

Maintaining a landscape that facilitates range shifts for terrestrial species

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Abstract

Range shifts are a well-documented species response to past episodes of climate change, reflecting a combination of dispersal pressure, suitable new habitat, and a permeable landscape that allows movement. There is abundant evidence that range shifts are already occurring in response to current climate change. They have been detected as expansions upslope and poleward, as downslope movement into riparian areas, or as extremely local movements that take advantage of proximate microclimates. The magnitude and pattern of contemporary range shifts are likely to differ from historic responses to climate because humans have modified the landscape, fragmenting habitats and disrupting natural movements. These modifications create resistance that may prevent species from colonizing new habitat, leading instead to range constrictions. We modeled landscape permeability to reveal where population expansions would be hampered by anthropogenic obstacles, and specifically to examine upslope, northward, and riparian movement patterns to identify key conduits and pinch points that if properly managed might facilitate the range shifts needed for species to adjust to a changing climate.

I. Objective and Introduction

The goal of this white paper is to describe the mechanisms by which climate change leads to species range shifts, and to understand how those shifts are influenced by the condition of the landscape through which species must move. The information is used to inform a spatially-explicit assessment of landscape permeability (the degree to which the landscape allows species and populations to pass through it) for Eastern North America. We translate the results into conservation priorities and strategies aimed at maintaining a landscape that facilitates range shifts for terrestrial species.

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 5-6⁰ C, cypress trees and alligators had moved north as far as the high Arctic (Krosby et al. 2010). More recently, most of Eastern North America and Eurasia were repeatedly ice-covered during 2.6 million years of glacial cycles, causing species to repeatedly shift their ranges. While they did so at different rates and in different directions, all the species that currently occur in these areas expanded their ranges north to occupy their current ranges in the last 12,000 years. Despite all the change of the last glacial period there were remarkably few known extinctions (Botkin et al. 2007).

Although there were periods of exceptionally rapid (e.g. > 10 C in a decade) warming and cooling in some places during the late glacial and early Holocene (Alley, Richard B. 2000. Mayewski et al. 2013, Steffensen et al. 2008), we are now facing a period of particularly 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 shift their distributions to adapt to these changing conditions. Indeed, in response to 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,

fragmenting natural land and creating obstacles to dispersal (Fischer and Lindenmayer 2007, Haddad et al. 2015). How do conservationists ensure that the landscape remains permeable enough to allow large-scale movements, particularly by species that disperse slowly or may be hindered by a variety of factors? Here we address this question for terrestrial landscapes in Eastern North America.

II. Climate Change and Range Shifts

A. Range Shifts

Species respond to changes in climatic conditions in several ways: 1) *individuals adapt* their behaviors or habitat niches while staying in the same location, perhaps choosing shadier nesting sites or spending more time in riparian areas or being less active during the day; 2) *populations evolve* new climate tolerances to adapt to changed conditions through natural selection. We often think of evolution as happening very slowly, but as was demonstrated by studies of the Galapagos Island finches (Weiner 1995, Visser 2008), species can evolve rapidly in response to dramatic changes in climatic pattern. Furthermore, many species, from trees to corals, 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.

The other way that species may respond to climate changes is that 3) *populations and species shift their distributions*. This can occur when climate change leads to previously unsuitable habitat becoming suitable for population persistence, allowing colonization of new habitat patches outside of the current range of a species. It can also result from differential survival of individuals at the range edge leading to a more gradual redistribution. For example, individual propagules that survive preferentially in shadier or moister areas can cause a local population to shift in elevation or to a more shaded aspect. It is likely that components of all three mechanisms occur for most species. Range shifts 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 such as amphibians that breed in 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 to disperse is driven by the number of source populations and the abundance of reproducing individuals within them. The probability of a disperser encountering a new habitat is partially a function of dispersal pressure and partially of the permeability of the landscape through which the species must traverse. 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 a population process that occurs over generations, and are sensitive to variation in three factors: dispersal pressure and vagility, the permeability of the landscape, and the availability and suitability of the receiving habitat for the species in question.

A range shift 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, barriers, or lack of dispersal pressure. If at the same time, new and climatically suitable areas remain remote from current distributions due to the loss and fragmentation of habitats, and beyond the dispersal capacity of many species, then, the concern is that species with low adaptability or dispersal capacity will be caught

between climate-forced range change and low likelihood of finding distant habitats to colonize, 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 which have not yet expanded 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 the current species (Roth et al. 2014). For example, alpine areas, which are demonstrably sensitive to climate change (Walter 2016) and offer resident species little potential for upslope or northward movements, have yet to show any local extinctions, apparently due to the abundance of local microclimates (Roth et al. 2014.)

A1. Dispersal and Dispersal pressure

Whether species arrive in a new location that may be suitable for colonization depends on the population size and the buildup of dispersal pressure, their dispersal ability, and the proximity, relative abundance, and size of patches of suitable habitat (Primack and Miao, 2002). Research has shown that dispersal limitations are often more important than recruitment limitations for forest plant species colonizing new areas (Honnay et al. 2002). Some wind dispersed plants and some animals are capable of long-distance dispersal in a single generation such as migratory birds and large mammals. Smaller mammals and herptiles are more likely to be restricted to shorter dispersal distances and therefore dependent on adjacent and proximal 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 travel 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 longer-distance dispersal, whether by natural vectors, or inadvertently assisted by ubiquitous and constant human movement such as 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 and 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.

A2: Landscape Permeability:

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 relative to their dispersal abilities and reproductive capabilities. If the goal was simply to maintain genetic connectivity among populations, a few individuals occasionally reaching the new area might be enough, as even a few new genes can make a difference in an isolated population (Soule and Simberloff 1986), and gene flow does appear to increase fitness among populations near their range limit (Sexton et al. 2011). However, range shifts to places not yet occupied by the given species are often dependent on many more successes, 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, 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 Eastern US now surrounded by development, or patches of grassland in the Midwestern US 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, shrubland, and 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 geographic information system (GIS) models, resistance values are assigned to individual cells in a raster based on the cell’s land cover type and the expected degree of resistance. Such a GIS resistance model forms the basis of the continuous permeability models used to model potential range shifts.

The resