified we pulled them out in the dataset. We assigned all above ground transmission lines a resistance of "7." Below ground powerlines were treated like dirt roads, adding one additional point of resistance to the cell. Pipelines were given a resistance score of "7". We compared the dataset to aerial photos to confirm that these widths were reasonable and to ensure that we added only features that made a distinguishable footprint on the ground.

Waterbodies

We adjusted the resistance score of waterbodies to reflect their size, because very large waterbodies impede the movement of terrestrial species more than small streams or ponds. To quantify the effect of waterbody size, we first created a waterbody file from the waterbodies in the landforms (see Chapter 2) and the NLCD cells classified as water. We assigned water within 200 m of a shoreline a resistance value of "1," water between 200 and 400 m of a shoreline received a resistance value of "3,"and water greater than 400 m from a shoreline was given a value of "5" to reflect a stronger barrier as the waterbody size increases (Figure 3.1). Streams and ponds that had less than 200 m of shoreline were all assigned a "1."

Figure 3.1. Waterbodies and the zones used in the resistance weighting.
Waterbodies are shown in blue on the right, with darker blues indicating higher resistance at 0-200, 200-400, and 400+ meters.

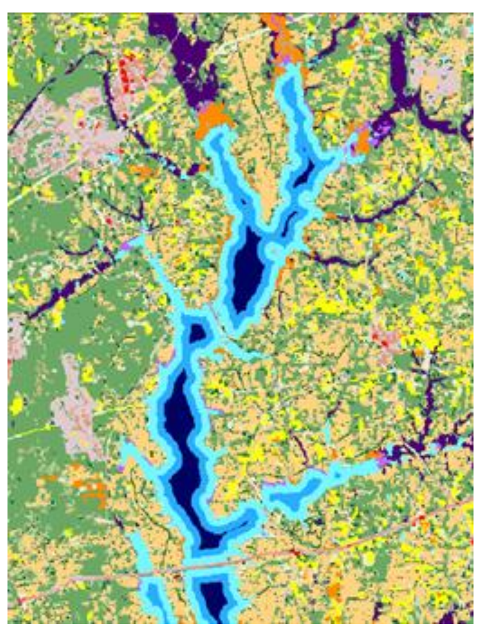


Table 3.3. Summary of Improvements to the Resistance Grid.

Roads and Railroads

Landcover	Region	Resistance Score	Source
Major Roads	Great Lakes and Tallgrass Prairie AND Great Plains	20	Tiger 2016 (US) & National Road Network (CA)
Minor Roads	Great Lakes and Tallgrass Prairie AND Great Plains	10	Tiger 2016 (US) & National Road Network (CA)
Dirt Roads	Great Lakes and Tallgrass Prairie AND Great Plains	Reistance + 1	Tiger 2016 (US) & National Road Network (CA)
Railraods	Great Lakes and Tallgrass Prairie AND Great Plains	9	BTS 2016

Industrial Forests

Landcover	Region	Resistance Score	Source
Forest Loss or Gain	Great Lakes and Tallgrass Prairie	3	Global Forest Change Dataset (2016)
Forest Loss or Gain on Secured Lands	Great Lakes and Tallgrass Prairie	1.5	Global Forest Change Dataset (2016) & Analysis of Secured Lands for the Great Lakes

Grassland and Prairie

Landcover	Region	Resistance Score	Source
Prairie/Grassland Areas	Great Lakes and Tallgrass Prairie	1	Nature Serce Eos, Remnant Prairies in Iowa, Gulf Hypoxia, Secured Lands

Grassland/Pasture

Landcover	Region	Resistance Score	Source
Grassland; Hay/pasture	Great Lakes and Tallgrass Prairie AND Great Plains	3	NLCD and Cropscape 2016: most years grassland
Grassland; Hay/Pasture	Great Plains	1	NLCD

High Intensity Agriculture

Landcover	Region	Resistance Score	Source
Corn and Soy Agriculture in 2016	Great Lakes and Tallgrass Prairie	9	Cropscape 2016 (US) or AAFC (CA)
Persistant Corn and Soy	Great Lakes and Tallgrass Prairie	9	Cropscape: Majority of years corn or soy

Oil and Gas Development and Wind Energy

Landcover	Region	Resistance Score	Source
Oil and Gas Well Pads	Great Plains	7	Ventyx 2017
Oil and Gas Buffer Area	Great Plains	0.2 and 1 additional point of resistance (Graduated weighting - well density)	Ventyx 2017
Wind Tower Buffer Area	Great Plains	0.2 and 1 additional point of resistance (Graduated weighting - well density)	Ventyx 2017

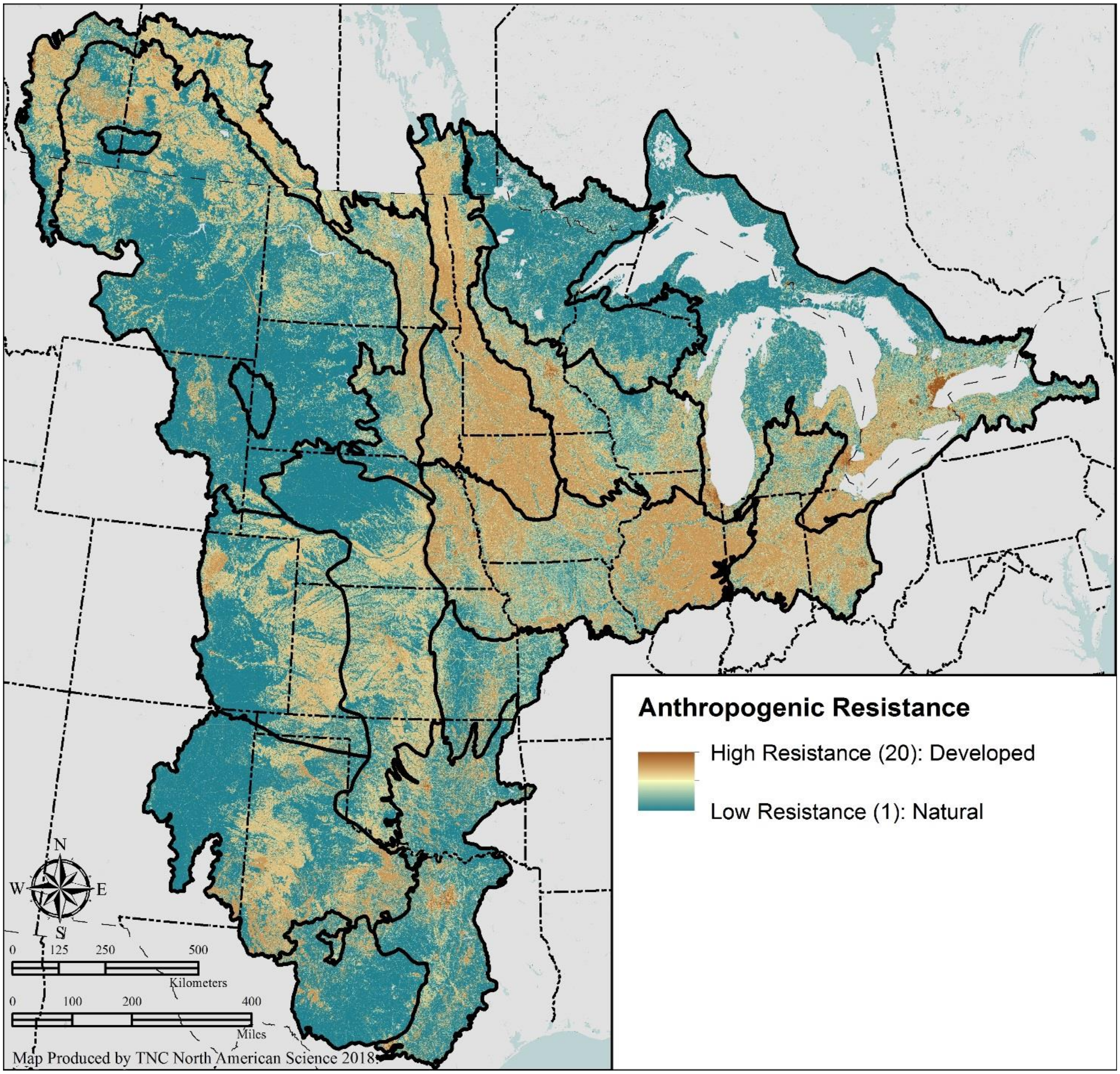
Transmission Lines, Powerlines, and Pipelines

Landcover	Region	Resistance Score	Source
Transmisison Lines	Great Lakes and Tallgrass Prairie AND Great Plains	7	Ventyx 2017
Pipelines	Great Lakes and Tallgrass Prairie	9	Ventyx 2017
Pipelines	Great Plains	7	Ventyx 2017

Water : Distance to Shoreline

Landcover	Region	Resistance Score	Source
<200 meters	Great Lakes and Tallgrass Prairie AND Great Plains	1	NLCD, NHD, NHN, ArcGIS Analysis
200 to 400 meters	Great Lakes and Tallgrass Prairie AND Great Plains	3	NLCD, NHD, NHN, ArcGIS Analysis
>400 meters	Great Lakes and Tallgrass Prairie AND Great Plains	5	NLCD, NHD, NHN, ArcGIS Analysis

Figure 3.2. Anthropogenic resistance grid used in the Circuitscape analysis. The figure shows the improved and integrated land cover map with each cell reclassified to its assigned resistance score.



Mapping Regional Flow

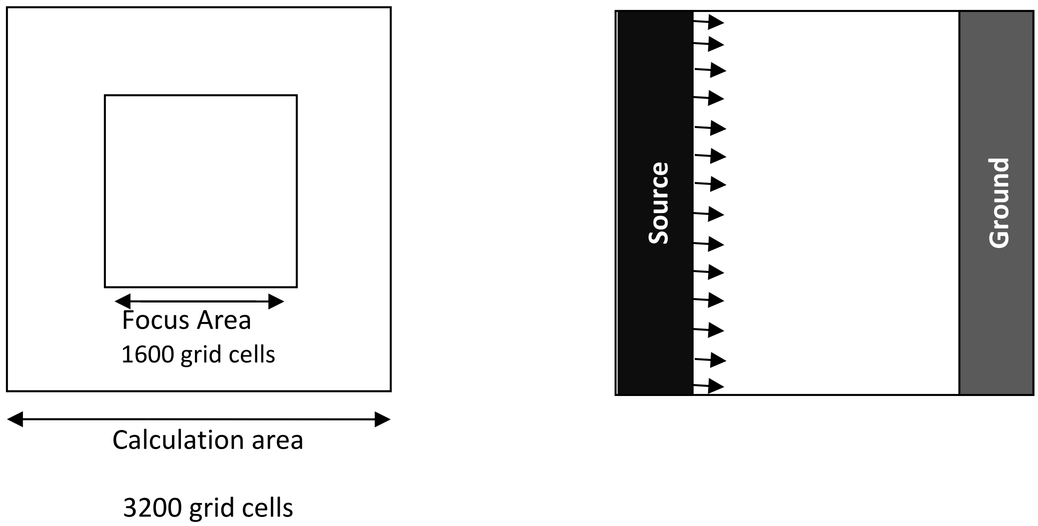
Circuitscape was originally designed to measure point-to-point connectivity, calculating resistance-based connectivity metrics from one discrete patch to another. The point-to-point approach has been widely used in conservation planning to measure the connections between two patches of suitable breeding habitat as defined by the habitat needs of a species (Beier et al. 2011). However, using a point-to-point approach can limit the utility of assessing connectivity over very large areas, or in evaluating the response of populations to climate change where there are so many habitat patches of interest that assessing connectivity among all possible combinations is prohibitive. Additionally, the point-to-point method is sensitive to the location of the starting points and may produce different results across the same landscape if different starting points are used. To overcome these conceptual and practical limitations, we used a minor adaptation of the Circuitscape model that allows for the "point free" creation of omnidirectional connectivity maps illustrating flow paths across large study areas. Our methods have been developed and refined over several years and were originally are described in Anderson et al. (2013) and Pelletier et al. (2014).

Briefly, to obtain complete wall-to-wall coverage of the region we ran the model in gridded landscape tiles where one whole side of the tile was assigned to be "source" and the other side to be "ground." Next "current" was injected along the entire source side and allowed to flow across the landscape (resistance surface) towards the ground side revealing the flow pathways across the landscape and highlighting where flow gets blocked or concentrated. Because current seeks the path of least resistance from the source cells to any grid cell on the ground side, a run with the west edge as source and the east side as ground will not produce the same current map as a run with the east edge as source and west edge as ground. Runs were thus repeated in each of four directions: east to west, west to east, north to south, south to north, and summed across all directions. Lastly, we clipped out the central quarter of each tile (focus area in Figure 3.3) and joined it to the central regions of all the other tiles. This last step was done because testing had shown that the central quarter gave stable, repeatable, and consistent results regardless of the size of the calculation area. In contrast, the outer margins of the tile had considerable noise in the results created by the tile's exact boundaries. All calculations were performed using the latest version of Circuitscape (4.0) with a cell size of 180 meters.

To run the analysis, we developed a systematic processing method and then used Python scripting to automate the process. First, the study area was divided into 216 tiles - calculation areas - comprised of 3200 cells by 3200 cells or roughly 480 square kilometers. Each tile was intersected with the resistance map and the analysis was run as described above. All tiles with land cover information were included except for those that were 100% water (Great Lakes).

To inject current in the tile with coastal regions, where a proportion of the tile was filled by the Great Lakes we used a new method developed by Jeff Cardille of McGill University (personal communication, December 2015). We created a random raster with the same mean and standard deviation as the land resistance and replaced the large waterbodies with this random raster on the resistance grid. When current is

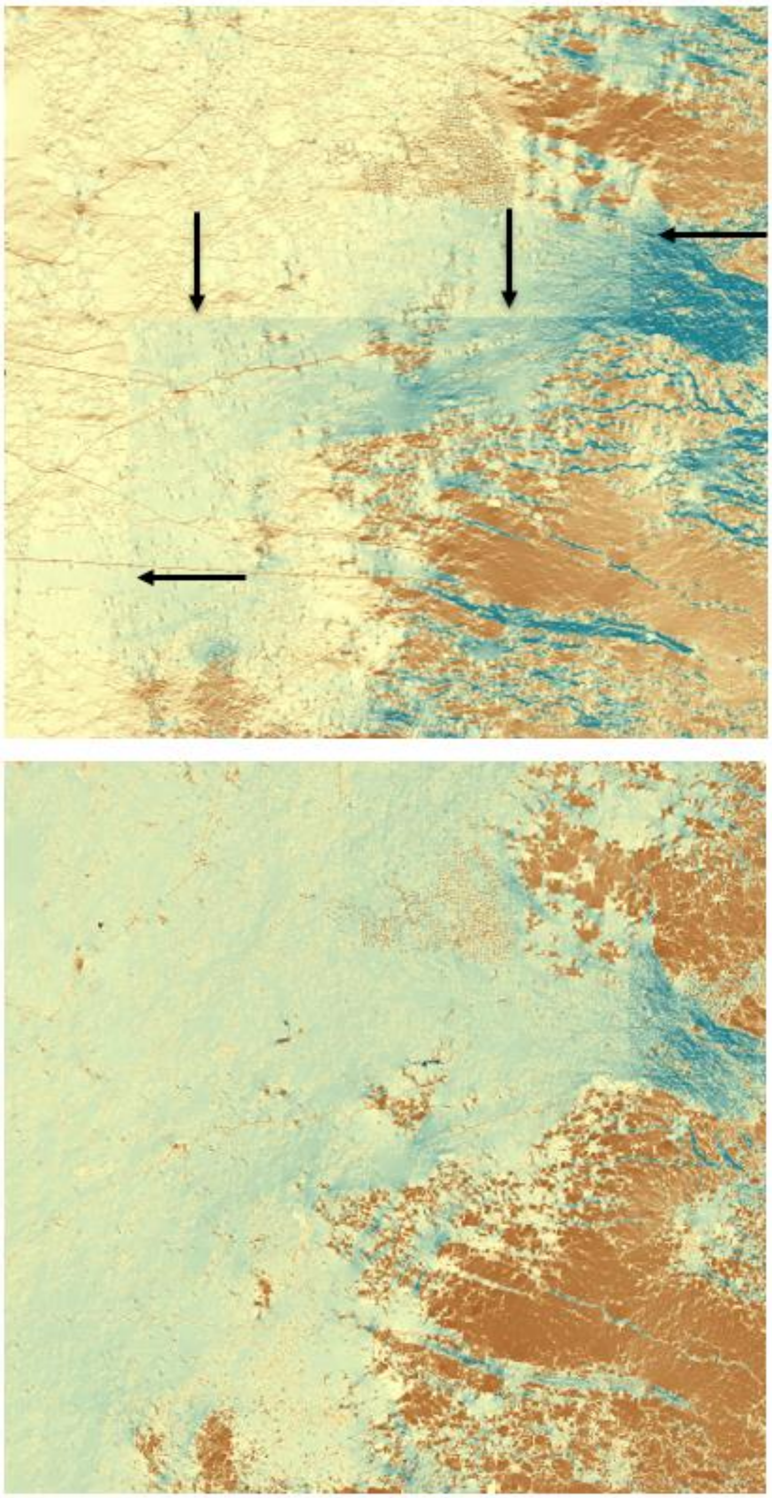
Figure 3.3. Diagram of tiles used in the Circuitscape analysis.
The image on the left shows the focus area in comparison to the calculation area. The image on the right shows how current is injected from every cell on the source (on the left) and can flow to any cell in the ground (right).



injected along the "water" side of the tile it runs equally along the grid until it encounters a shoreline, allowing for equal current flow potential for coastal areas.

Lastly, the focus area was clipped out of each tile and joined together to create a single continuous coverage for the region. To standardize the scores across tiles, a cell of overlap was retained between all adjacent focus areas. Theoretically the scores within the overlap area should be the same between two adjacent tiles since they are the same area. To enforce this, the neighboring cell's score was adjusted so the overlapping areas had the same mean score as the starting tile, and this was repeated for all cells starting at the center and working outward in a starburst pattern. This created a more seamless surface than our previous method (Anderson et al. 2013) of using a standard normal transformation (Z-score) to convert focus areas to the same scale and then joining the focus areas together (Figure 3.4). That method minimized differences between areas that in some cases had very different mean scores, such as a largely agricultural focal area adjacent to a largely natural focal area.

Figure 3.4. Edge mapping overlap. The figure on the top shows the artifacts of tiling on the middle bottom tile. The bottom figure shows the same tile with the edge artifacts smoothed out using the method described above.



Regional Flow Results and Patterns

The final map of wall-to-wall regional flow based on the anthropogenic resistance grid highlights areas of highest flow in dark blue, areas of moderate flow in medium blue, and areas of blocked or low flow in brown (Figure 3.5). A particularly useful feature of the wall-to-wall permeability results is that they reveal spatial patterns in current flow that reflect how the human-modified landscape is configured (Figure 3.6). Thus you can identify where population movements and potential range shifts may become concentrated or where amount of natural cover is less of a constraint, and it is possbile to quantify the importance of an area by measuring how much flow passes through it, and how concentrated that flow is. The results can be used to identify important pinch points where movements are predicted to concentrate, or diffuse intact areas that allow for more random movements. These four prevalent flow types each suggest different conservation strategies:

- Diffuse flow: areas that are intact (high proportion of natural landcover) and consequently facilitate high levels of dispersed flow that spreads out to follow many different and alternative pathways. The related conservation strategy is to keep these areas intact and prevent the flow from becoming concentrated. This might be achievable through maintaining or improving land management and/or procuring broad-scale conservation easements to prevent conversion.

- Concentrated flow: areas where large quantities of flow are concentrated through a narrow area. Because of their importance in maintaining flow across a larger network, these pinch points are good candidates for land conservation/protection.

- Constrained flow: areas of low flow that are neither concentrated nor fully blocked but instead support movement across the landscape in a weak reticulated network. With respect to strategy, these areas present large conservation challanges. In some cases restoring a riparian network might end up concentrating the flow and creating a linkage that will be easier to maintain over time.

- Blocked/Low flow: areas where little flow gets through and is consequently deflected around these features. Depending on the landscape context, some of these might be important sites where restoring native vegetation or altering road infrastructure might reestablish a historic connection, potentially shifting the site to an area of concentrated flow.

Figure 3.5. Results of the wall-to-wall Circuitscape model applied to the anthropogenic resistance grid. Brown indicates areas with low permeability where movement is blocked. Medium blue indicates areas of moderate flow; these are often highly natural settings were patterns of species movements are expected to be diffuse. Dark blue indicates areas of concentrated flow where movements will accumulate or be channeled due to a combination of high flow and somewhat limited options.

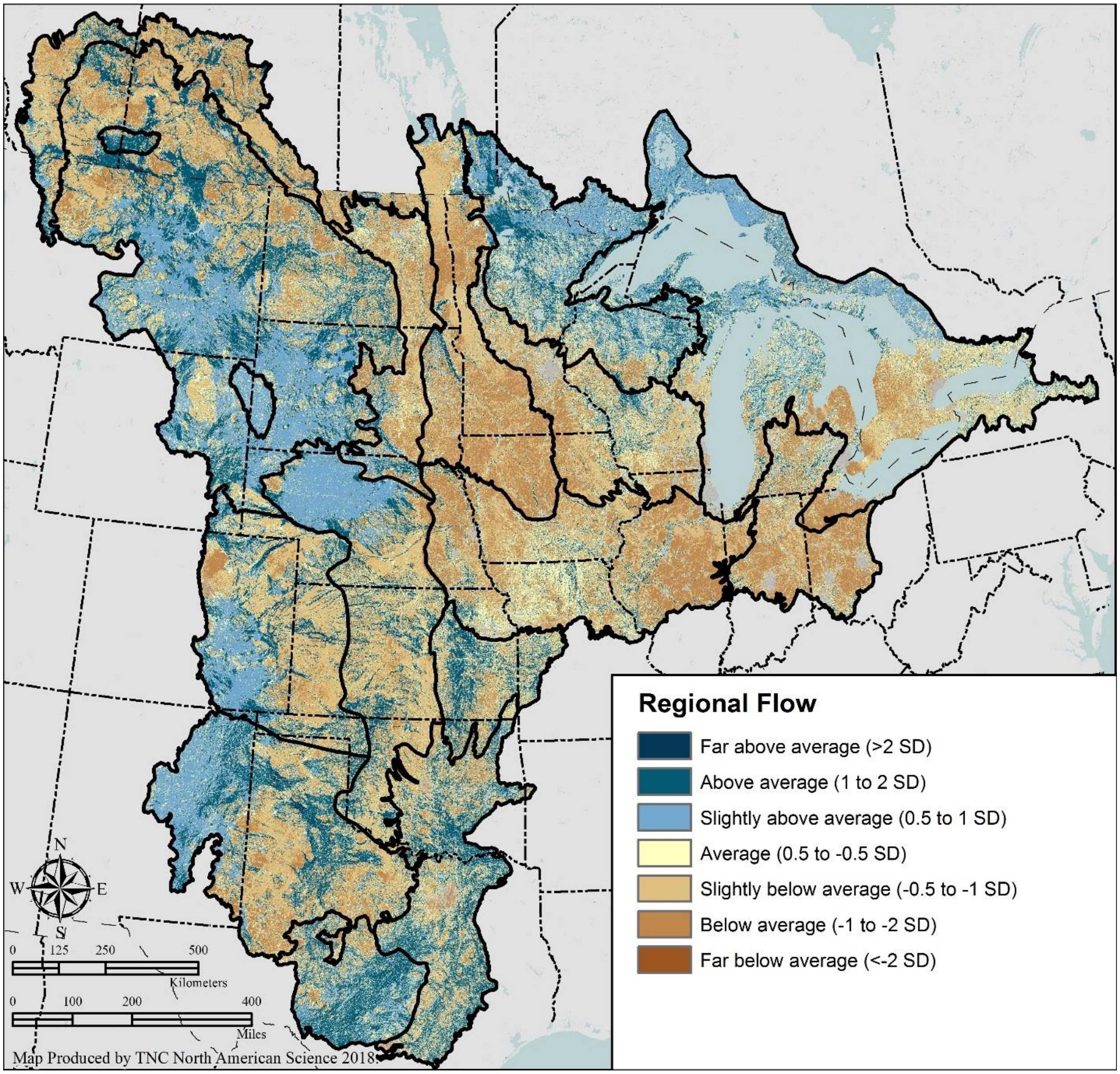
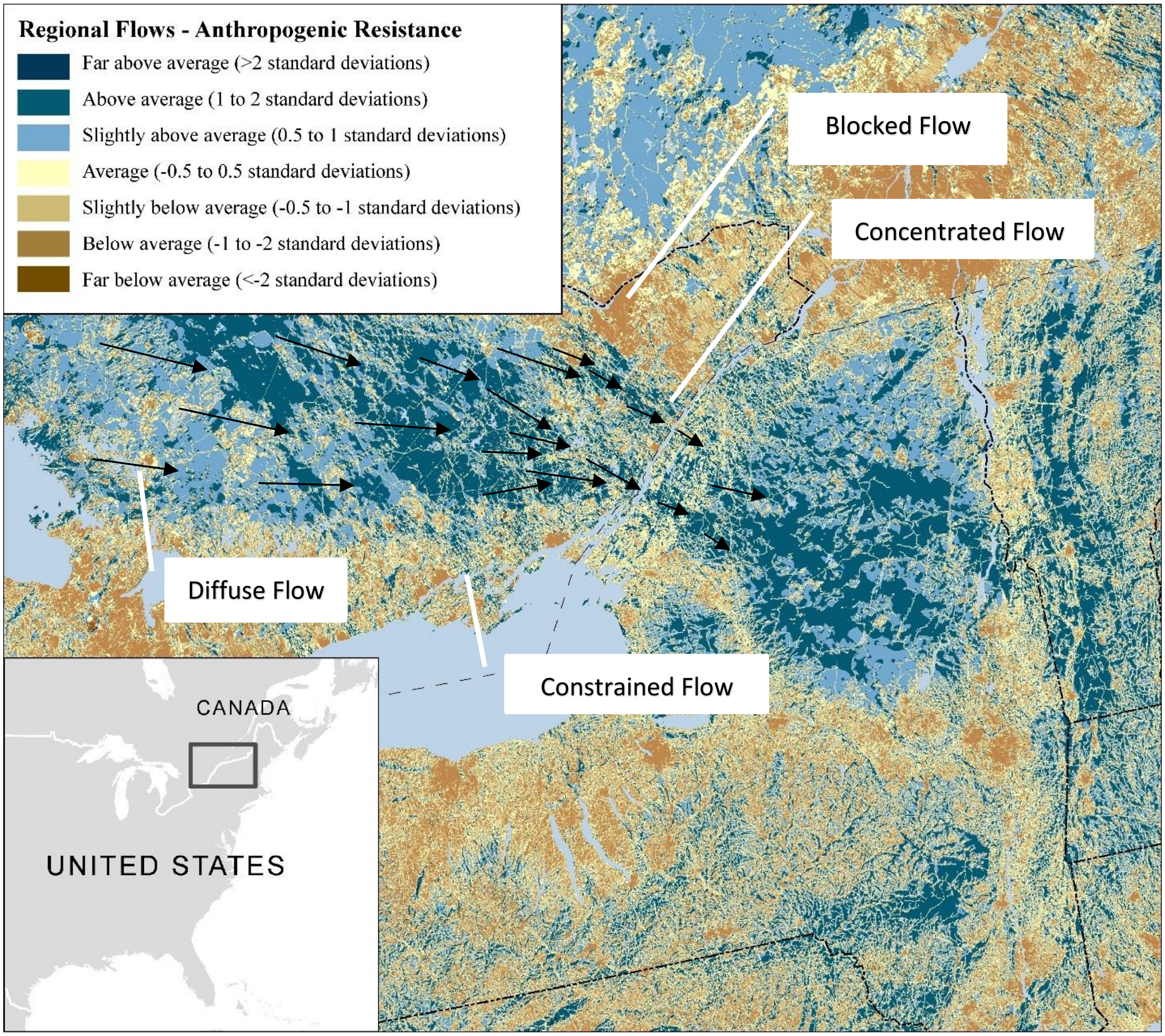


Figure 3.6. Flow types. An zoomed-in illustration of the four flow types. (St Lawrence Valley between the Algonquins and the Adirondacks).



To create a categorical classification of flow patterns, we calculated the amount and the variation of flow in a local neighborhood of 1000 acres (440 hectares, 1.135 km radius circle). The size of the neighborhood was determined by testing a variety of distances and picking the one that seemed to best capture flow patterns without too much smoothing. Within each neighborhood we calculated the mean amount of flow, and the variation in flow as indicated by the standard deviation. Areas that had high flow and a high standard deviation were considered "concentrated" because they channel a large amount of flow and are different from their surrounding cells. Areas that had above-average flow and low standard deviation were considered "diffuse" because they have the potential to convey a lot of flow and are in a neighborhood of similar high flow cells. We divided the mean and standard deviation into 7 quantile classes by area and analyzed the combinations to classify the wall-to-wall continuous grid (Figures 3.7 and 3.8).

Figure 3.7. Diagram illustrating categorization from wall-to-wall map to catagorized results . Blue areas are concentrated flow that have high flow (high means) and are different from their neighbors (high standard deviations). Green areas are diffuse areas that have high flow (high means) and are like their neighbors (low to medium standard deviations). Gray areas have average flow (average means) and are different from their neighbors (high standard deviation). Areas not shown (lightest gray in the diagram or white on the map have average or below average current values and are considered areas of blocked flow.

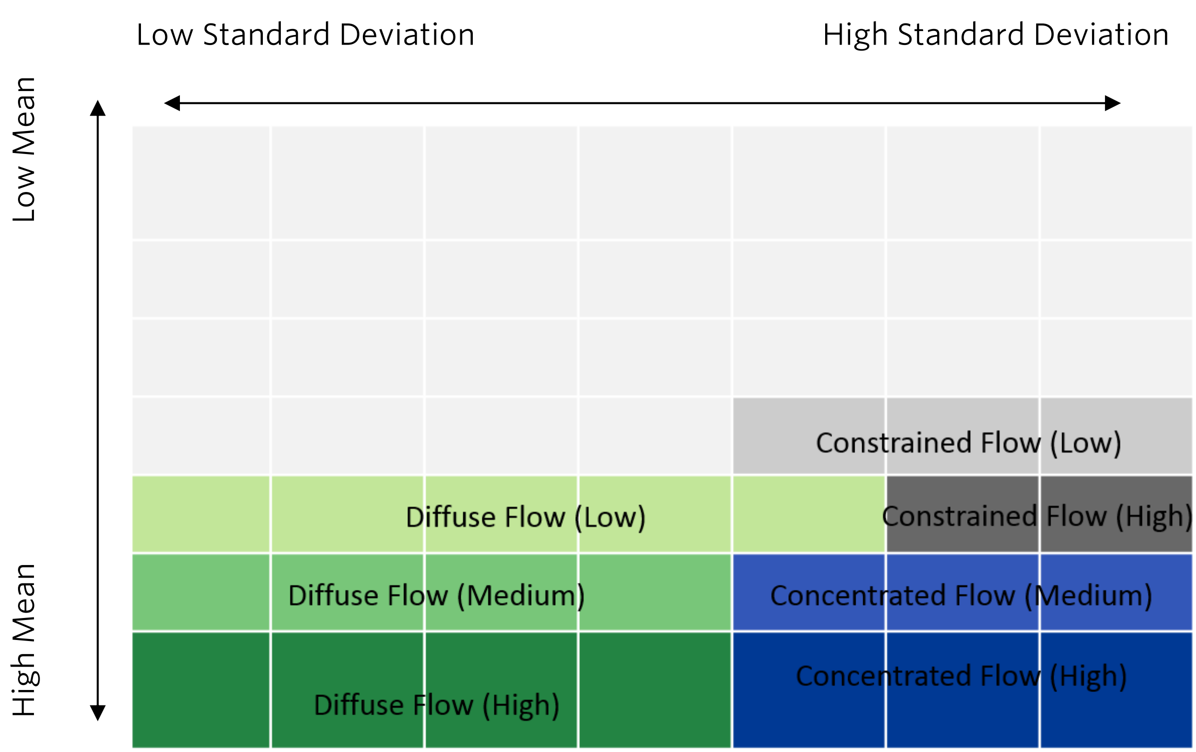
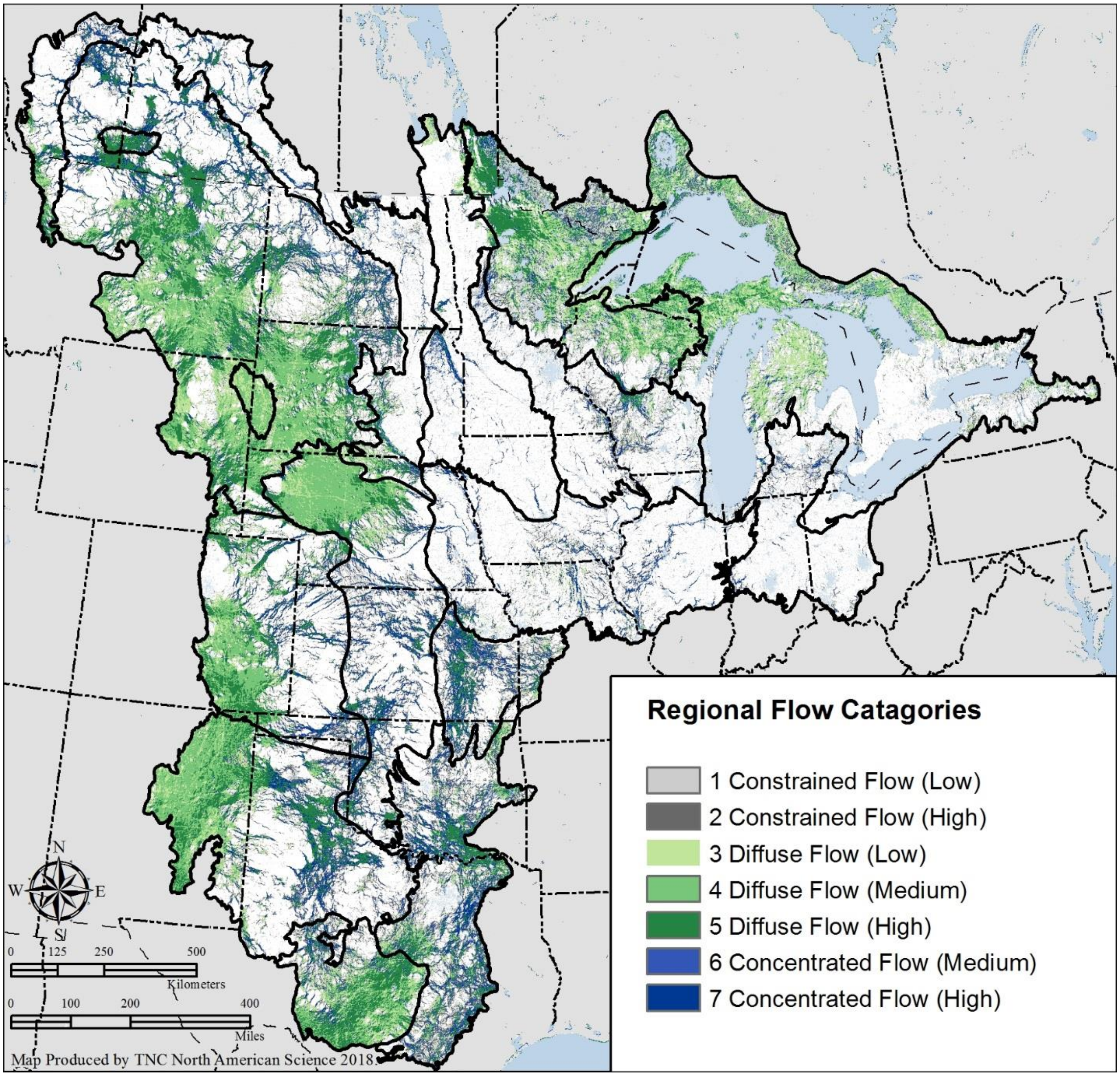


Figure 3.8. Categorized results of the wall-to-wall Circuitscape model applied to the anthropogenic resistance grid. Grey indicates areas with low permeability where movement is blocked. Green indicates areas of moderate flow; often highly natural settings where species movements are diffuse. Blue indicates areas of concentrated flow where movements will accumulate or be channeled through a pinch point.



Climate Flow

This section descriped how we modified the regional flow model to specifically highlight connections that we expect will cross gradients in temperature and/or moisture availability, which we refer to as providing “climate relief.” Paleoecological studies show that movement was a near universal response to past changes in climate (Pardi and Smith 2012), but not every directional movement provides equivalent climate relief. Although all parts of the landscape are important in allowing and maintaining population movements, current evidence suggest that areas that offer cooler temperatures or higher moisture are particularly critical in providing local relief from a warming climate (Chapter 2). Our goal was to evaluate how these features are arranged on the landscape and whether access to them is limited or prevented by fragmentation, or conversely enhanced by the contours of the topography. We refer to the regional flow analysis informed by features with strong climatic gradients: **climate flow**. In the previous section we defined “regional flow” as the gradual movement of populations tracking a set of changing conditions over time, and here we define the term “climate flow” to refer to specific directional movements in response to temperature and moisture changes.

A variety of approaches to incorporating climate gradients into connectivity models have been developed. The most straightforward are models that directly connect temperature gradients based on global or national climate data (see McGuire et al. 2016). The climate gradient approach is logical and promising but is currently hindered for our purposes by the coarse scale of the temperature models (typically 1 km or larger. Our approach empahsizes gradients, and builds from our understanding of how fine-scale topography and microclimate relief create the local climate environments experienced by most species.

As described in Chapter 2, the evidence for upslope and northward movements in response to temperature change is strong and consistent across many taxa groups and across several continents. In response to moisture and precipitation changes there is rapildy growing evidence for the important role of downslope basins and riparian areas, as well as for longitudinal movements in some parts of the US. Following these findings in the research litererature, we focused our attention on the four best documented and mappable patterns of species response to climate change:

1) **Upslope** toward higher elevations,
2) **Downslope** toward moist basins or riparian areas,
3) **Northward** toward cooler latitudes, and
4) **Locally** toward suitable microclimates.

In this section, we model the movement patterns expected from these responses and integrate them into the regional flow map. As with the regional flow map, we incorporate the arrangement and resistance of fragmentation and other human modifications into each model to explore the implications of such modifications on directional movements driven by climate change.

We integrate these directional factors into the flow map as a boost, and not as a fixed determinate of movement. Although these factors are correlated with population expansions and range shifts, it is also clear that a variety of ecological factors may create variation in a species response to climate such as competitive release, habitat modification, or changes in amounts and patterns of precipitation, snow cover duration, water balance, or seasonality (Groffman et al. 2012). Our decision to give weight to these factors but not to override the land cover-derived drivers acknowledges that many things might cause a range shift to differ substantially from straightforward poleward or upslope movement largely driven by temperature or moisture (Garcia et al. 2014).

The wall-to-wall Circuitscape approach is well suited to exploring how species will move in response to shifts in climate because it assumes that every cell in the region is a starting point for some species, and the directional movement along elevation gradients could be conceived in terms of resistance and latitudinal movement as source-ground flow. In the following sections we first look at 1) upslope movement primarily driven by temperature change, and 2) downslope movement primarily driven by moisture changes and 3) northward movement driven by regional temperature gradients. Finally, we integrate these factors into the regional flow model to create a map of climate flow.

Upslope Model: Local Temperature Relief

To model upslope movement we created a 30-m continuous landform model based on each cell's relative land position and slope (Anderson 1999, Anderson et al. 2012). We converted this to a resistance grid by first isolating the relative land position value and assigning increased resistance to moving downslope and decreased resistance to moving upslope. Next, we modified the resistance score using the cell's slope value, to reflect the relative degree of effort versus gain in temperature differences (Table 3.4). For example, moving upward along a gentle slope is easy but provides little gain in temperature differences (moderate resistance), moving upward along a moderate slope provides larger gains in temperature differences for moderate effort (low resistance), moving upward along a steep slope is too difficult for most species despite the temperature gains (high resistance) (Figures 3.9 and 3.10). We combined the land position and slope values into one resistance score that scales the model such that a theoretical species would move upslope preferentially along areas of moderate slope where they would experience the greatest temperature differences relative to effort.

Although mountainous areas may produce the largest amount of pure elevation change, elevational gradients still influence temperature regimes in the more gentle topographies that characterize most of the Central US. Species also experience temperature relief from slopes relative to their local landscape (e.g. a 10-m slope in a flat landscape may provide more relief to nearby species than a 10-m slope in an already mountainous landscape). To ensure that the upslope resistance grid was scaled to both local relief and larger regional relief we calculated both a regional resistance score and a local neighborhood resistance score around each cell and then integrated them. For regional relief we calculated the absolute amount of upslope resistance in a 3 km focal area around each cell and converted it to a Z-score using the mean and standard deviation for the whole region. For local relief, we used the same focal statistic algorithm to calculate the mean and standard deviations of upslope resistance for a 3 km radius around each cell and converted the flow to a Z score using only these local means and deviations. The regional and neighborhood resistance Z scores were combined by adding the two grids. We were aiming to give them equal weight, highlighting areas of both absolute upslope flow and neighborhood upslope flow, but the distributions of the two datasets were very different such that the local neighborhood resistance score overwhelmed the regional score. To carry forward a regional influence, we gave twice the weight to the regional resistance grid. The results provide a single upslope resistance grid that was a weighted combination of regional and local resistance.

To incorporate anthropogenic resistance, we combined the upslope resistance grid with the anthropogenic resistance grid weighting the scores so that the final resistance score of each cell was 20% from the upslope resistance value and 80% from the anthropogenic resistance value. In Circuitscape, we ran current through the combined upslope/anthropogenic resistance grid in all directions (as described previously for the regional flow model) to create an output of upslope current flow incorporating anthropogenic resistance (Figure 3.11).

Table 3.4. Resistance scores applied to the landform model. Land position ranks (LP rank) were ordered so they decrease towards higher land positions. Slope ranks (S rank) were ordered so that they increase at the extremes of no slope (no temperature gain) and steep slopes (too difficult to transverse) and are lowest at moderate values (most gain for least effort). NA = not applicable.

Landform	code	Slope	Position	LP rank	S rank	Sum	Weight
Slope crest	13	3mod	highest	1	1	2	1
Ridgetop	12	2gentle	highest	1	4	5	2.5
N-sideslope	23	3mod	high	4	1	5	2.5
S-sideslope	24	3mod	high	4	1	5	2.5
Flat summit	11	1flat	highest	1	7	8	4
hill/gentle slope	22	2gentle	high	4	4	8	4
Lower side	33	3mod	low	7	1	8	4
Hilltop flat	21	1flat	high	4	7	11	5.5
Valley/toeslope	32	2gentle	low	7	4	11	5.5
N-cove	43	3 mod	lowest	10	1	11	5.5
S-cove	44	3 mod	lowest	10	1	11	5.5
Dry flat	30	1flat	low	7	7	14	7
Wet flat	31	1flat	low	7	7	14	7
Slopebottom	42	2gentle	lowest	10	4	14	7
Slopebottom flat	41	1flat	lowest	10	7	17	8.5
Steep slope	4	4 High	any	NA	9	18	9
Cliff	5	5 Highest	any	NA	10	20	10

Figure 3.9. Conceptual model of how a species population (black arrows) might move upslope and northward over five generations.

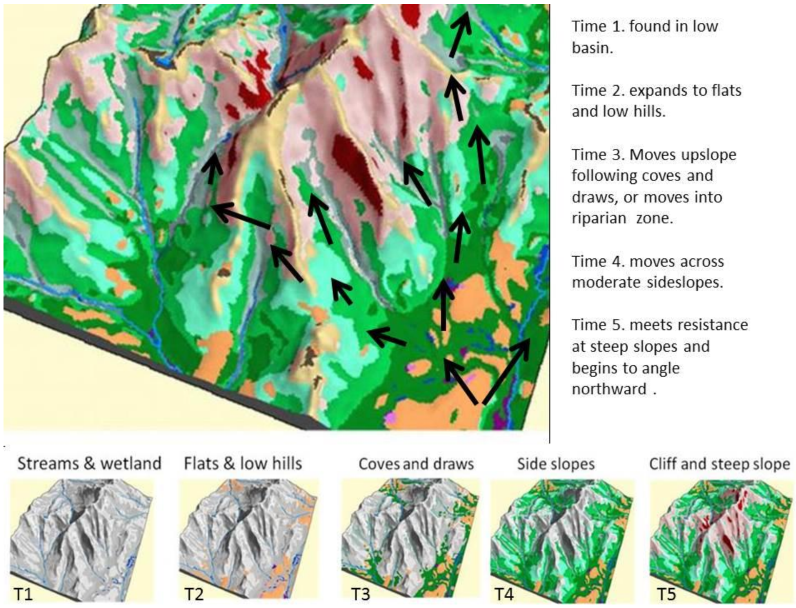


Figure 3.10. The resistance scores applied to the landform model. This picture shows a three-dimensional model of Mt Mansfield in Vermont. The left image shows the landform model with the low land position flats in purple and blue, mid land position and moderately sloped sideslopes in green, and high position and steep slopes and cliffs in orange and red. The second image shows the resistances where low resistance corresponds to areas with the most temperature gain for the least effort (moderately steep sideslopes). Flat valley bottom and steep slopes have higher resistance.

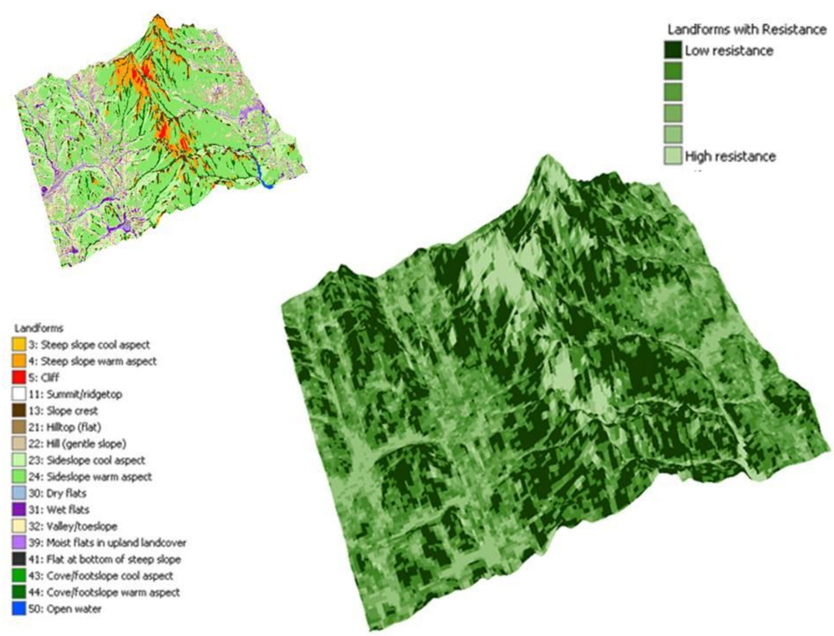
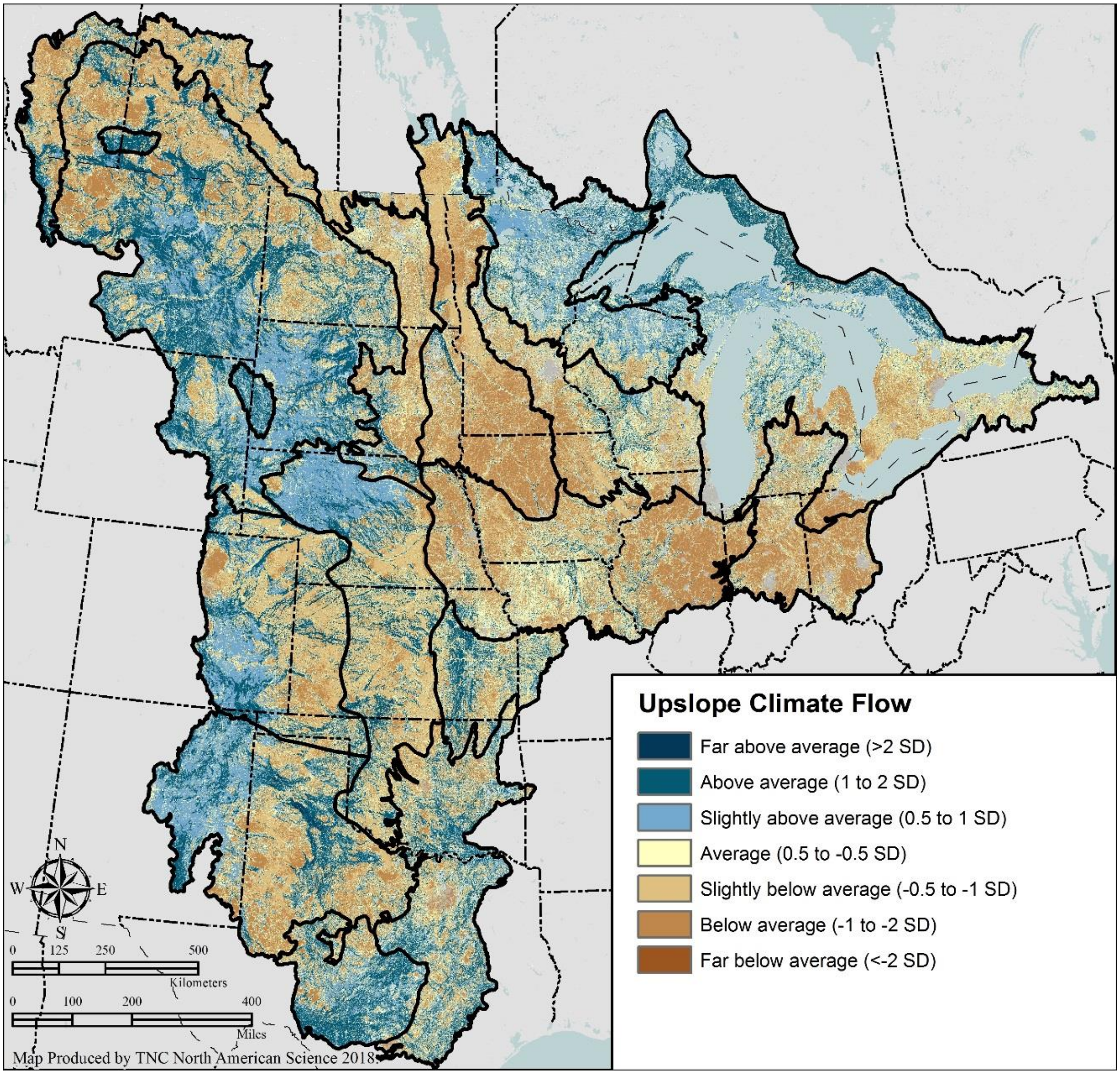


Figure 3.11. The Upslope model applied to the whole study area. As in Figure 3.5, the color scheme in the legend describes differences in permeability and flow rate, with flow rate "boosted" for upslope movements.



The upslope model highlights areas with high potential for upslope range shifts are arranged locally and across the region (Figures 3.12 and 3.13). The realistic effect of the local scaling (Figure 3.12) is to create a much more distributed picture of where upslope movements may be available to species for local climate relief. This takes the emphasis off the region's few mountains and highlights a wide range of moderate slopes that might play a large role in providing local climate relief (Figure 3.12).

Figure 3.12. Zoom in of upslope model in Sandhills region.

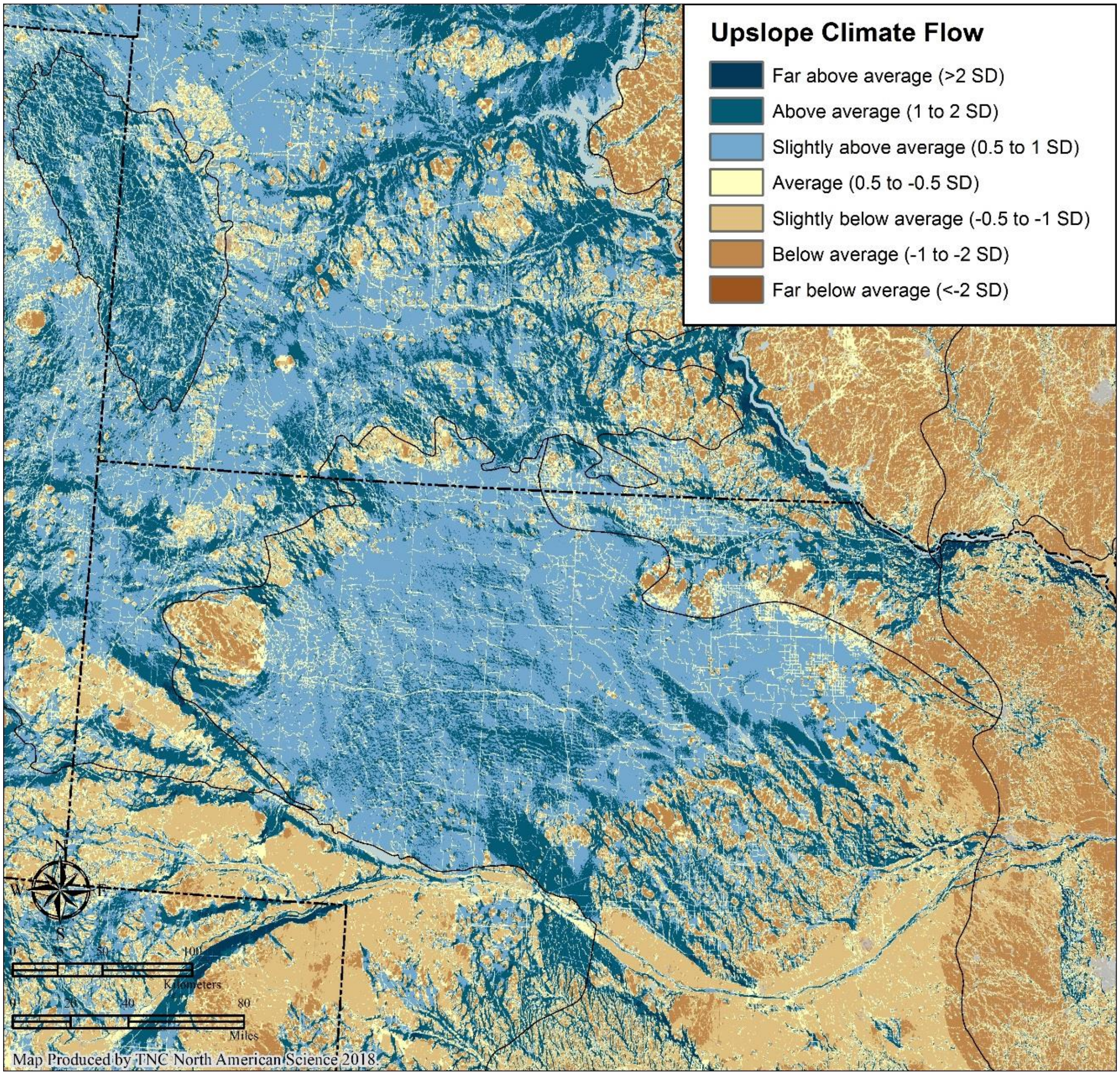
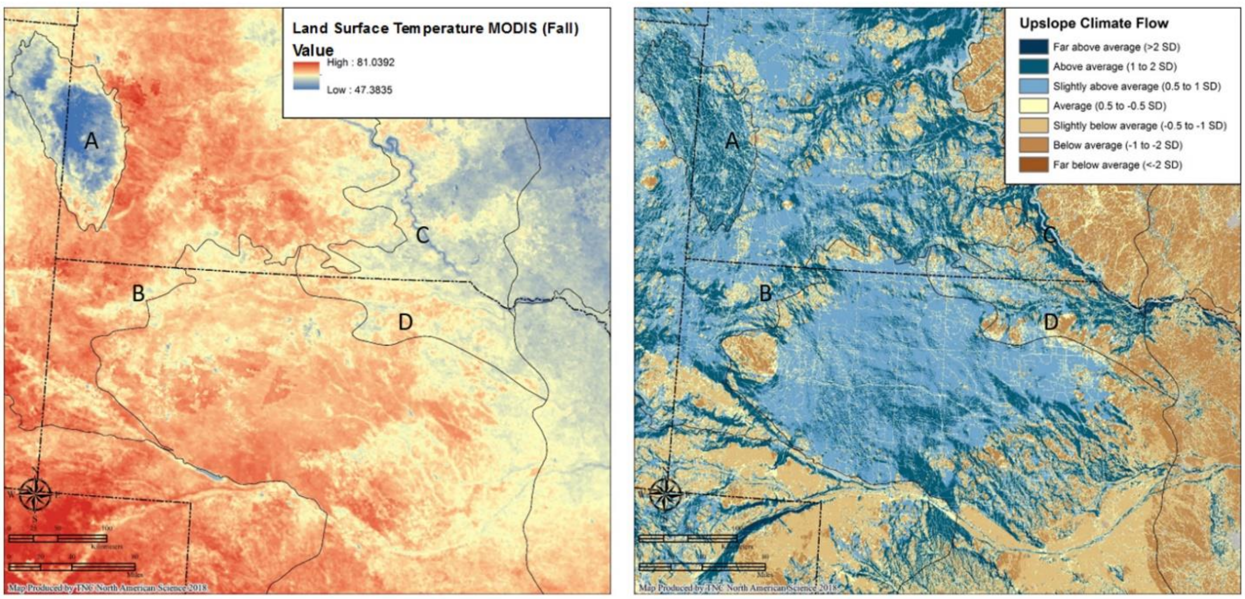


Figure 3.13. Comparison of upslope model with MODIS land surface temperature (LST) for the Sandhills Region. This figure shows the correspondence between topography and surface temperature in fall. The LST model is MODIS (MOD11A2.006) Terra Land Surface Temperature and Emissivity 8-Day Global average at a 1km scale for September 2018 in Fahrenheit. Although the scale of the LST model is coarse, local cool spots can be seen to correspond with the topography and the upslope model especially in: A) higher elevation of the Black Hills; B) finely dissected hills within Nebraska National Forest; C) cliffs and bluffs along the Missouri river, D: riparian slopes along the Niobrara river.



Downslope Model: Access to Local Moisture

As described in Chapter 2, riparian areas are usually a minor proportion of any landscape but they serve and outsize role in facilitating adaptation to climate change. In a previous study (Anderson et al 2013) we identified distinct riparian climate corridors (RCC) for the Eastern US and measuring a variety of characteristics about each RCC unit such as its size, length, intactness, temperature change. That work was inspired by Krosby et al.'s (2014) analysis for the Pacific Northwest where they identified potential riparian areas that spanned large temperature gradients, had high levels of canopy cover, were relatively wide, had low solar insolation, and low levels of human modification – characteristics expected to enhance their ability to facilitate climate-driven range shifts and provide microclimatic refugia from warming.

Here, we present a new approach that measures the potential contributions of downslope movement continuously across the whole landscape, rather than identifying individual corridors and summarizing their attributes. As with upslope movement, we evaluated where downslope movements were likely to concentrate or where they facilitate high current flow. This new approach emphasizes downslope and riparian areas as collectors of climate-driven movement from the surrounding landscape. It decreases the emphasis on directional movement within the riparian areas, although many of the resulting corridors traverse and connect large parts of the landscape and may facilitate movement for many species. We hypothesized that species could experience additional moisture, deeper soils, and local temperature relief by moving into these relatively lower areas.

Mapping Downslope Movement

To model downslope movement, we first identified areas that were downslope and lower in elevation than the surrounding landscape. We did this by creating a continuous 30-m dataset that assigned a relative elevation value to every cell by comparing its elevation to its neighbors within a 3 km radius neighborhood (the same radius used calculate upslope local flow and to calculate local connectedness in the resilience analysis). We used a focal statistic to calculate the mean and standard deviations of the elevations within a 3 km radius, and then calculated a Z-score for each cell based on the neighborhood mean and standard deviation. Values below the mean were lower than their neighborhood and values higher than the mean were higher in elevation than their neighborhood, and these values became the resistance values.

We used the Z-Scored relative elevation surface as a resistance grid in Circuitscape to force current to flow more easily into and throughout the downslope areas as they had less resistance. To give additional benefit to flow in moist areas, we integrated the landform model (described earlier in this section) into the resistance grid and further lowered the Z score within "wet flat" and "moist flat" landforms. Areas with these two landforms were extracted from the landform dataset and their Z-Score was lowered to one half of a standard deviation below average (-0.5 SD) for moist flats and one standard deviation below average (-1.0 SD) for wet flats if the elevation-based Z score was not already less than the respected scores. This lessened the resistance slightly in moist and wet areas allowing current to flow more easily. This moisture enhanced Z-scored resistance surface was used as the downslope resistance grid in further Circuitscape flow modeling. We tested the model in Circuitscape by running current through it in all directions ("wall-to-wall" as described for the regional flow model) to create an output of "current" flow based on the downslope and moisture-enhanced resistance surface. The output tracked downslope moisture patterns at a fine scale.

To create the final downslope model we combined the downslope, moisture-enhanced resistance grid with the anthropogenic resistance grid to create a resistance surface that favored moving downslope but was sensitive to anthropogenic barriers. We found that in a 50/50 weighting, the anthropogenic grid had little influence on the results. To create a more realistic model we increased the weight of the anthropogenic resistance dataset so that the final resistance score of each cell was 10% from the downslope resistance value and 90% from the anthropogenic resistance value.

The Circuitscape analysis on the resultant resistance grid shows how the areas with high potential for downslope and moist range shifts are arranged locally and across the region, and how they intersect with anthropogenic resistance (Figures 3.15 -3.16).

Figure 3.14. Downslope model. This map shows the results of the moisture-enhanced downslope model with anthropogenic resistance weighted at 90% and downslope flow weighted at 10%.

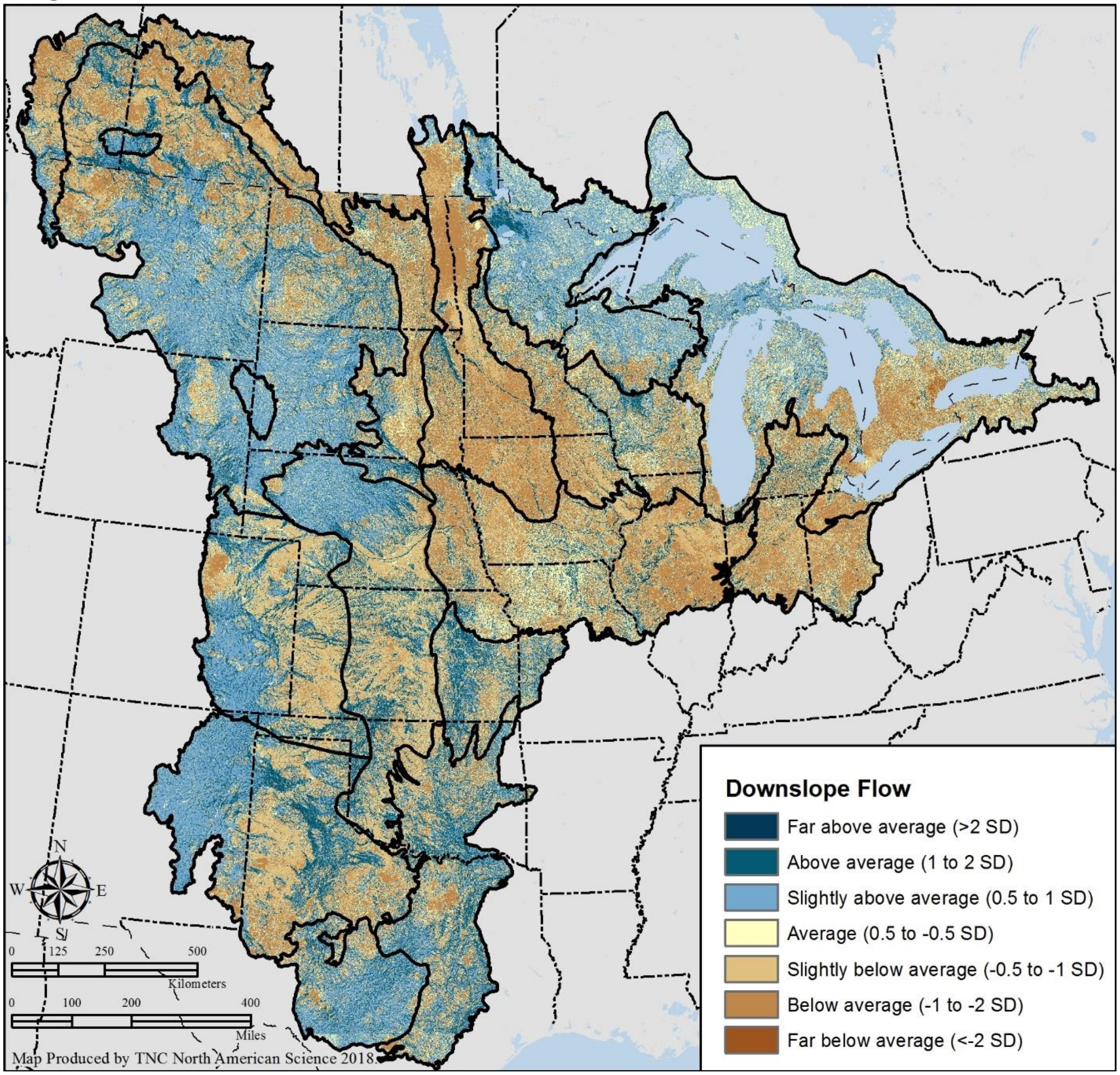
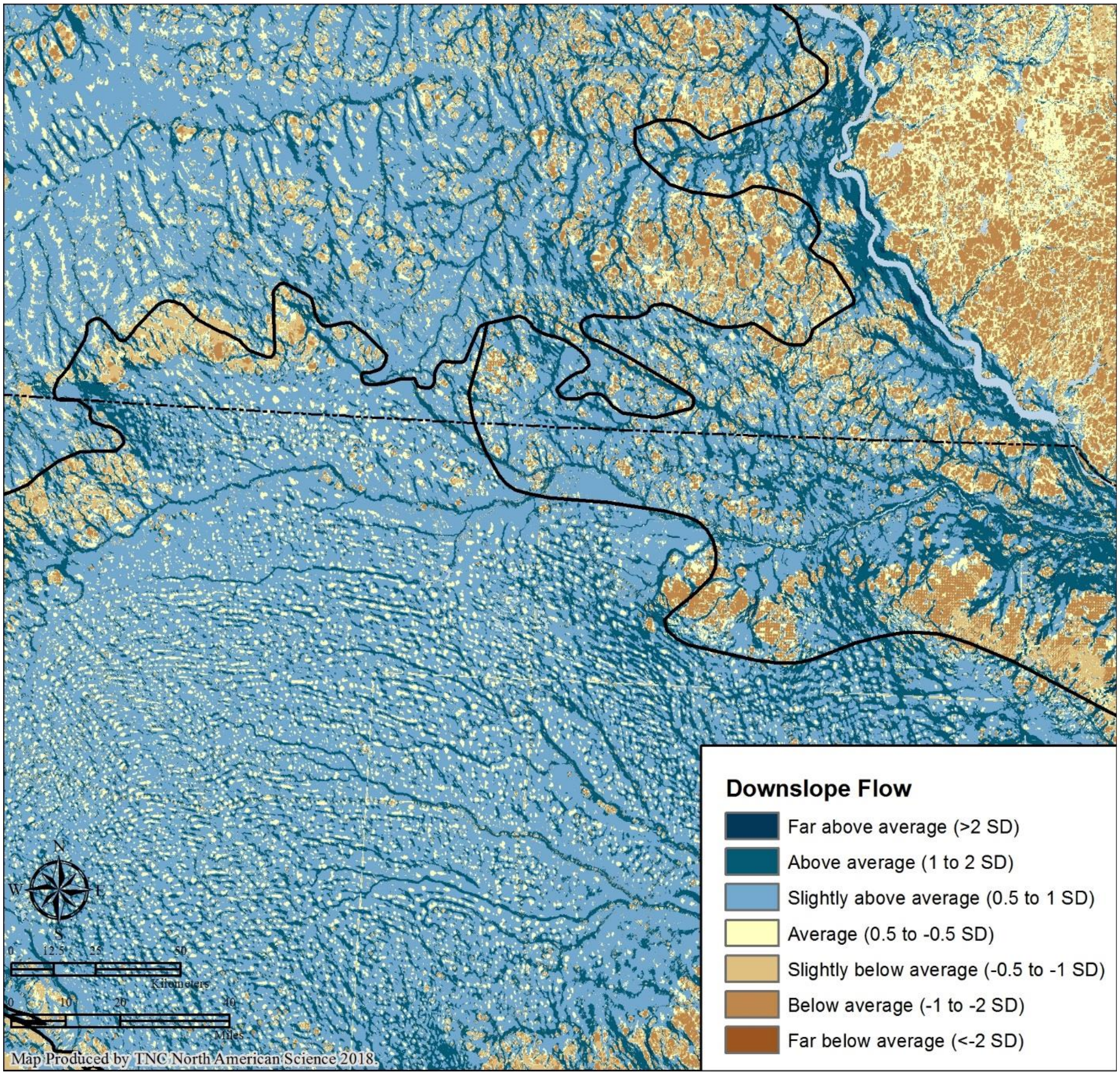


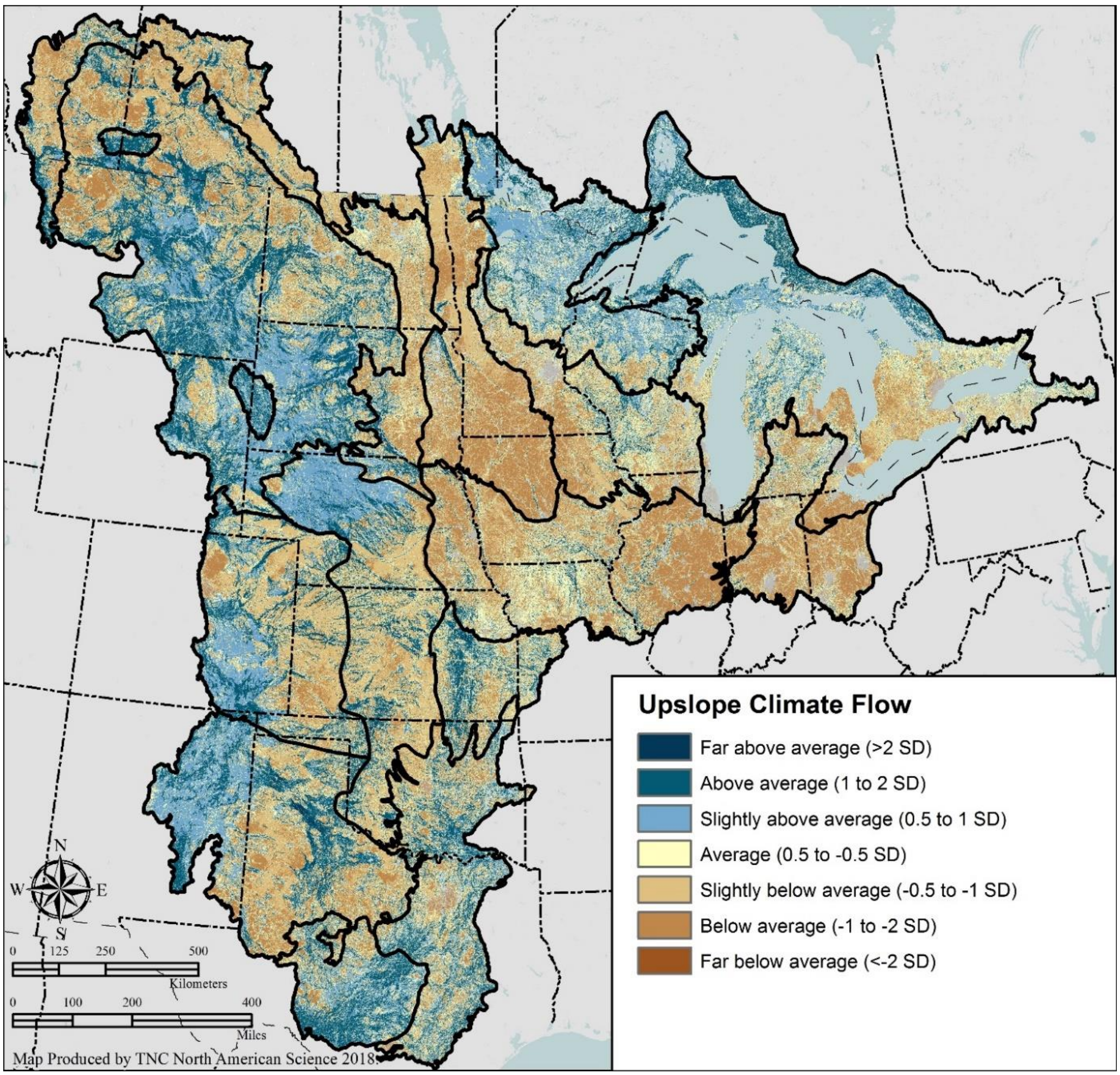
Figure 3.15. Zoom in of the downslope models. This map shows a zoom in of the same model as 3.19 for the Sandhills region of Nebraska. Current flow clearly tracks small and large rivers as well as swales and basin wetlands, except in areas with high anthropogenic resistance such as the industrial farmland in the upper right.



Northward Model: Regional Temperature Relief

To simulate long-term climate relief for populations that expand or shift northward, we added latitudinal direction into the climate flow model. We did this by modifying the four directional runs we used to develop the regional flow model (i.e., north to south, south to north, east to west, and west to east, see previous section for details) to emphasize the northward flows. We did this by combining the four individual runs so the north-south runs contributed 60% of the flow value and east-west runs contributed 40% of the flow value (Figure 3.16).

Figure 3.16. Northward model. This map shows regional flow model with north-south movements weighted at 60% and east-west movements weighted at 40%.



Final Climate Flow Model: Integration of Slope and Latitude

For our final model, we weighted the regional flow model with the upslope, downslope and northward models to simulate species populations flowing through the natural landscape finding climate relief moving up or down slopes, mostly in a northward direction. The goal was to approximate a species population expanding locally then northward as allowed by the anthropogenic resistance within its neighborhood.

As with all spatial analyses that involve expert-derived weighting of multiple factors, we faced the challenge of how to weight the influence of each factor in a way that most closely approximates the real world. We wanted to keep the emphasis on the areas that are important for regional flow, while boosting slightly the areas that channel slope-based and northward movements. We met this goal by using the regional flow map as our based dataset, and then boosting the score of cells if they were important for upslope, downslope or northward movement. For each of the three factors we took the areas that were above-average with respect to their factor:

Upslope = >1 SD above the mean,

Downslope = >0.5 SD above the mean,

Northward = >1 SD above the mean

We overlaid each factor on the regional flow map and replaced the cell score if the cell score for the factor was higher. For example, a cell score of 1.2 for Upslope would replace a Regional Flow score of 1.0, giving a slight bump-up to the cell reflecting its slope. If several factors had scores higher than the regional flow score we replaced the latter with the highest score. This approach had the effect of raising the scores in areas with above-average current flow for upslope, downslope, or northward movement but still retaining the regional flow score, and thus not penalizing areas for not having slopes or a northward orientation (Figure 3.17, with comparison of components in Figure 3.18).

Classified Version of the Climate Flow Map

To produce our final climate flow map (Figure 3.19) we used the same method described previously for the regional flow. The amount of flow was calculated by looking at the mean flow within a 1000-acre circle (440 hectares, 1.135 km radius circle) of each cell. We calculated the variation in a local neighborhood by looking at the standard deviation in a local neighborhood. Areas that had high flow and high standard deviation in flow were classified as concentrated flow areas. Areas that had above average flow and low standard deviation were classified as diffuse flow. Areas with less flow were classified as constrained or blocked flow.

Figure 3.17. Climate flow model. The results of a Circuitscape analysis applied to the regional flow grid and weighted for above-average upslope flow, downslope flow or northward flow. Areas of high current flow are predicted to be important for temperature or moisture driven range shifts because of their physical characteristics and because human fragmentation patterns channel flow through these areas.

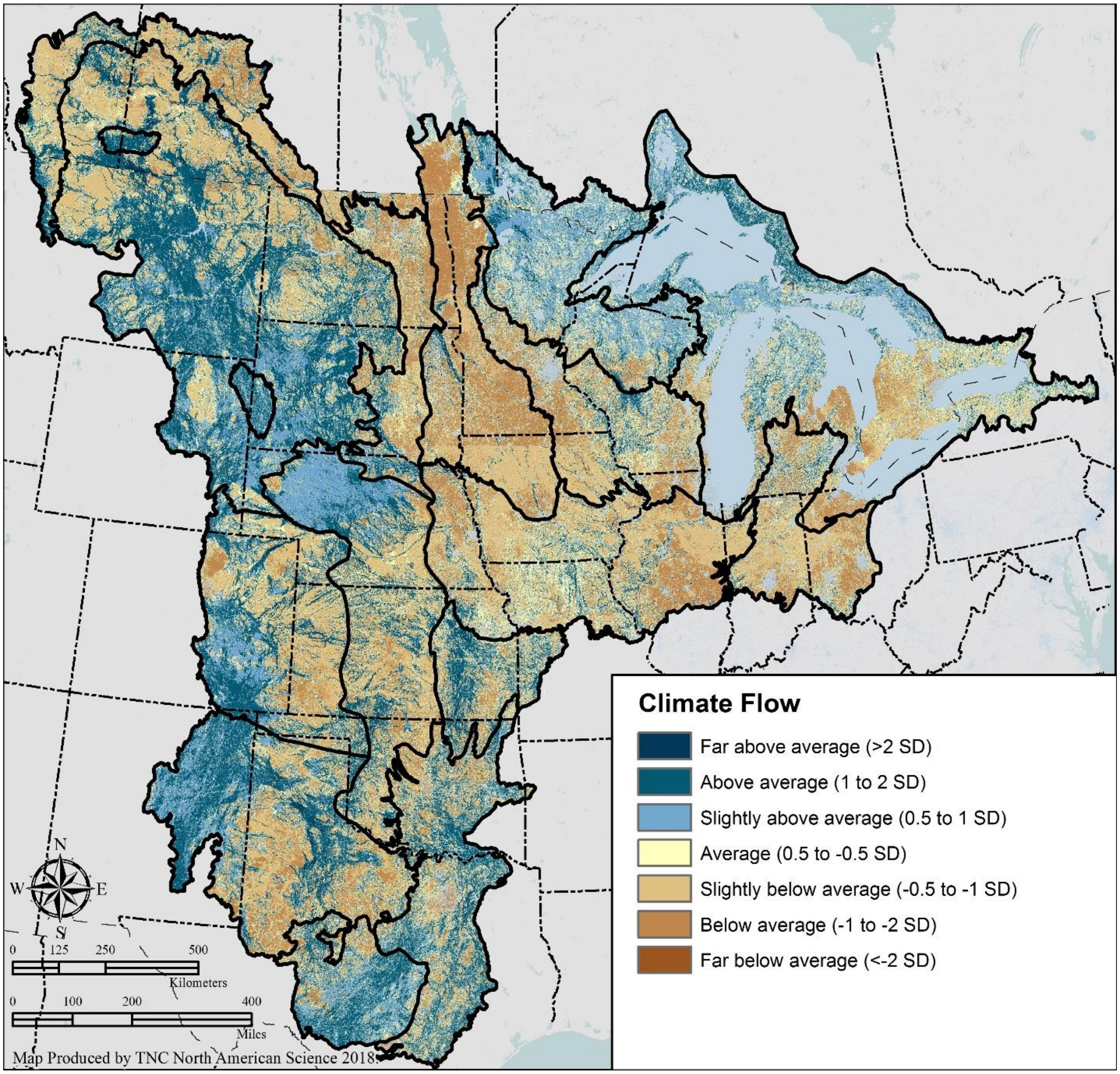


Figure 3.18. Comparision of results. These maps for the Sandhills region compare the Circuitscape results for Regional Flow based on anthropogenic resistance only, with the enhanced versions that include upslope flow, downslope flow, northward flow and the integrated Climate Flow.

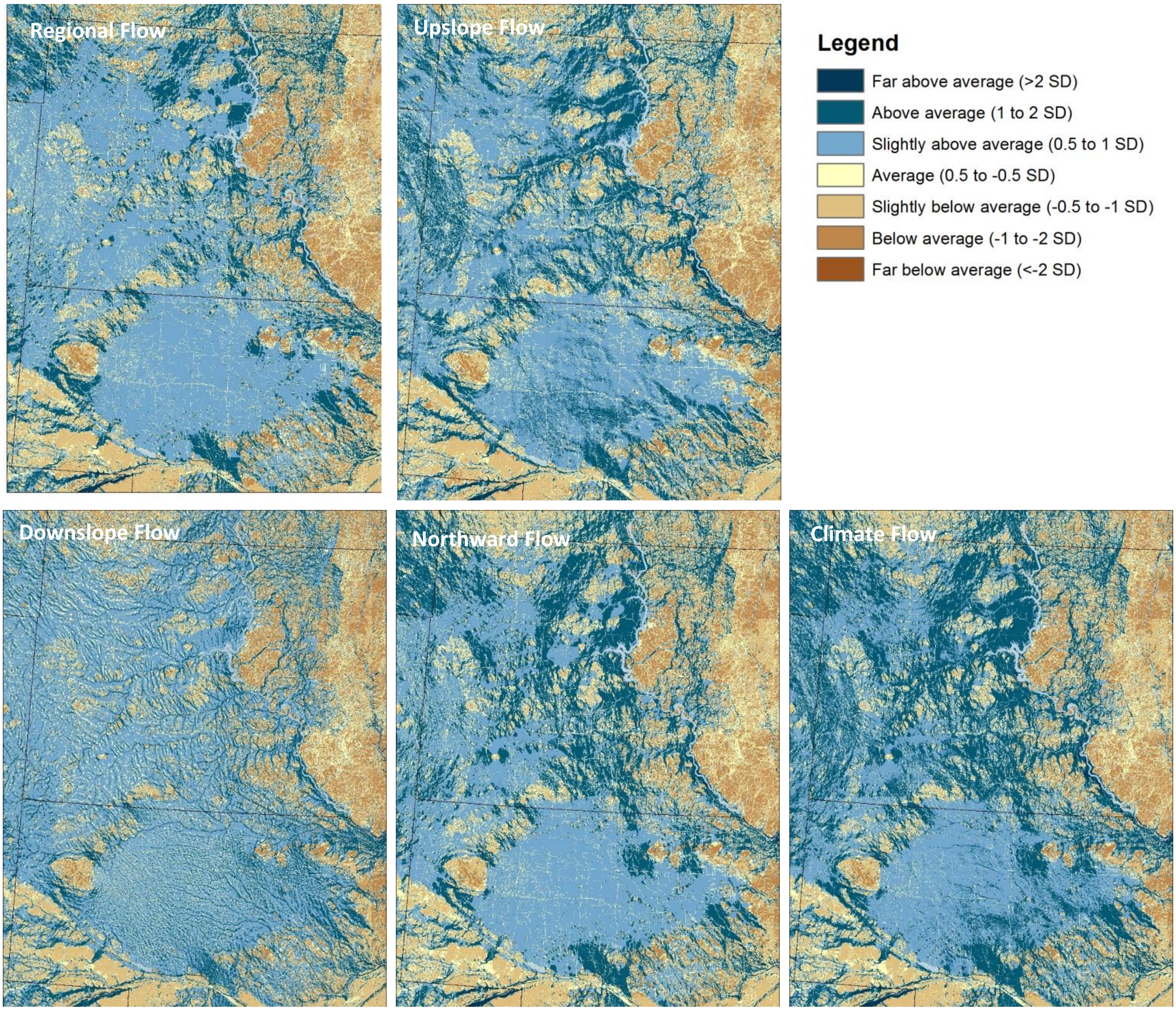
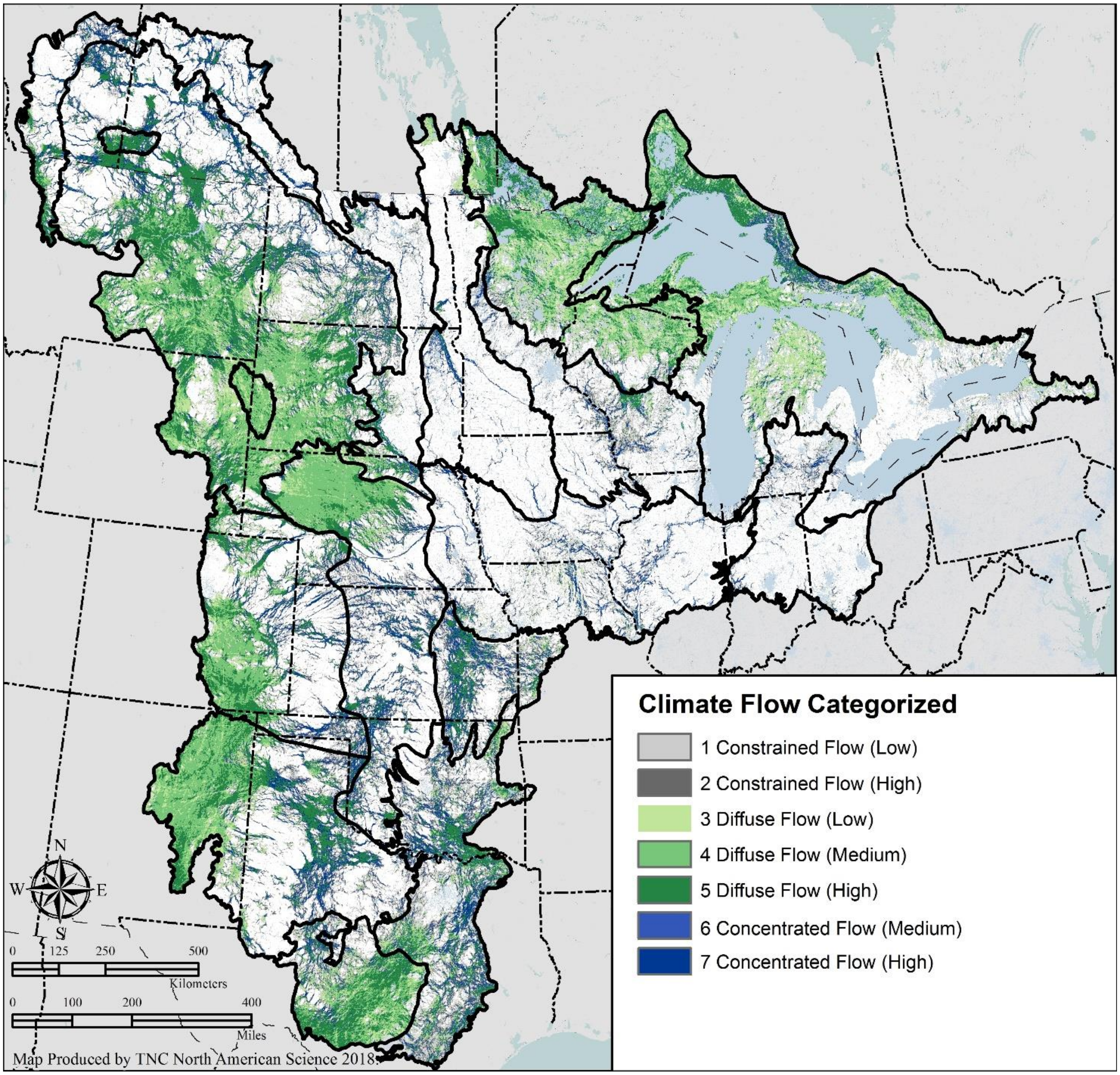


Figure 3.19. Classified climate flow model. The results of classifying the climate flow map into 7 categories of flow density and spread. White areas indicate places where flow is impeded.



Access to Local Microclimates

This section built upon the literature review in Chapter 2 showing evidence for contemporary range shifts. We suggested that population movement responses to climate change could be grouped into four main patterns: upslope toward higher elevations, northward toward cooler latitudes, downslope toward moist riparian areas, and locally toward suitable microclimates. The former three have been discussed previously and represent larger scale responses. The latter is a very small-scale response where a population shifts slightly over time to take advantage of a moist spot or cool microclimate and thus persist at a site.

Local microclimates may be the primary mechanism for species persistence under a changing climate for most organisms. Species experience climate at extremely local scales and the available moisture and temperature in the near-ground "boundary layer" can differ greatly from the local average (Geiger et al. 2009). Thus, a topographically diverse landscape is experienced by its resident species as a heterogeneous mix of microclimates, many of which might be suitable for persistence even where the average background climate appears unsuitable. Landscape-based climatic variation can be substantial, on par with or greater than a 1.5°C warming. Vegetation cover also has a large influence of ground-based microclimates and can amplify or buffer the effects of topography.

The focus of this report has been on mapping larger scale, between-site responses to climate change, and because mapping the distribution of microclimates is the basis of the climate resilient site analysis (Anderson et al. 2018a&b), we do not address it further here. However, microclimates are an important part of how species respond to climate change. Further, areas of high microclimate diversity are an important part of the upcoming chapter "Resilient and Connected Landscapes" because they are integrated into the resilient sites which form the base of the connected networks.

CHAPTER

4

BIODIVERSITY

Confirmed Areas for Biological Diversity

The central idea of a conserving-the-stage approach to conservation is that rather than trying to protect biodiversity one species at a time, the key is to conserve the geophysical "stages" that create diversity in the first place at local and regional scales (Anderson & Ferree 2010, Beier & Brost 2010, Lawler et al. 2014). Species ranges are not fixed, and the world has always experienced some measure of climate change. Thus, protecting the full spectrum of physical environments that provide habitat for distinct sets of species offers a way to conserve diversity under both current and future climates (Hunter et al. 1988). Toward that end, a separate analysis of resilient sites (Anderson et al. 2018a&b) identified examples of each distinct geophysical setting that had the most microclimates and local connectedness but did not consider the confirmed diversity present at each location. Here we integrate information on the current location of species and communities with the physically based resilience map.

To identify a network of sites that could likely sustain biological diversity into the future, we wanted the network to be composed of climate resilience sites that contained the maximum amount of current biodiversity. Thus, in this section, we prioritized sites that scored high for resilience and contained viable rare species populations, exemplary natural communities, or served as critical migratory bird stopover sites. We began by identifying and prioritizing climate-resilient areas that had been recognized as important areas for biological diversity in previous studies by TNC or state agencies, and we supplemented this with known locations of biodiversity elements in those settings that were not well represented in the existing studies.

To identify areas of high biodiversity value we compiled the results of two sets of intensive, multi-year studies on the locations of exemplary habitats and rare species populations: TNC's Ecoregional Plans, and Conservation Opportunity Area maps or related map products developed as part of State Wildlife Action Plans (SWAPs). We assessed how well these two sets of maps represented the full suite of geophysical settings. In cases where specific geophysical settings were not well represented in the mapped priorities, we supplemented these maps with known occurrences of rare species and communities (NatureServe element occurrences, or EOs) when available; otherwise, for those settings, we identified the largest areas of very high estimated resilience within the relevant ecoregion.

The Nature Conservancy's Ecoregional Portfolios

From 1998 to 2006, The Nature Conservancy implemented a series of biodiversity assessments across each of the United States' 81 terrestrial ecoregions. The goal of each assessment was to identify a portfolio of sites that, if conserved, would collectively protect multiple viable examples of a set of focal conservation targets -

species and communities characteristic of, or unique to, each ecoregion. Although the assessments were performed independently by ecoregion, the data are relatively consistent because the teams followed a similar methodology and applied a standard set of criteria (Anderson et al. 1999, Groves et al. 2003). Viability criteria were based on the size, condition, and landscape context of each biodiversity element (EO), and the results were reviewed by local experts familiar with the species and communities of the ecoregion. The assessments were performed and evaluated by teams of scientists from both TNC and other NGOs or agencies. The final selection of sites was based on the viability of each target occurrence combined with a set of numeric distribution and representation goals set for each target. In most regions, "sites" were drawn around clusters of viable targets using roads, property boundaries, or some other delineating feature. In a few ecoregions (i.e. Central and Southern Shortgrass Prairie) optimization tools were used to map a portfolio of "sites" using hexagons as a consistent sampling unit. In addition to describing the targets, assessment process, and final portfolios, the reports detail the extent to which the portfolio met the stated goals for each conservation target. In some cases, lack of data, low numbers of occurrences, or poor target viability were important constraints to identifying a robust portfolio. Published versions of each report are publicly available on TNC's Conservation Gateway along with many of the supporting datasets: http://www.conservationgateway.org/ConservationPlanning/SettingPriorities/EcoregionalReports/Pages/EastData.aspx

We obtained the national "roll-up" version of the TNC ecoregional portfolios and overlaid it on the spatially continuous map of resilience scores for the Great Plains and the Great Lakes and Tallgrass Prairie assessment regions. To identify areas of confirmed biodiversity value, we selected the portion of each portfolio site that scored above-average for resilience (cells that were greater than one standard deviation above the mean resilience value for the respective ecoregion). This resulted in 35% (102 million acres) of the resilient land in the study area being identified as having confirmed diversity value.

Across all the TNC portfolios, 58% of areas within the focal polygons scored "above-average" for resilience, with 30% scoring "average" and 13% "below-average." To test how well the known locations of biodiversity elements were concentrated in the resilient portion of the TNC portfolios we overlaid the individual locations of species and communities (known as "element occurrences" or "EO") in the states where we had relatively comprehensive data on the locations of biodiversity element. We found that 76% of the EO locations in the Great Lakes and Tallgrass Prairie ecoregions and 70% of the EO locations in the Great Plains ecoregions were located on the above-average resilience portion of the portfolio roll-up. Additionally, the pattern of the majority of EOs occurring on above-average resilience sites was consistent across taxonomic groups: 75% of animal, 81% of plant, and 73% of community EOs in the Great Lakes and Tallgrass Prairie region, and 65% of animal, 86% of plant, and 76% of community EOs in the Great Plains were on these resilient sites. This gave us confidence that identifying the resilient portion of each portfolio site would do a good job of capturing biodiversity elements across the region, thus allowing us to incorporate an indicator of known biodiversity in data-poor areas.

State Wildlife Action Plans

In the US portions of the focal ecoregions, we supplemented the TNC ecoregional portfolio data with datasets and priority maps developed by the states as part of their State Wildlife Action Plans (SWAPs). The SWAPs were created by each state's Fish and Wildlife agency (or equivalent), in collaboration with academic and agency scientists, conservation practitioners, private landowners, and other stakeholders, with the goal of providing resource assessments and blueprints for conserving the state's fish and wildlife. To be approved by the US Fish and Wildlife Service (USFWS), each plan had to address eight requirements laid out by the US Congress. USFWS approval is required for states to be eligible to receive funding through the State and Tribal Wildlife Grants program. First iterations of the plans were completed in 2005, and they were updated in or by 2015, with some pursuing additional revisions.

To develop the SWAP, the assessment teams identify "Species of Greatest Conservation Need" (SGCN) and then assess habitats, risks, and actions needed. States vary in their approach for developing these lists –all include mammal, bird and fish species, and many also include insects and other invertebrates, and some include rare plants or habitats. Many plans from our focal regions developed a map of "Conservation Opportunity Areas," which incorporate key locations for focal species, and are similar in concept to TNCs ecoregional plans, though COAs may be prioritized based on other factors, such as partnerships that are already in place, or available funding. In many states, TNC's ecoregional plans were important inputs to the assessment process. The methods for developing COAs varied, with some states creating detailed maps of terrestrial and aquatic biodiversity, and others working primarily with existing prioritizations from partners and stakeholders. Several states in the Great Plains assessment area incorporated use of a modeling tool called the "Crucial Habitat Assessment Tool" or CHAT, which uses a consistent hexagonal assessment unit, and focuses on habitat. Applications of this tool include development of maps intended to reduce potential wildlife-development conflicts by highlighting essential habitat areas (http://www.wafwachat.org/about).

With assistance from our Steering Committee, we reached out to SWAP coordinators to obtain the SWAP COA spatial dataset, and/or other spatial data that represented the distribution of wildlife/biodiversity priorities in their state. In cases where there were multiple data layers available and it was not clear which was most equivalent to the TNC biodiversity portfolio (i.e., a COA, a CHAT map, and maps indicating highest overlap in SGCN range maps, for example), we talked with the developers via phone or Web Ex to understand the intricacies of the data. For a few states, potentially useful datasets were not yet complete (some states are continuing to develop additional map products). In all, we obtained spatial data for all states except Oklahoma and Arkansas, which do not currently have a COA or similar map. For Wyoming we used (with permission) a COA map that was in an earlier SWAP but removed during the update process in favor of providing individual component maps to stakeholders.

In Canada, we compiled a biodiversity portfolio identified by Nature Conservancy Canada (a Canadian NGO, not affiliated with the US Nature Conservancy) that was similar in scope and assessment methods to the TNC portfolio. Details on the sources of data for each state are shown in Table 4.1.

Table 4.1. Spatial data from State Wildlife Action Plan (SWAP)s or similar state assessments, and Nature Conservancy of Canada, to identify wildlife/biodiversity priority areas.

Note: Most datasets were obtained directly from SWAP coordinators (current contact info can be found on the web pages that we link to for each state), but in cases where these data are publicly posted, we have included the web link. Acronyms: SGCN = Species of Greatest Conservation Need; COA = Conservation Opportunity Area, CHAT = Crucial Habitat Assessment Tool.

State & plan date, Title of map	Comments & link to the plan and dataset if publicly posted
Arkansas (2015): None.	In the plan they rank the ecoregions by number of SGCN (Fig 3.3 in the SWAP), but do not present mapped priorities at more local scales. www.wildlifearkansas.com
Colorado (2015): Crucial Habitat for Tier 1 Terrestrial Animal and Plant SGCN (Figure 21).	The state was mapped into 5 priority levels for crucial habitat for SGCN, and we incorporated the two highest levels into our composite SWAP map. Details on the map methodology are in Chapter 8 of the Colorado plan. http://cpw.state.co.us/aboutus/Pages/StateWildlifeActionPlan.aspx
Iowa (2015): High Opportunity Areas for Cooperative Conservation Actions (Map 8-25).	This map sums the priorities from 22 terrestrial and aquatic assessments from field staff and many partners. Values range from 1-12, indicating the number of plans that highlighted each pixel. We selected areas that scored 4 or above (i.e. were identified in four or more of the component maps). The sources and methods are in Chapter 8. http://www.iowadnr.gov/Conservation/Iowas-Wildlife/Iowa-Wildlife-Action-Plan
Illinois (2016): COAs currently recognized through the Illinois Wildlife Action Plan (Figure 1).	Defined as "areas with significant existing or potential wildlife and habitat resources; places where partners are willing to plan, implement, and evaluate conservation actions; where financial and human resources are available, and where conservation is motivated by an agreed-upon conservation purpose and set of objectives" Centered on dataset of state's key blocks of habitat & the corridors that connect them. We removed polygons identified as rivers. https://www.dnr.illinois.gov/conservation/iwap/pages/default.aspx
Indiana (2015): Indiana conservation opportunity areas (Figure 5-22).	COAs were designated based on SGCN distribution data, unique habitat communities, assessment of long term viability, current conservation actions and partnerships, threat assessment, and connectivity/potential to reconnect, and likelihood of obtaining funding. We used just the terrestrial polygons. https://www.in.gov/dnr/fishwild/7580.htm
Kansas (2016): Terrestrial Ecological Focal Areas (Chapter 2, Figure 3B).	Designated "Ecological Focus Areas" – landscapes where conservation actions can be applied for maximum benefit to all Kansas wildlife (Ch. 2, p. 8). Each includes a suite of SCGN and priority habitats, and a "unique set of conservation actions designed to address the specific resource concerns facing these species and habitats." Data layers include large natural areas & connectivity from the CHAT. https://ksoutdoors.com/Services/Kansas-SWAP
Michigan: Biodiversity Stewardship areas	Not from the SWAP but recommended and shared by the SWAP coordinator as the most appropriate dataset for Michigan. Developed through an intensive statewide process to develop a map of high priority areas for protecting biodiversity approximately 10 years ago. Informed the current SWAP, but map not presented in the 2015 plan.

Minnesota (2015): The Wildlife Action Network map, terrestrial components (Fig 1.3)	The Wildlife Action Network incorporates SGCN populations and sites with high SGCN richness, as well as viability. It serves three purposes: 1) addresses large-scale habitat stressors such as climate change, fragmentation, and invasive species; 2) increase the efficiency of actions by the conservation community; 3) prioritize and focus conservation through an additional step of identifying Conservation Focus Areas (a prioritization for the next 10 years). https://www.dnr.state.mn.us/mnwap/index.html https://gisdata.mn.gov/dataset/env-mnwap-wildlife-action-netwrk
Missouri (2015): 2015 Conservation Opportunity Areas separated by habitat systems (Fig. 4)	In the MO SWAP, COAs were divided by type (grassland, forest, river, etc.) and each had a different set of scoring criteria. For grasslands, the criteria include a pre-settlement prairie layer, current land condition from NLCD, and community records from the Heritage Program database. We used just the terrestrial system COAs. https://mdc.mo.gov/sites/default/files/downloads/SWAPopt.pdf
Montana (2015): Tier 1 Terrestrial Focal Areas (Fig. 133)	The plan delineates habitat (plant communities) of most critical conservation need as well as SGCN, emphasizing SGCN with state ranks of S1 or S2. The plan notes differences in the process east and west of Continental Divide; the east focused more on intact landscapes, while teams in the west focused more on connectivity between protected areas. http://fwp.mt.gov/fishAndWildlife/conservationInAction/actionPlan.html
Nebraska (2015): Nebraska Natural Legacy Project: Biologically Unique Landscapes and Demonstration Sites	Identified Biologically Unique Landscapes (BULs) – based on key habitats, Heritage Program data on locations of natural communities, and at-risk species. Incorporated a fine filter of Tier 1 and Tier 2 species; the list includes vertebrates, mollusks, insects, and plants (768 species). Incorporated Spatial Analysis Optimization Tool (SPOT) and Natural Heritage Program Hotspot analysis but did not attempt to capture corridors/connectivity. Map also includes Natural Legacy demonstration sites. We removed rivers and streams. http://outdoornebraska.gov/naturallegacyproject/
New Mexico (2016): Conservation Opportunity Areas (Fig. 11)	Defined as areas considered to have superior potential for conserving SGCN. Incorporates priority habitats from assessments with the New Mexico CHAT tool. This priority habitat layer was intersected with 5 other GIS layers, including SCGN point locations, species distribution model polygons for SCGN, large intact blocks from CHAT. The weighting scheme included availability of funding. Clusters with scores in the top 10% were selected as COAs. http://www.wildlife.state.nm.us/conservation/state-wildlife-action-plan/
North Dakota (2015): North Dakota State Wildlife Plan focal areas (Figure 7)	The plan notes that "focus areas typically exhibited unique or easily identifiable differences in vegetation, soils, topography, hydrology, or land use. Focal areas are highly variable in size and often represent an area of native vegetation or a natural community type rare to North Dakota." We removed the river and stream focal areas. https://gf.nd.gov/wildlife/swap
Ohio (2015): COAs in individual maps – for example, Appalachian Foothills Forest COA (Fig 11).	A set COAs were developed by habitat type. "The idea is to concentrate efforts and resources to provide all the necessary habit requirements in a few, relatively large landscapes of major habitat types, along with the remnants of several unique habitats, for species that are of limited distribution or have low populations." COAs tend to connect nearby public lands/protected areas. We obtained a shapefile

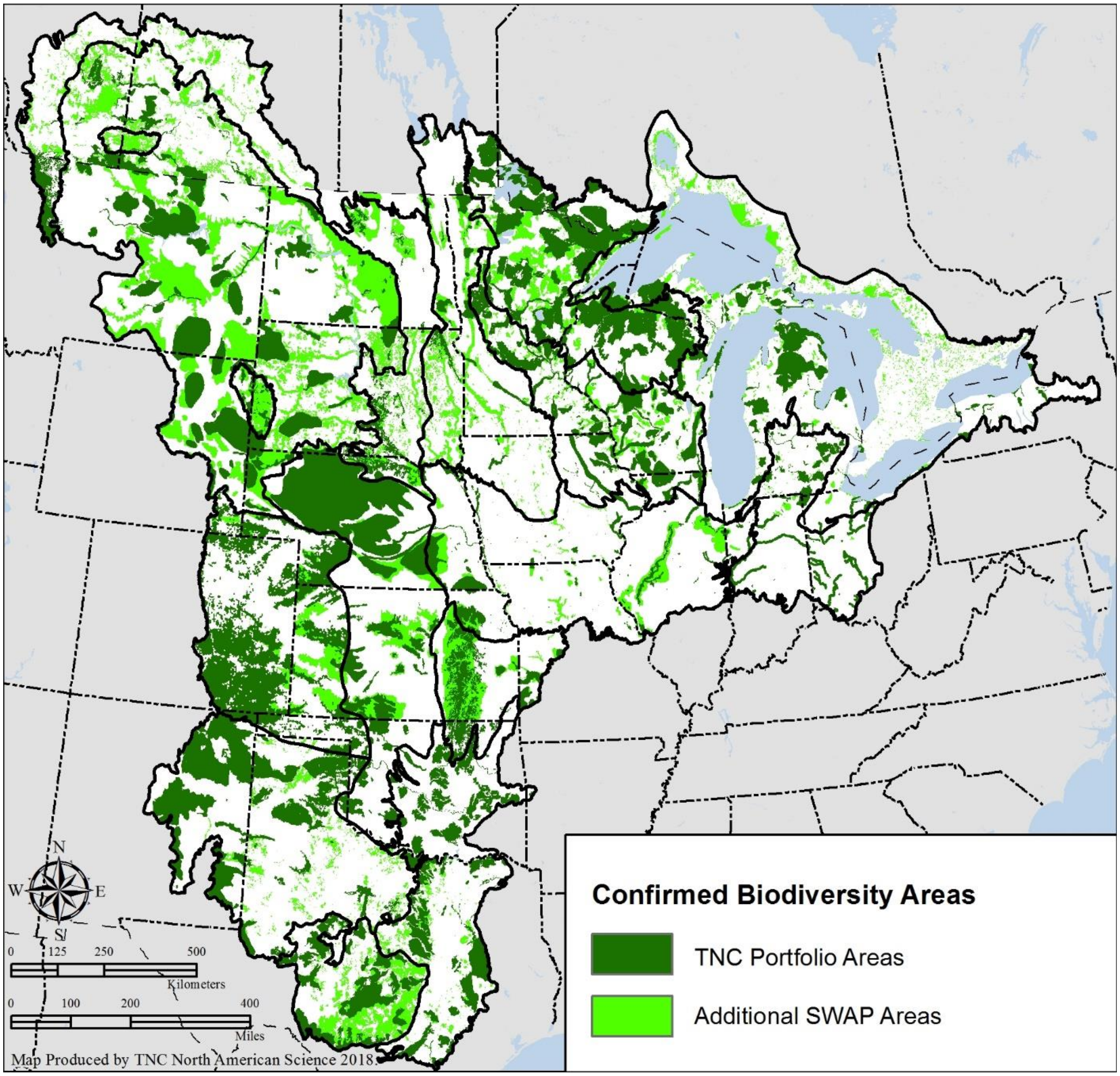
	with all terrestrial COAs from the plan coordinator. http://wildlife.ohiodnr.gov/ohioswap
Oklahoma (2015): None.	Focus area delineation is in progress.
South Dakota (2015): Map of terrestrial conservation opportunity areas (Fig. 6.6).	Terrestrial and aquatic COAs were proposed to encourage voluntary ecosystem restoration with an emphasis on the occurrence of SGCN and intact native habitats (101 SCGN were identified). Used NRCS Major Land Resource Areas as framework, then within each, attempted to meet the goal of maintaining more than or restoring at least 10% of primary historical ecological ecosystems for each ecological site type. Incorporated large intact blocks from CHAT model, species richness data & other sources. https://gfp.sd.gov/wildlife-action-plan/
Texas (2012, revising now):	Texas in in the process of revising their plan and has two types of assessments that were appropriate for this application, but only one was complete at the time of our compilation. We have incorporated an assessment a CHAT product, which incorporates SCGN distributions, but is primarily intended to identify sensitive resources and direct development away from them. This map draws information from an aggregated biodiversity value metric that is not yet complete for the state. The CHAT map uses these terrestrial maps as input, prioritizing areas that have confirmed presence and high-quality habitats. These "in progress" products were shared directly by the plan developers and are not in the current SWAP.
Wisconsin 2015: Wisconsin Conservation Opportunity Areas (multiple regional maps).	COAs were defined as places on the landscape that contain significant ecological features, natural communities, or SCGN habitat for which WI has responsibility. These were ranked by global, continental, Upper Midwest, and state priority. The report presents separate terrestrial and aquatic COAs. We incorporated all these levels. https://dnr.wi.gov/topic/wildlifehabitat/actionplan.html A compiled statewide map is here: https://dnr.wi.gov/topic/WildlifeHabitat/documents/MapCOA_statewide.pdf
Wyoming (2010): No map in the 2017 revision, but we incorporated SGCN priority areas from the 2010 plan.	Wyoming defined COAs in the 2010 SWAP based on a MARXAN analysis of priority habitats for SCGN for a suite of habitat types (input maps are shown in Figs 1-10 and 15 in the 2010 plan). This prioritization was not included in the 2017 SWAP revision, as stakeholders in Wyoming preferred access to input datasets on overlap in SCGN ranges, landscape intactness, etc., rather than the final prioritization product. We included this 2010 product but note that this is not a product that WY is currently using to guide implementation. Links to the 2017 and the 2010 plan: https://wgfd.wyo.gov/Habitat/Habitat-Plans/Wyoming-State-Wildlife-Action-Plan
Canada (2007) – Conservation Blueprint for the Prairie and Parkland ecoregions (Fig. 33)	The methods for the Nature Conservancy of Canada's Prairie and Parklands Conservation Blueprint are like those used in TNC's ecoregional planning – a combination of coarse and fine filter conservation targets were used to identify and map biodiversity priorities. http://support.natureconservancy.ca/pdf/blueprints/Prairies_and_Parklands.pdf?_ga=2.200626025.670120404.1537991172-628480056.1533841894

Using the same overlay methods as for the TNC portfolio described above, the SWAP analysis identified 79 million acres of resilient land of which 47% overlapped with the resilient portions of the TNC portfolio. We added the additional 42 million acres to those identified by the TNC portfolio, bringing the total acres of resilient land with confirmed biodiversity to 144 million acres. The amount of resilient land with confirmed biodiversity varied widely by ecoregion and region and ranged from a low of 19% in the Central Tallgrass Prairie to a high of 79% in the Black Hills (Table 4.2). Over the entire study area, the confirmed biodiversity areas comprised 50% of the resilient area and 18% of the total land assessed (Figure 4.1).

Table 4.2. Percent overlap of confirmed biodiversity sites with resilient areas. The final column (% represented) is the proportion of resilient land identified as having confirmed biodiversity value. Total resilient area per ecoregion indicated the amount of area that scored above-average for resilience (31% if the cells had a perfect normal distribution) plus the amount that scored above average for the entire ecoregion or region (the regional override). Actual scores ranged from 32% to 63%. We include the Aspen Parkland although we assessed only a small portion of the ecoregion.

REGION / ECOREGION	Total Acres	Total Resilient (%)	Total Biodiversity (%)	% Represented
Great Lakes	**306,309,729**	**41**	**15**	**38**
Aspen Parkland	3,423,273	26	10	**37**
Central Tallgrass Prairie	63,329,349	39	7	**19**
Dakota Mixed-Grass Prairie	24,627,338	35	18	**53**
Great Lakes	68,532,781	46	13	**29**
North Central Tillplain	25,139,939	37	9	**25**
Northern Tallgrass Prairie	43,726,410	32	12	**37**
Prairie-Forest Border	33,489,422	40	20	**49**
Superior Mixed Forest	44,041,219	49	32	**66**
Great Plains	**461,215,295**	**37**	**22**	**59**
Black Hills	3,251,093	63	50	**79**
Central Mixed-Grass Prairie	58,541,151	40	29	**73**
Central Shortgrass Prairie	55,135,360	37	26	**69**
Crosstimbers and Southern Tallgrass Prairie	47,003,449	34	13	**38**
Cypress Upland	2,027,502	36	28	**76**
Edwards Plateau	23,165,699	32	23	**73**
Fescue-Mixed Grass Prairie	30,465,772	35	14	**40**
Northern Great Plains Steppe	153,874,542	38	23	**60**
Osage Plains/Flint Hills Prairie	19,367,508	35	20	**59**
Southern Shortgrass Prairie	68,383,219	38	19	**49**
Grand Total	**767,525,025**	**39**	**19**	**50**

Figure 4.1. Confirmed biodiversity areas. This map shows resilient areas within the TNC portfolio supplemented by areas identified in the State Wildlife Action plans and the Nature Conservancy of Canada's Prairies and Parklands Blueprint.



Balancing Representation

The stability of geophysical settings and their influence on diversity make them a natural target for evaluating representation. As described in our landscape resilience mapping reports for these two geographies (Anderson et al. 2018a&b), the representation of settings in current protected areas, and in TNC portfolios, is known to be uneven – in particular, settings that support agriculture are often poorly represented. In this section we address this problem by identifying a few more sites with confirmed biodiversity using the raw Natural Heritage element occurrence data in order to capture the full suite of geophysical settings in the network.

We defined a geophysical setting as a distinct physical environment in which specialized biota and characteristic natural commities have developed. Geology defines the available environments and shapes species diversity patterns through its influence on the chemical and physical properties of soil and water, and by creating topography that redistributes climatic effects to create predictable weather patterns and microclimates (Anderson et al. 2014, Dobrowski 2010). While climate factors may drive species diversity patterns at continental scales (Currie 1991, Currie & Paquin 1987), geophysical factors often take precedence over climate in explaining diversity patterns at local scales and can overwhelm local biotic interactions (Rosenzweig 1995, Willis & Whittaker 2002, Benton 2009). As the climate changes, we assume the physical differences in the land will continue to influence the composition of habitats even as the species change in response to temperature and precipitation.

The geophysical settings used in the resilience analysis, and a list of their associated species, are described in the individual reports for the Great Lakes and Tallgrass Prairie, and Great Plains region (Anderson et al. 2018a&b). For example, the setting "coarse sand" refers to surficial soils comprised of >90% pure sand. In the Great Lakes region, this setting supports communities such as oak-pine barrens, sand prairies, and wooded dunes, as well as species such as: Greater Prairie-chicken, Kirtland's Warbler, Plains Pocket Gopher, Blandings Turtle, Karner Blue Butterfly, Wild Lupine, and Sand Cherry.

An overlay of the confirmed biodiversity areas on the map of geophysical settings revealed that the selected areas encompassed most settings, but some were either missed completely or the amount captured was low. Specifically, five settings had less than 15% of their area identified in the confirmed biodiversity assessment (Table 4.3).

We calculated whether the setting was still likely to be underrepresented after areas of high flow were added to the network by estimating the area likely to be captured by flow alone, and adding that to the amount captured by confirmed biodiversity (Table 4.3). After this step, only one setting, clay/silt in the Northern Tallgrass Prairie, a very highly converted setting, was still underrepresented. For this setting we identified more sites of confirmed biodiversity by overlaying the natural heritage element occurrences on the areas of above-average resilience and adding in contiguous patches of resilience if they contained an A or B ranked natural community. This increased the representation of clay/silt slightly from 7% to 8%.

Table 4.3. Underrepresented settings within the study area. This table show geophysical settings with <15% of their area identified by the confirmed biodiversity overlay of TNC, SWAP, and NCC Blueprint sites. We caclulated how much of the setting was captured by confirmed biodiversity (column 4) and how much additional acreage was estimated to be captured by flow (column 5). Using the total of biodiversity and flow we calculated the percent representation (%Rep) of the resilient land. Only clay/silt in the Northern Tallgrass Prairie ecoregion had <15% represented in the network, and for this setting we supplemented the 7% representation with more sites for confirmed diversity using the Natural Heritage element occurrences.

Ecoregion	Setting	Total Acres of setting	Acres Resilient	Acres Confirmed Biodiversity	Acres Estimated Flow	Total Diversity +Flow	% Rep
Aspen Parkland	Acidic Sedimentary	9,106	8,378	0	2,473	2,473	30%
Central Tallgrass Prairie	Calcareous Loam	28,732,578	11,493,031	344,791	1,700,800	2,045,591	18%
Northern Tallgrass Prairie	Clay/Silt	7,608,824	1,750,030	35,001	85,067	120,068	7%
Superior Mixed Forest	Calcareous Sedimentary	2,589	1,139	46	903	949	83%
Osage Plains/Flint Hills Prairie	Circumneutral Sedimentary	519,210	166,147	4,984	29,160	34,144	21%

Rare Species and Natural Communities

To support the analyses described above, we compiled 163,514 point-locations of rare species and natural communities for this study. The data came from NatureServe and the State Natural Heritage programs and was used with their permission (Great Lakes/Tallgrass = 93,204, Great Plains = 70,310). Each location, called an element occurrence or "EO" represented location where a species or community is present, and which has practical conservation value. EOs are the basic unit of record for documenting and delimiting the presence and extent of a species on the landscape (populations or subpopulations) or an exemplary example of a natural community. In our work, EOs were used primarily to measure and document the distinctiveness of each geophysical setting (Anderson et al. 2018a&b), but we also used them to increase the confirmed diversity sites for the underrepresented clay/silt geophysical setting.

The Natural Heritage programs create EOs for native species that are considered at-risk within their jurisdictions, with an emphasis on the most imperiled. Species that are critically imperiled or imperiled globally (G1 or G2) are the most consistently tracked throughout their range. Vulnerable (G3) or apparently secure (G4) species are tracked in most states but coverage can vary. Data are more complete for vertebrates and vascular plants, and for some invertebrate groups such as: freshwater mussels, snails, crayfishes, butterflies, dragonflies and damselflies. Data are highly variable for other invertebrate groups and non-vascular plants. Global rank definitions are as follows:

- G1 Critically Imperiled: At very high risk of extinction due to extreme rarity (often 5 or fewer populations), very steep declines, or other factors.
- G2 Imperiled: At high risk of extinction due to very restricted range, very few populations (often 20 or fewer), steep declines, or other factors.
- G3 Vulnerable: At moderate risk of extinction due to a restricted range, relatively few populations (often 80 or fewer), recent and widespread declines.
- G4 Apparently Secure: Uncommon but not rare; some cause for long-term concern due to declines or other factors.
- G5 Secure: Common; widespread and abundant.

The location of an EO has a recorded level of mapping accuracy that can range from highly precise, where the locality is very well understood and documented, to very low precision, which is used to identify older records that may have been vague as to the exact locale. For this analysis we used only precise records for G1-G4 (or T1-T4) species. More common species (G5) were excluded due to inconsistent survey effort.

Natural Heritage Programs also track natural communities. These are repeating assemblages of species that occur within a distinct set of environmental parameters such as a unique geophysical setting (e.g., sandstone pavement barren, calcareous cliff, loess prairie), or a climatically driven dominant vegetation type (e.g., northern hardwood forest, dry oak-heath forest). Each state has developed its own classification of its natural communities, and the rarer ones are inventoried, mapped and described in a manner analogous to mapping the extent of a species population. Canadian provinces do not currently track natural communities. The quality of each community EO is ranked by the field biologist based on the size, condition, and landscape context.

Current Condition:
- A: mature example of the community type; natural processes intact; no exotics.
- B: minor alteration of vegetation structure, composition, and ecological processes; few exotics.
- C: significant alteration of vegetation structure, composition and ecological processes; exotic species abundant.
- D: highly altered vegetation composition, structure, and ecological processes, restoration/recovery is unlikely; exotic species abundant.

Landscape Context:
- A: highly connected; surrounding area largely intact natural vegetation
- B: moderately connected; surrounding area moderately intact
- C: moderately fragmented; surrounding area a mix of cultural and natural.
- D: highly fragmented; surrounding area agriculture or urban development

Size: No Generic ranking applicable. Record actual size of community.

We included only communities that were located on resilient lands and were ranked A-C or were unranked.

RESILIENT AND CONNECTED CONSERVATION NETWORKS

CHAPTER 5

The goal of this section was to identify a network of resilient sites that if adequately managed or conserved would sustain the diversity of the region under a dynamically changing climate. Our approach to mapping such a network was to first combine the resilience and flow datasets into a single coverage, and then to overlay the confirmed diversity areas. We used this integrated coverage to identify a connected network of resilient sites which maximized resilience, diversity, and flow.

The resilient site analysis upon which this is based (Anderson et al. 2016a) highlights a fixed portion (approx. 33%) of each of the region's geophysical settings based on the distribution of microclimates and degree of local connectedness. We used a statistical distribution to calculate the average resilience score for each geophysical setting, and then identified the places that scored above average for each setting within an ecoregion (>0.05 SD). On top of this we added a regional override to add sites that scored only average in their setting and ecoregion but were nevertheless among the highest scoring sites for the whole region (>1 SD for the region). This increased the portion of the region identified as resilient to 38%. In this study we prioritize among that 38% based on documented value for biodiversity and flow, to identify the places most essential for conserving and sustaining diversity under a changing climate.

One approach to prioritizing sites is to use a higher resilience score threshold. For example, selecting sites that score far above average (>1 SD) for resilience identifies the top scoring sites in each ecoregion based solely on their resilience characteristics and will maintain almost perfect representation of the geophysical settings. An alternative approach, and the one that we used here, is to explicitly address the spatial configuration needed to produce an ecologically coherent network that allows for adaptation and change. The latter required that we study how the natural flow patterns are arranged across the region, where the rare species are currently located, which riparian corridors naturally connect critical features, and where a stepping stone pattern will have to be relied upon because there is no realistic way to functionally connect the sites. By incorporating these characteristics into the network design, we hoped to strengthen its collective long-term ability to sustain diversity while allowing for range shifts and adaptation.

Go with the Flow

Our approach to creating a network differs from similar studies in that we did not first identify sites and then try to connect them, instead we used the natural flow patterns as a spatial template and integrated the resilient and confirmed biodiversity areas with the flow pattern. In effect, we prioritized resilient and diverse sites that were aligned with the natural flow patterns. By ensuring that resilient source areas representing the region's diverse species and environments are situated in places that naturally intercept and transmit population movements, we can facilitate the adaptation and persistence of nature's diversity.

We prioritized the study area based on three themes – resilience, diversity, and flow. Resilience criteria were based on microclimates and local connectedness applied to each geophysical setting (summarized in Chapter 2; see Anderson et al. 2018a&b). The goal of the resilience criteria was to ensure that the network was designed around representative areas of every habitat were species could persist in to the future due to the climatic variability and connectedness of the site. Diversity criteria were based on the TNC and SWAP portfolios of critical sites for biodiversity, supplemented with confirmed rare species and natural community occurrences (Chapter 4). The goal of the diversity criteria was to include confirmed features in the network that were particularly hard to capture by random chance, and thus ensure that the network contained the full spectrum of biodiversity. Flow was based on an analysis of circuit flow to a landscape of variable resistance as defined by the arrangement and resistance of land uses, weighted by key upslope, northward and riparian corridors (Chapter 3). The idea was to take advantage of the natural flow patterns in the region by selecting resilient and diverse sites that enhanced or reinforced those patterns.

We did not set a numeric acreage goal for this prioritization, but we aimed to identify the half (19%) of all the resilient areas that were the most connected and diverse, and by implication, the most critical to protect. In the Eastern US this amounted to 23% of the region (Anderson et al. 2016), and subsequently rose to 26% when we added coastal sites. The prioritization forced us to study how the resilient sites interweave and are juxtaposed with the flow and diversity patterns. The prioritization is not necessarily intended as an estimate of how much conservation is needed to sustain diversity over time but rather to provide a starting point for focusing conservation on the most critical network of sites and linkages. If the most resilient areas were protected in totality in the region it would equal 38% of the area and include the prioritized network. This approaches E.O. Wilson's Half Earth goal (Wilson 2016) and is probably closer to the actual area that we need to be concerned about if we want to maintain all the natural benefits and services we derive from nature. Currently only 8% of the Great Lakes and Tallgrass region and 7% of the Great Plains is in some form of permanent conservation, so it will be a challenge to protect, or sustainably manage, the full network.

Site Prioritization: Resilience, Flow, and Diversity

Resilience and Flow

The resilience analysis and flow analysis are both continuous and geographically comprehensive. To identify an ecologically coherent network, we first combined these two datasets in their categorical forms to create a map that included all 42 possible combinations: seven levels of resilience scores and seven types of flow based on pattern and intensity. These were as follows:

Flow Type **Resilience Score**

Medium to High

- Concentrated flow: FBA, BA, SBA, A, SAA, AA, FAA
- Diffuse flow: FBA, BA, SBA, A, SAA, AA, FAA
- Constrained flow: FBA, BA, SBA, A, SAA, AA, FAA

Low

- Concentrated flow: FBA, BA, SBA, A, SAA, AA, FAA
- Diffuse flow: FBA, BA, SBA, A, SAA, AA, FAA
- Constrained flow: FBA, BA, SBA, A, SAA, AA, FAA
- Blocked flow: FBA, BA, SBA, A, SAA, AA, FAA

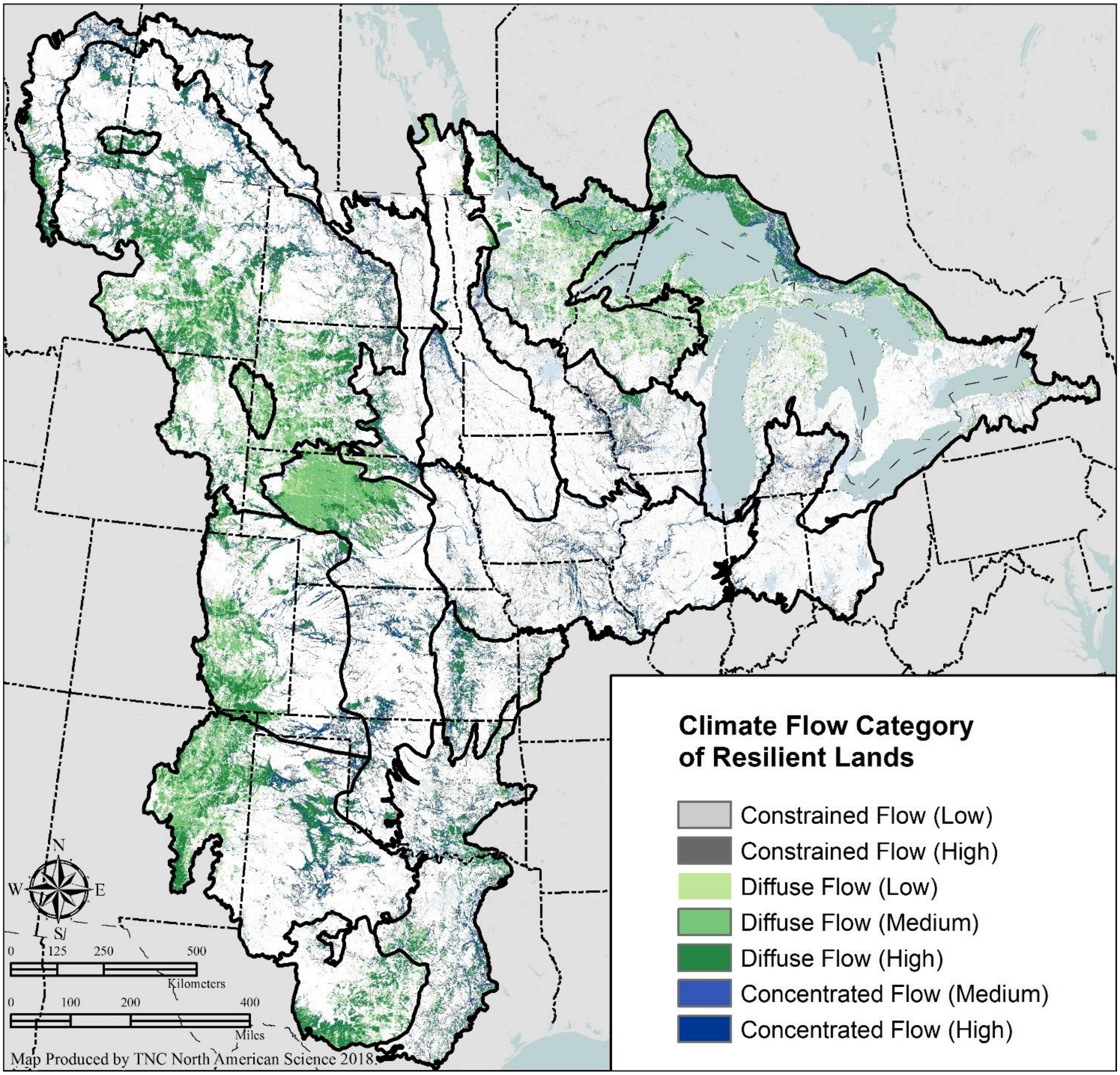
The resilience categories are: FBA = far below average (<-2 SD), BA = below average (<-1 SD), SBA = slightly below average (<-0.5), average (-0.5-0.5), slightly above average (>0.5 SD), above average (>1 SD), and far above average (>2 SD).

Using the categorical map, we selected places that met the criteria of above-average resilience and high concentrated or diffuse flow (red box above), thus selecting the places that maximized geophysical representation, resilience, and flow. Collectively these areas covered 17% of the region and delineated the structure, outline, and the majority of the network area. We augmented the network in highly agricultural ecoregions that had less than 20% of the undeveloped land area showing up in the network. In these ecoregions, we expanded the criteria to include constrained flow with high resilience (dashed boxes above). This augmentation added only 1% more land but identified natural connections in regions where restoration may be necessary to increase the flow. Ecoregions that were augmented included:

- Aspen Parkland
- Central Tallgrass Prairie
- Crosstimbers & Southern Tallgrass Prairie
- Dakota Mixed-Grass Prairie
- Fescue-Mixed Grass Prairie
- North Central Tillplain
- Northern Tallgrass Prairie
- Osage Plains/Flint Hills Prairie
- Prairie Forest Border

The results formed a connected network covering 18% of the study area (Figure

Figure 5.1. Resilience and flow. This map shows the areas that met the criteria for above-average resilience and high concentrated (blue) or diffuse (green). To identify important linkages that may need restoration, the network is enhanced in the prairie ecoregions by including areas with constrained flow and above-average resilience.



Confirmed Diversity & the Network

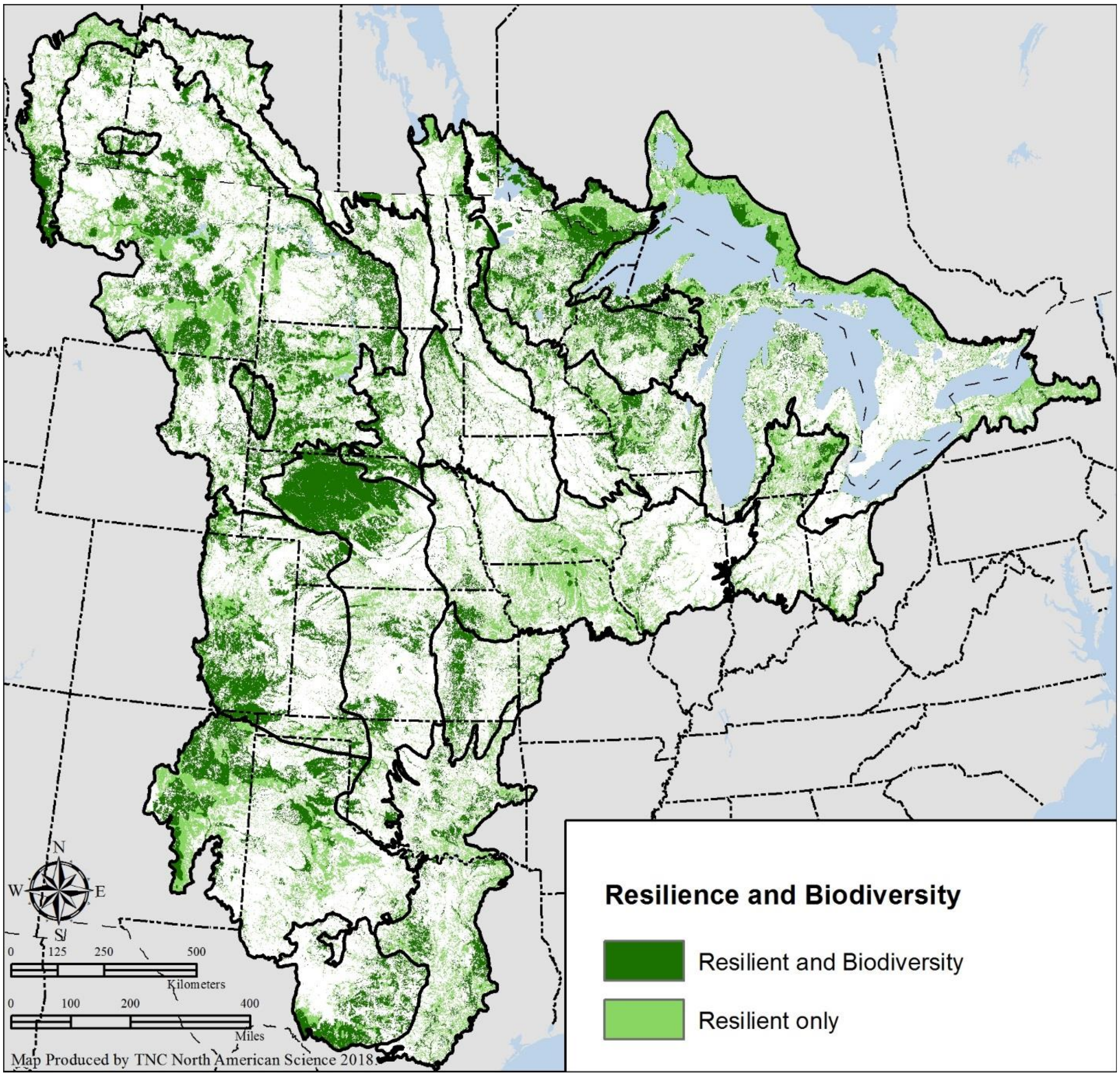
The confirmed diversity criteria identified the resilient portions of the TNC ecoregional portfolio sites or the SWAP sites (augmented in one ecoregion by known locations of species and communities on geophysical settings that were underrepresented in the TNC and SWAP sites; Figure 5.2). Although in total, the confirmed diversity sites covered 16% of the study region when we overlaid them on the network of resilience and flow, they only added 5% more to the network because the other 11% overlapped with the flow network. Specifically:

• Resilience, Flow and Diversity	11%
• Resilience and Diversity	5%
• Resilience and Flow	7%
Total	23%

The goal of the confirmed diversity criteria was to ensure that the prioritized resilient areas contained as many known rare species populations or high quality natural community examples as possible. Unlike common species which are relatively easy to represent in a wide variety of configurations, rare species, because of their small populations, are difficult to pick up based on random chance. Building them into the prioritization ensured that we selected the sites where they are most likely to persist and that have the characteristics to support similar species as the species composition changes in response to climate drivers.

The confirmed diversity criteria also ensured that the network was capturing high quality natural communities in good condition, or viable species populations. As the resilience analysis was based on enduring features alone, this was the first time that finer-scale criteria on the structure and composition of the vegetated communities or size of the population was brought into the analysis. Although we expect the communities to rearrange and the species to move over time, this gives us confidence that the starting materials, the soils, topography, and existing vegetation, are likely to be in suitable condition.

Figure 5.2. Confirmed diversity and above-average resilience. This map shows the distribution of sites that were identified for their biodiversity features in a TNC ecoregional portfolio or a State Wildlife Action Plan, and which also met the criteria for above-average resilience. The map was augmented in one ecoregion by resilient examples of individual geophysical settings that were missed or underrepresented by the TNC/SWAP site. The biodiversity features on this small set of sites were confirmed by Natural Heritage Program species or community occurrences.



Integration: Resilient and Connected Landscapes

We combined the network identified by the combination of resilience, flow, and confirmed biodiversity into a single prioritized network. The network is designed to represent resilient examples all the characteristic environments of the Central US while maximizing amount of diversity contained within in them and the natural flow that connects them. By building the network around the natural flows and pathways that allow species populations to shift and expand and then identifying representative resilient sites situated within those pathways, the network is specifically configured to sustain biological diversity while allowing nature to adapt and change.

The results delineate a network of resilient and connected sites that covers 23% (205 million acres) of the region. Half of the network (50%) met all three criteria: flow, confirmed diversity and resilience. The rest of the area met at least two criteria: flow and resilience (30%) or confirmed diversity and resilience (20%). The breakdown of the network was as follows:

Prioritized Network	**23%**
o Climate Corridor	2%
o Climate Corridor w Confirmed Biodiversity	3%
o Climate Flow Zone	4%
o Climate Flow Zone w Confirmed Biodiversity	9%
o Resilient w Confirmed Biodiversity	5%
o Resilient Secured	0%
Resilient Only (not in Network)	8%

In total, the network represents: resilient examples of all geophysical settings, contains the resilient portions of over 142 M acres of sites identified by TNC/SWAP portfolios for biodiversity, and includes over 43 million acres of climate corridors equaling 6% of the region. (Table 5.1, Figures 5.3–5.6 and inside front cover).

The prioritized network identifies 23% of the region, of which 19% is already permanently secured (Table 5.4, Figure 5.9).

Table 5.1. Percentages of prioritized resilient areas. This table shows the percent of each region's land identified by the respective network classes. Vulnerable = resilience score average or below-average, and diversity = confirmed biodiversity. The Great Lakes had 19% of its area in the Resilient and Connected Prioritized Network, whereas the Great Plains had 30%. Note: water (8% of region) is excluded.

Region and Ecoregion	Develop-ed (%)	Vulner-able (%)	Resilient Only (%)	Climate Corridor (%)	Climate Corridor with Diversity (%)	Climate Flow Zone (%)	Climate Flow Zone with Diversity (%)	Resilient with Diversity (%)	Resilient Secured (%)	Priority RCN (%)
Great Lakes	9	60	12	2	2	3	5	5	1	19
Aspen Parkland	5	72	10	4	5	0	0	4	1	13
Central Tallgrass Prairie	9	66	15	5	3	0	0	2	0	10
Dakota Mixed-Grass Prairie	5	67	9	2	4	1	6	6	0	20
Great Lakes	11	49	14	2	1	10	6	5	1	25
North Central Tillplain	16	62	14	2	2	0	0	4	0	9
Northern Tallgrass Prairie	6	76	8	1	2	1	1	5	1	10
Prairie-Forest Border	11	60	11	2	5	0	1	9	0	18
Superior Mixed Forest	4	49	7	1	2	7	18	11	1	39
Great Plains	1	63	6	3	3	6	14	5	0	30
Black Hills	1	36	3	0	0	10	42	8	0	60
Central Mixed-Grass Prairie	0	61	6	2	3	1	19	6	0	32
Central Shortgrass Prairie	1	63	6	2	3	3	16	7	0	30
Crosstimbers & S. Tallgrass	2	65	6	8	5	6	4	3	0	27
Cypress Upland	1	63	1	1	3	7	24	1	0	35
Edwards Plateau	1	68	2	1	1	5	19	3	0	29
Fescue-Mixed Grass Prairie	3	63	14	5	4	1	6	3	0	20
Northern G. Plains Steppe	1	62	5	2	3	8	14	5	1	32
Osage Plains/Flint Hills	1	67	6	5	9	2	7	4	0	26
Southern Shortgrass Prairie	0	62	6	3	2	10	13	4	0	31
Grand Total	4	62	8	3	3	5	10	5	0	26

Figure 5.3. Prioritized resilient and connected sites. This map shows the resilient areas that met criteria for confirmed biodiversity and concentrated or diffuse flow. The network covers 23% of the region and 75% of the resilient sites.

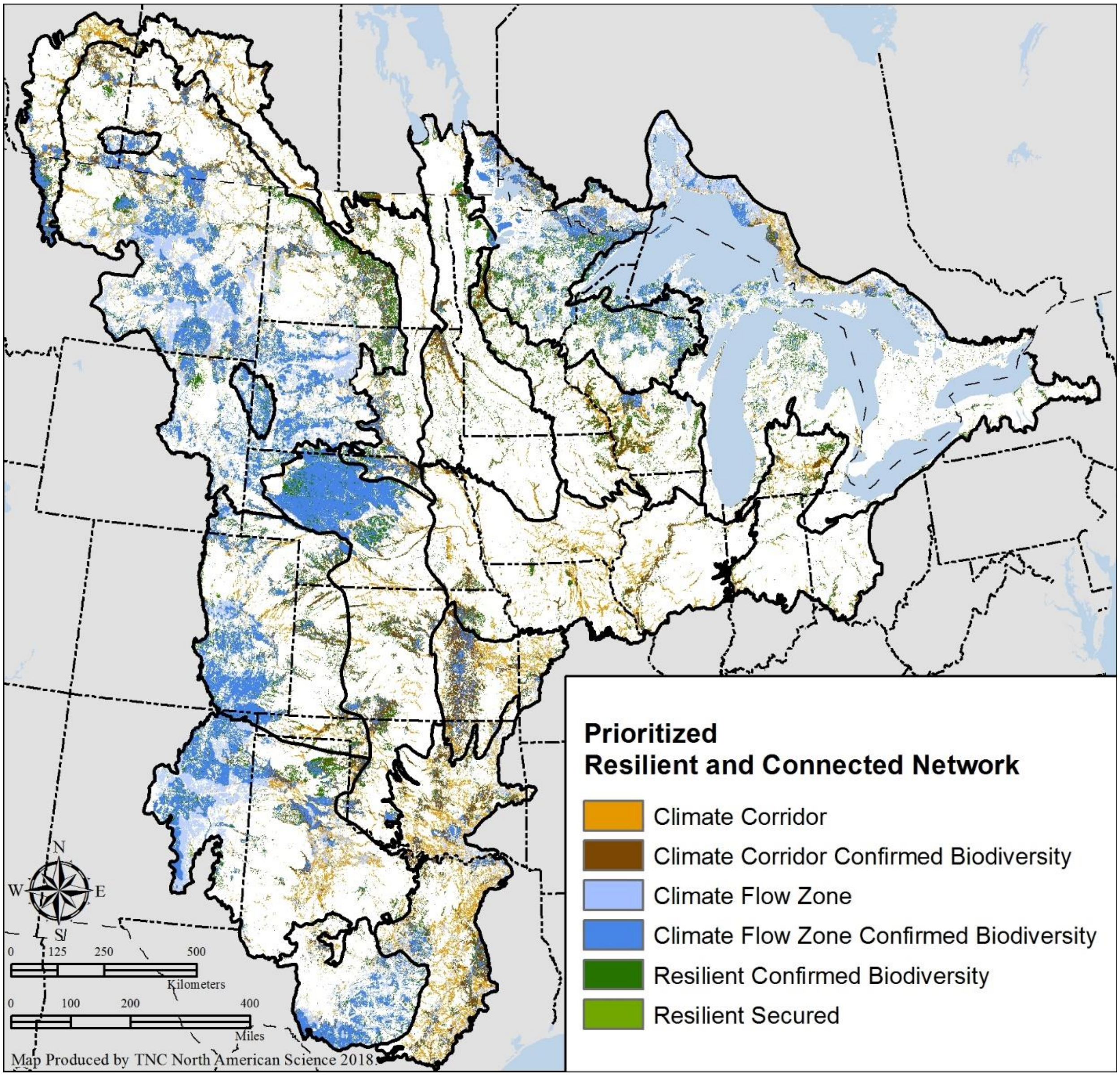


Figure 5.4. All resilient and connected sites. This map shows the resilient and connected network including seven categories of resilient sites. Climate corridors and flow zones with confirmed diversity are in darker colors.

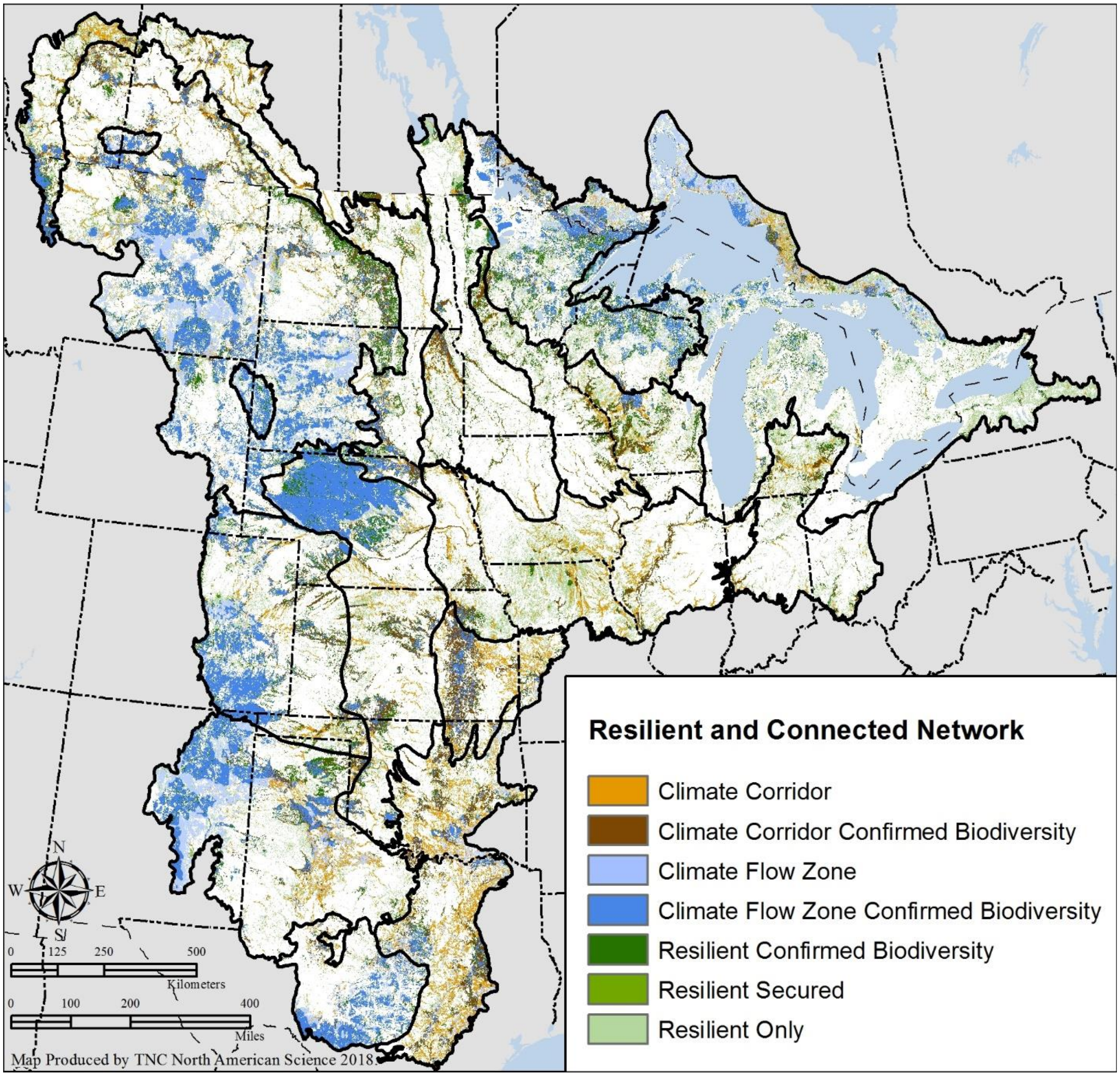


Figure 5.5. Continuous map of resilient and connected sites. This map shows all of the categories of resilience for sites and linkages, including the areas that score average or below average. This map is the counterpart to the estimated resilience map in Anderson et al. (2018a&b) which is based solely on score.

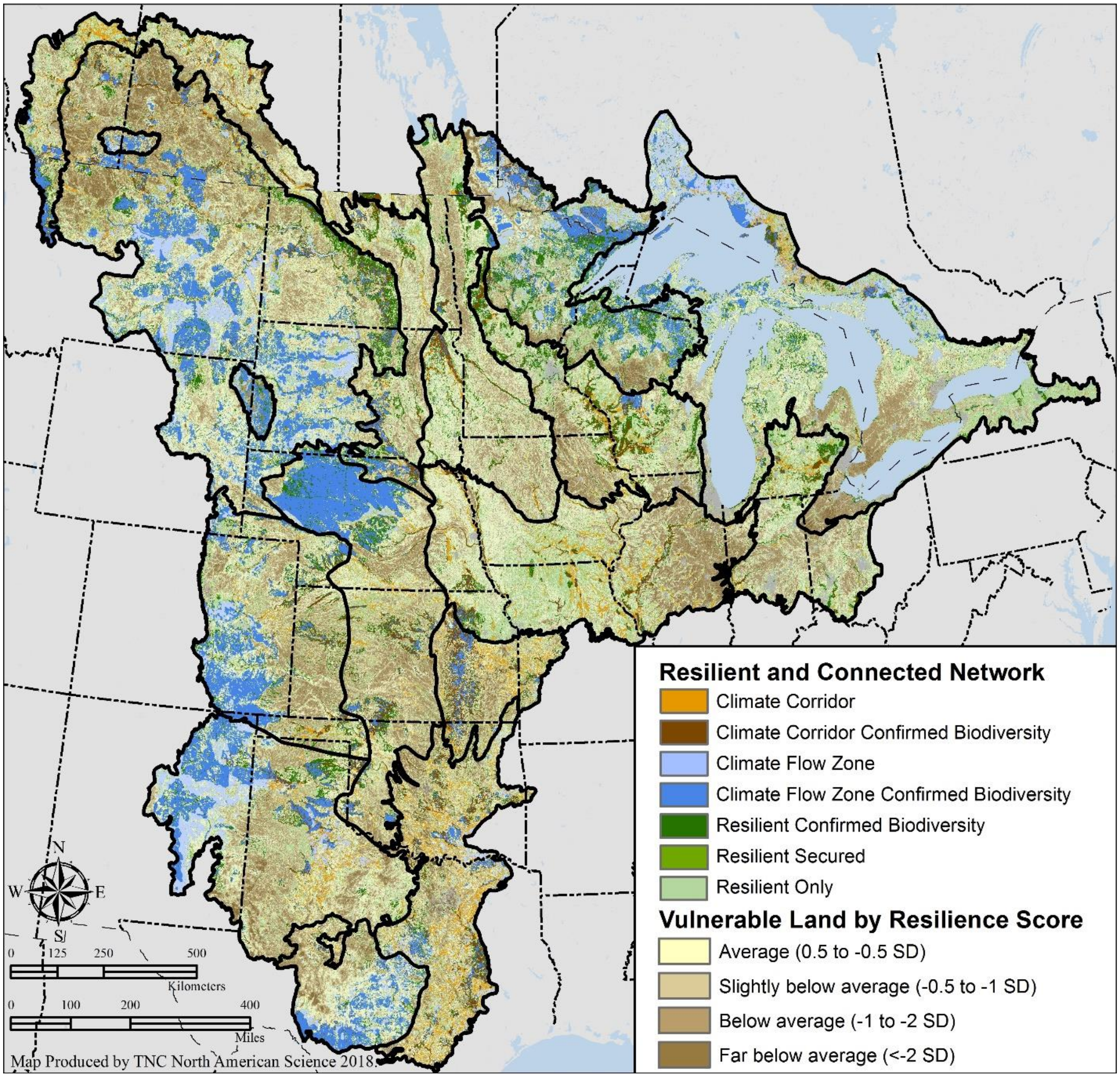
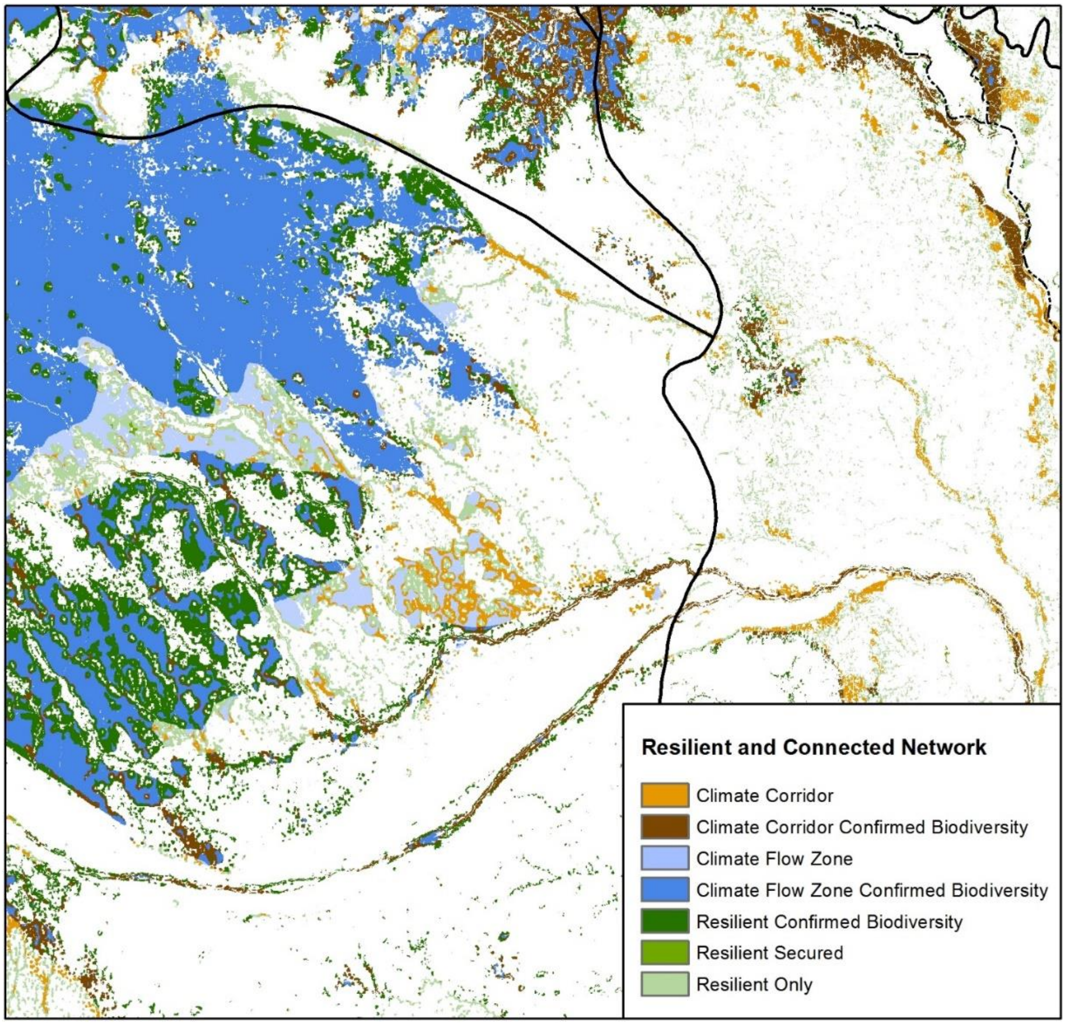


Figure 5.6. Zoom-in of Northeastern Nebraska. This map shows the resilient and connected network including seven categories of resilient sites. Climate corridors and flow zones with confirmed diversity are shown in darker colors.



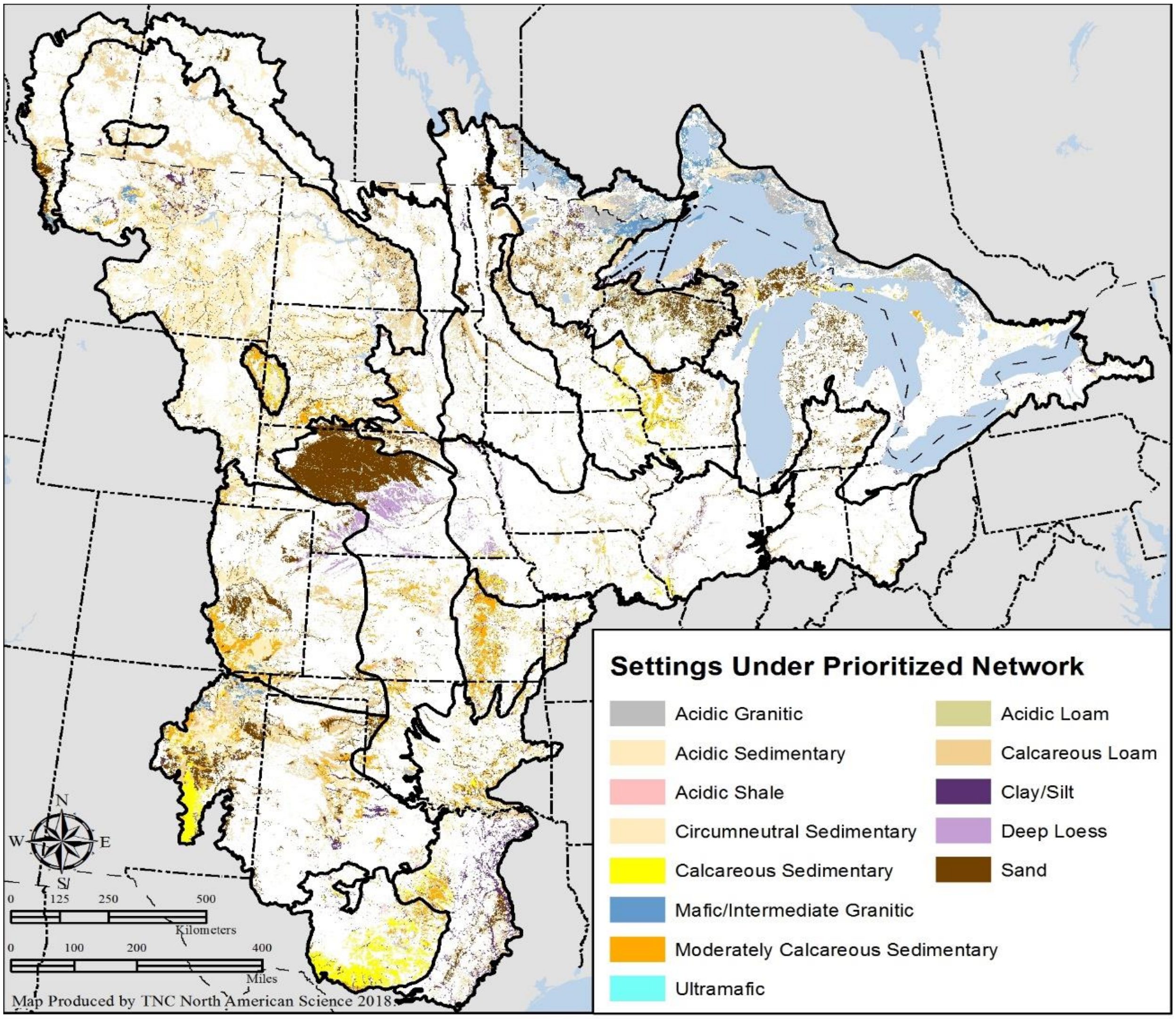
Representation of Geophysical Settings

The prioritized network represents all geophysical settings in the region, but because we used connectivity values as prioritization criteria we were concerned that the network might be biased towards more acidic settings that tend to be more intact. An assessment showed that several settings were under-represented in the network, and that these were the fertile settings that once underlain prairie and now are mostly agricultural: Clay/Silt, Calcareous Loam, Deep Loess. These settings may require restoration and sustained management to ensure that they retain their natural diversity into the future.

Table 5.2. Representation of Geophysical Settings in Network.
This table is arranged by the % representation of the setting in the priority network. Settings below 20% may be considered under-represented in the network and will need restoration and management. Settings above 30% may be considered over-represented in the network. Results are for land only; water (8% of region) is excluded.

Geophysical Setting		Priority Network		Distribution across Network						Not in Network		
Type	Total Acres	Acres	%	Corridor (%)	Corridor w Diversity (%)	Flow Zone (%)	Flow Zone w Diversity (%)	Resilient Only w Diversity (%)	Resilient Only Secured (%)	Resilient Only (not in RCN -%)	Vulnerable (%)	Developed (%)
Ultramafic	39,914	31,598	79	3	2	53	18	4	0	4	13	4
Mafic/Intermediate	9,060,321	5,931,083	65	4	4	22	29	7	0	8	23	4
Acidic Granitic	15,835,057	10,249,626	65	6	4	28	22	5	0	13	19	3
Acidic Sedimentary	6,786,840	3,689,253	54	5	7	17	18	7	0	11	29	5
Circumneutral Sed.	129,136,619	46,847,679	36	2	2	10	18	3	0	5	59	1
Mod. Calcareous Sd	65,363,161	21,229,765	32	4	5	6	13	5	0	7	59	2
Acidic Loam	8,595,972	2,781,852	32	0	1	5	17	9	1	6	58	4
Calcareous Sed.	30,994,025	9,938,319	32	3	3	7	15	4	0	8	57	3
Sand	160,243,223	45,131,450	28	2	3	3	13	7	1	7	59	5
Acidic Shale	3,103,161	723,508	23	2	4	2	10	6	0	10	66	1
Clay/Silt	50,995,505	8,562,428	17	5	2	3	3	3	0	10	67	6
Calcareous Loam	286,076,380	44,241,261	15	3	2	2	3	5	0	11	68	6
Deep Loess	35,764,911	5,314,223	15	3	3	1	3	5	0	8	71	5
Grand Total	801,995,089	204,672,046	26	3	3	5	10	5	0	8	62	4

Figure 5.7. Geophysical representation of the prioritized network. This map shows geophysical settings that underlie the prioritized network (26% of land area, 23% of total area including water). See Table 5.2 above for exact proportions of each setting in the network. Note acidic sedimentary in the Great Lakes &Tallgrass Prairie region is shown in the same color as circumneutral sedimentary in the Great Plains region as the two settings are roughly similar in properties.



Secured Lands

We compiled information on tracts of permanently protected conservation land covering all states in this study region. The information is part of TNC's "secured land" dataset defined as land that is permanently secured against conversion to development. This definition was developed by an international group of scientists to differentiate "secured land" from the International Union for Conservation of Nature (IUCN) term "protected areas" which refers to land with a formal designation of conservation value (Dudley 2008).

The secured lands dataset includes many tracts of land with no formal designation but substantial conservation value, such as reserves held by The Nature Conservancy, forest management lands held by the Canadian Crown, or "forever wild" easements held by a non-governmental conservation entity. In contrast, the dataset excludes some designated protected areas such as world biosphere preserves, as these areas are not formally protected from development.

To classify secured lands, we used a modified version of USFWS' GAP Status (Crist et al. 1998). Our version (TNC GAP) was similar in concept but used criteria that can be applied more easily than the USFWS criteria (Table 5.4). The criteria were:

1) Intent: the degree that owner, or managing entity is focused on maintaining natural diversity.
2) Duration: the owner or managing entity's temporal commitment to maintaining the land.
3) Effective management potential: the apparent capability of a managing entity to implement the intent and duration based on governance, planning, and resource levels. In the US, local, state and federal agencies, conservation NGOs, and land trusts are considered as effective managers.

TNC GAP is a land classification system and it does not necessarily describe how protected the contained conservation targets are within a secured area (Table 5.3). For example, a species breeding on a secured parcel may be only partially conserved if their conservation calls for securement of multiple breeding areas and sufficient winter habitat. In this case, meeting the species conservation goal would require a network of secured lands each with the appropriate level of securement.

The Secured Lands dataset was compiled from over seventy sources and reflects land securement status through the end of the year 2018. Only parcels with permanent ownership duration were included in the mapped dataset. All parcels were assumed to meet the criterion of effective management. Management intent can change over time and it is not uncommon for conservationists to have a goal of moving the GAP status of a parcel from GAP 3 (secured for multiple-uses) to GAP 1 (secured for nature).

Table 5.3. Comparison of GAP status, IUCN and TNC GAP status definitions.

TNC GAP	GAP STATUS	IUCN	Selected Examples
TNC GAP 1 **Intent:** Nature conservation with little human interference **Duration:** Permanent	**GAP 1:** Areas having permanent protection from conversion of natural land cover and a mandated management plan in operation to maintain a natural state within which disturbance events can proceed without interference or are mimicked through management.	**Category Ia**: Strict Nature Reserves set aside to protect biodiversity **Category Ib:** Wilderness Areas are usually large unmodified or slightly modified areas, retaining their natural character and influence, without permanent or significant human habitation, which are managed to preserve their natural condition.	Research Natural Areas (RNA) Some TNC preserves where TNC controls management Wilderness Areas and Wilderness Study areas Forever wild easements
TNC GAP 2 **Intent:** Nature conservation with heavy management where needed **Duration**: Permanent	**GAP 2:** Areas having permanent protection from conversion of natural land cover and a management plan in operation to maintain a primarily natural state, but which may receive uses or management practices that degrade the quality of existing natural communities, including suppression of natural disturbance.	**Category III**: Natural Monument or Feature protected areas **Category IV**: Habitat/species management protected areas aim to protect species or habitats and management reflects this priority.	National Wildlife Refuges Areas of Critical Environmental Concern Some National Parks and county open space lands US Forest Service Special Interest Areas Some TNC conservation easement lands and preserves
TNC GAP 3 **Intent:** Multiple Uses. Typically, resource extraction, recreation and nature conservation **Duration:** Permanent.	**GAP 3** Areas having permanent protection from conversion of natural land cover for most of the area, but subject to extractive uses of either a broad, low-intensity type (e.g., logging) or localized intense type (e.g., mining).	**Category V:** Protected landscape/seascape where the interaction of people and nature over time has produced an area of distinct character with significant ecological, biological, cultural and scenic value. **Category VI**: Protected area with sustainable use of natural resources, generally large, with much of the area in a more-or-less natural condition and where a proportion is under sustainable natural resource management and exploitation is one of the main aims of the area.	State Forests and State Wildlife Areas US Forest Service and BLM land Most TNC Easements Most National/ State/ City /County Parks National Recreation Areas Open Space and Natural Areas

Table 5.4. Land securement across the prioritized network. The GAP categories are defined in Table 5.3.

Region and Category	Acres	Secured (%)	GAP 1 (%)	GAP 2 (%)	GAP 3 (%)	Unsecured (%)
Great Lakes and Tallgrass Prairie						
Priority Network	63,679,298	29	2	11	15	71
Climate Corridor	8,100,897	6	0	2	4	94
Climate Corridor w/ Biodiversity	8,329,515	27	2	11	14	73
Climate Flow Zone	11,755,072	16	1	4	10	84
Climate Flow Zone w/ Biodiversity	15,458,543	55	6	23	26	45
Resilient w Biodiversity	18,349,679	20	1	8	11	80
Resilient Secured	1,685,591	100	1	38	61	0
Resilient Only (Not in Network)	39,588,824	0	0	0	0	100
Vulnerable	203,044,652	5	0	2	3	95
Water	76,591,084	9	1	3	5	91
Development	29,798,749	4	0	2	2	96
Total	**412,702,606**	**9**	**1**	**3**	**5**	**91**
Great Plains						
Priority Network	140,993,780	15	1	3	12	85
Climate Corridor	13,112,762	5	0	2	3	95
Climate Corridor w Biodiversity	14,273,475	12	0	3	9	88
Climate Flow Zone	27,073,619	14	0	2	12	86
Climate Flow Zone w Biodiversity	63,246,186	19	1	3	15	81
Resilient w Biodiversity	22,031,295	9	0	2	7	91
Resilient Secured	1,256,443	100	1	24	75	0
Resilient Only (not in network)	28,574,360	0	0	0	0	100
Vulnerable	291,647,736	5	0	0	4	95
Water	3,874,246	23	1	14	8	77
Development	4,671,642	2	0	0	2	98
Total	**469,761,764**	**8**	**0**	**1**	**6**	**92**
Total : Priority Network	**204,673,078**	**19**	**1**	**5**	**13**	**81**
Grand Total	**882,464,369**	**8**	**0**	**2**	**6**	**92**

Figure 5.8. Secured lands. This map shows the secured lands in the Central US by Gap code (see Table 5.3).

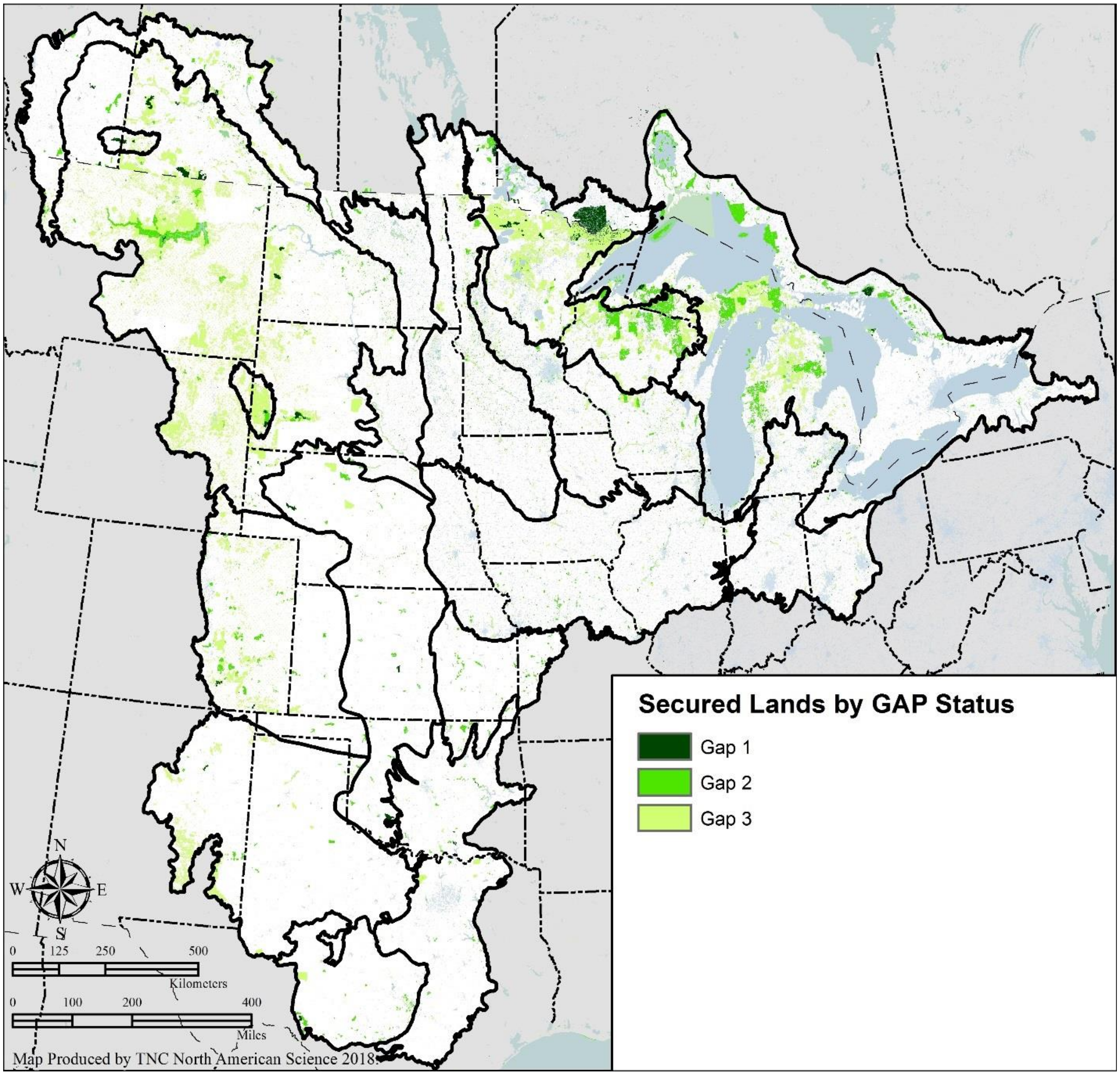
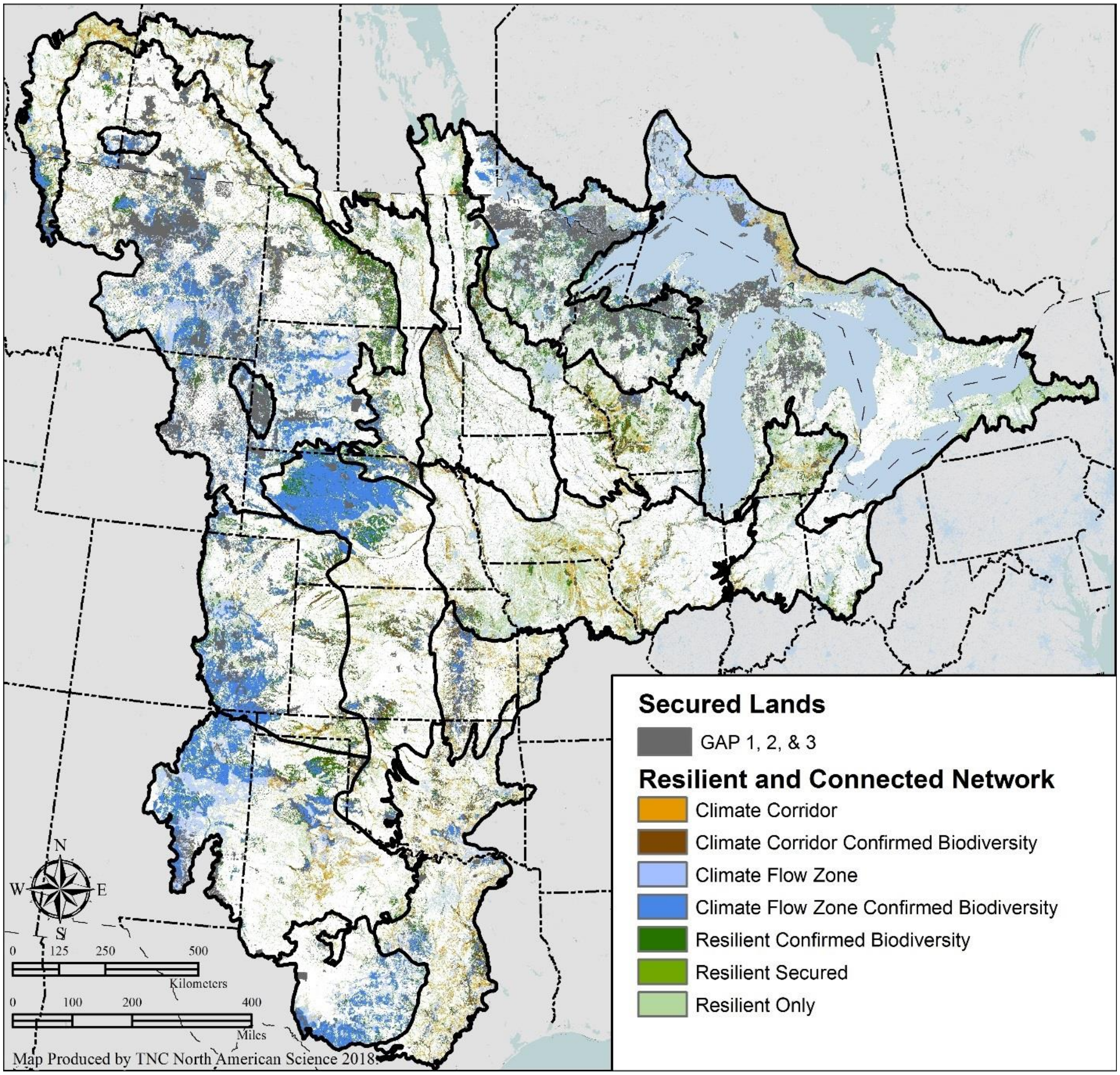


Figure 5.9. Secured land with the resilient and connected network . The map shows the secured lands in gray on top of the prioritized network. In sum the network is 19% secured (see Table 5.4) by conservation land in Gap 1-3 status (categories are defined in Table 5.3).



REFERENCES

Ackerly, D.D., S.R. Loarie, W.K. Cornwall, S.B. Weiss, H. Hamilton, R. Branciforte, and N. J. B. Kraft. 2010. The geography of climate change: implications for conservation biogeography. Diversity and Distributions 16:476–487.

Anderson, M.G., M.M. Clark, M.W. Cornett, K.R. Hall, A. Olivero Sheldon, J. Prince. 2018a. Resilient Sites for Terrestrial Conservation in the Great Lakes and Tallgrass Prairie. The Nature Conservancy, Eastern Conservation Science and North America Region. 179 pp.

Anderson, M.G., M.A. Ahlering, M. M. Clark, K.R. Hall, A. Olivero Sheldon, J. Platt and J. Prince. 2018b. Resilient Sites for Terrestrial Conservation in the Great Plains. The Nature Conservancy, Eastern Conservation Science and North America Region. 196 pp.

Anderson, M.G., A. Barnett, M. Clark, C. Ferree, and A. Olivero Sheldon, J. Prince. 2016a. Resilient Sites for Terrestrial Conservation in the Eastern North America Division. The Nature Conservancy, Eastern Conservation Science. 127 pp.

Anderson, M. G., A. Barnett, M. Clark, A. Olivero Sheldon, and J. Prince. 2016b. Resilient and Connected Landscapes for Conservation across Eastern North America. The Nature Conservancy, Eastern Conservation Science, Boston. http://www.nature.ly/TNCResilience

Anderson, M.G., A. Barnett, M. Clark, C. Ferree, A. Olivero Sheldon, and J. Prince. 2014. Resilient Sites for Terrestrial Conservation in the Southeast Region. The Nature Conservancy, Eastern Conservation Science. 127 pp.

Anderson, M. G., and C. Ferree. 2010. Conserving the stage: climate change and the geophysical underpinnings of species diversity. PLoS ONE 5(7):E11554. DOI:10.1371/journal.pone.0011554

Anderson, M.G., M. Clark, and A.O. Sheldon. 2014. Estimating climate resilience for conservation across geophysical settings. *Conservation Biology* 28:959-970.

Anderson, M.G. 1999. Viability and Spatial Assessment of Ecological Communities in the Northern Appalachian Ecoregion. PhD Dissertation. Univ. of New Hampshire. 224 pp.

Anderson, M.G., M. Clark, and A. Olivero Sheldon. 2012. Resilient Sites for Terrestrial Conservation in the Northeast and Mid-Atlantic Region. The Nature Conservancy, Eastern Conservation Science. 168pp

Beier, P., and B. Brost. 2010. Use of land facets to plan for climate change: conserving the arenas, not the actors. *Conservation Biology* 24:701–710.

Beier, P., W. Spencer, R.F. Baldwin, and B.H. McRae, B.H. 2011. Toward best practices for developing regional connectivity maps. *Conservation Biology 25*:879-892.

Botkin, D. B., H. Saxe, M.B. Araujo, R. Betts, R.H. Bradshaw, T. Cedhagen and D.R. Stockwell. 2007. Forecasting the effects of global warming on biodiversity. *Bioscience 57*:227-236.

United States Bureau of Transportation Statistics (BTS). 2016. Railroad Network. http://osav-usdot.opendata.arcgis.com/datasets/2553aa5e457349efb600502050bf9c3c_0

Chen, I.C., J.K. Hill, R. Ohlemüller, D.B. Roy, and C.D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science 333*:1024-1026.

Cook, K.L. 2007. *Space use and predictive habitat models for American Black Bears (Ursus Americanus) in Central Georgia, USA.* (Master's Thesis). University of Georgia, Athens, Georgia.

Corlett, R.T. and D.A. Westcott. 2013. Will plant movements keep up with climate change? *Trends in Ecology & Evolution* 28(8): 482-488.

Davis, M. B. and R.G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science 292*:673-679.

Dobrowski, S. Z. 2010. A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology.* 17:1022-1035. DOI:10.1111/j.1365-2486.2010.02263x

Duke Energy 2014. Transmission Rights of Way. http://www.duke-energy.com/safety/right-of-way-management/transmission.asp

Faith, D. P., and P. A. Walker. 1996. Environmental diversity: on the best-possible use of surrogate data for assessing the relative biodiversity of sets of areas. *Biodiversity and Conservation* 5:399–415

Fischer, J., and D.B. Lindenmayer. 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography 16*:265-280.

Fisette, T., A. Davidson, B. Daneshfar, P. Rollin, Z. Aly, and L. Campbell. 2014. Annual space-based crop inventory for Canada: 2009–2014. Geoscience and Remote Sensing Symposium (IGARSS), 2014 IEEE International, Issue Date: 13-18 July 2014. http://open.canada.ca/data/en/dataset/ba2645d5-4458-414d-b196-6303ac06c1c9.

Groves C. R. 2003. Drafting a Conservation Blueprint: a practitioner's guide to planning for biodiversity. Island Press, DC

Groves, C. 2003. *Drafting a Conservation Blueprint: A Practitioners Guide to Planning for Biodiversity*. Island Press, Washington, D.C.

Gunderson, L. H. 2000. Ecological resilience–in theory and application. *Annual Review of Ecology and Systematics* 31:425–439.

Guthrie, J.M. 2012. *Modeling movement behavior and road crossing in the black bear of south central Florida.* (Master's Thesis). University of Kentucky, Lexington, Kentucky.

Hansen, J., R. Ruedy, M. Sato, and K. Lo. 2010. Global surface temperature change. *Reviews of Geophysics*, 48(4) 1-29.

Hansen, M.C, Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A. Thau, D. Stehman, S.V. Goetz, J. Loveland, T.R. Kommareddy, A. Egorov, A. Chini, L, Justice, C.O. Townshend, J.R.G. 2013 High-Resolution Global Maps of 21st-Century Forest Cover Change Science 342: 850-853.

Heller, N. E., and E.S. Zavaleta. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological conservation 142*:14-32.

Hilty, J. A., and A.M. Merenlender. 2004. Use of riparian corridors and vineyards by mammalian predators in northern California. *Conservation Biology 18*: 126-135.

Hunter, M. L., G.L. Jacobson, and T.Webb. 1988. Paleoecology and the coarse-filter approach to maintaining biological diversity. *Conservation Biology* 2:375–385.

Krosby, M., J. Tewksbury, N.M. Haddad, and J. Hoekstra. 2010. Ecological connectivity for a changing climate. *Conservation Biology* 24:1686–1689.

Krosby, M., Norheim, R., Theobald, D. M., and B. H. McRae. 2014. Riparian climate-corridors: Identifying priority areas for conservation in a changing climate. Technical Report. Available at http://nplcc.databasin.org/datasets/46caec8762194138a8a6421322ea170d

Lawler J.J, D.D. Ackerly, C.M Albano, M.G. Anderson, S.Z. Dobrowski, J.L. Gill, N.E. Heller, R.L. Pressey, E.W. Sanderson, and S.B. Weiss. 2015. The theory behind, and challenges of, conserving nature's stage in a time of rapid change. *Conservation Biology* 29:618–629

Lenoir, J., J.C. Gégout, A. Guisan, P. Vittoz, T. Wohlgemuth, N.E. Zimmermann, and J.C. Svenning. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography 33*:295-303.

Lenoir, J., J.C. Gégout, P.A. Marquet, P. De Ruffray and H. Brisse, H. 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320: 1768-1771.

Lindenmayor, D. and J. Fischer. 2006. *Habitat Fragmentation and Landscape Change*. Island Press, Washington, D.C. 352 pp.

Loarie, S.R., P.B. Duffy, H. Hamilton, G.P. Asner, C.B. Field, and D.D. Ackerly. 2009. The velocity of climate change. *Nature* 462:1052–1055.

Luoto, M., and R.K. Heikkinen. 2008. Disregarding topographical heterogeneity biases species turnover assessments based on bioclimatic models. *Global Change Biology* 14:483–494.

Manci, K.M. 1989. Riparian ecosystem creation and restoration: A literature summary. US Fish and Wildlife Service Biological Report 89(20):1-59.

McGuire, J.L., J.J. Lawler, B.H. McRae, T.A. Nuñez, and D. M. Theobald. 2016. Achieving climate connectivity in a fragmented landscape. *Proceedings of the National Academy of Science*s 113:7195-7200. www.pnas.org/cgi/doi/10.1073/pnas.1602817113

McRae, B. H., and P. Beier. 2007. Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences 104*:19885-19890.

McRae, B. H., V.B. Shah. 2009. Circuitscape user guide. ONLINE. The University of California, Santa Barbara. http://www. circuitscape.org

McRae, B. H., B.G. Dickson, T.H. Keitt, and V.B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* 89: 2712-2724.

McRae, B.H., V.B. Shah, and T.K. Mohapatra. 2013. Circuitscape 4 User Guide. The Nature Conservancy. http://www.circuitscape.org.

McRae, B.H., K. Popper, A. Jones, M. Schindel, S. Buttrick, K.R. Hall, R.S. Unnasch, and J. Platt. 2016. Conserving Nature's Stage: Mapping Omnidirectional Connectivity for Resilient Terrestrial Landscapes in the Pacific Northwest. The Nature Conservancy, Portland, Oregon. 47 pp. http://nature.org/resilienceNW

Meiklejohn, K., R. Ament, and G. Tabor. 2010. Habitat Corridors & Landscape Connectivity: Clarifying the Terminology. Center For Large Landscape Conservation. www.climateconservation.org.

Olson, D. H., P.D. Anderson, C.A. Frissell, H.H. Welsh, and D.F. Bradford. 2007. Biodiversity management approaches for stream–riparian areas: perspectives for Pacific Northwest headwater forests, microclimates, and amphibians. *Forest Ecology and Management 246*: 81-107.

Olson, D. H. and K.M. Burnett. 2013. Geometry of forest landscape connectivity: pathways for persistence. In: Anderson, Paul D., Ronnenberg, Kathryn L., eds. Density management for the 21st century: west side story. Gen. Tech. Rep. PNW-GTR-880. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station:220–238

Open Street Map 2014. Open Street map. http://www.openstreetmap.org

Pachauri, R. K., and A. Reisinger. 2007. Contribution of WorkingGroups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Core Writing Team, R. K. Pachauri,and A. Reisinger, editors. IPCC, Geneva, Switzerland.

Pardi, M.I. and F.A. Smith. 2012. Paleoecology in an era of climate change: how the past can provide insights into the future. In Paleontology in Ecology and Conservation (Louys, J., ed.), pp. 93–115, Springer-Verlag.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*: 37-42.

Pelletier, D., M. Clark, M.G. Anderson, B. Rayfield, M.A. Wulder, and J.A. Cardille 2014. Applying circuit theory for corridor expansion and management at regional scales: tiling, pinch points, and omnidirectional connectivity. *PloS One 9*(1) e84135.

Pressey, R. L., M. Cabeza, M.E. Watts, R.M. Cowling, and K.A. Wilson. 2007. Conservation planning in a changing world. *TRENDS in Ecology and Evolution* 22:583–592.

Randin, C. F., R. Engler, S. Normand, M. Zappa, N. Zimmermann, P.B. Pearman, P. Vittoz, W. Thuiller, and A. Guisani. 2008. Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology* 15:1557–1569.

Robidoux, C. 2010 - Identification et validation préliminaire des corridors naturels du territoire de Corridor Appalachien – 2009-2010. Phase I. ACA - Corridor Appalachien. *Report is in French.*

Rodrigues, A.S.L., and T.M. Brooks. 2007. Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annual Review of Ecology, Evolution, and Systematics* 38:713–737.

Rouget, M. and D.M. Richardson. 2003. Inferring Process from Pattern in Plant Invasions: A Semimechanistic Model Incorporating Propagule Pressure and Environmental Factors. The American Naturalist 162(6). 713-724.

Schloss, C.A., J.J. Lawler, E.R. Larsron, H.L. Paperndick, M.J. Case, D.M. Evanse, J.H. DeLap, J.G. R. Landgon, S.A. Hall, and B.H. McRae. 2011. Systematic conservation planning in the face of climate change: bet-hedging on the Columbia Plateau. *PLoS One* 6 DOI: 10.1371/journal.pone.0028788

Seavy, N. E., T. Gardali, G.H. Golet, F.T. Griggs, C.A. Howell, R. Kelsey, and J.F Weigand. 2009. Why climate change makes riparian restoration more important than ever: recommendations for practice and research. *Ecological Restoration 27*: 330-338.

Shah, B.V. and B.H. McRae. 2008. Circuitscape: a tool for landscape ecology. In proceeding of the 7th Python in Science Conference (SciPy 2008). http://conference.scipy.org/proceedings/scipy2008/SciPy2008_proceedings.pdf, Pasadena CA.

US Census Bureau. 2014. 2014 TIGER/Line Shapefiles (machine-readable data files). http://www.census.gov/geo/maps-data/data/tiger.html

Ventyx Corporation. 2014. Velocity Suite: Transmission lines constrained or congested, transmission lines (In service by voltage class), and Natural Gas Pipelines (In service). http://www.ventyx. Accessed October 2014. com/en/enterprise/business-operations/business-products/velocitysuite.

Weiss, S. B., D.D. Murphy, and R.R. White. 1988. Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha bayensis*. *Ecology* 69:1486–1496.

Willis, K. J., and S. A. Bhagwat. 2009. Biodiversity and climate change. *Science* 326:806–807.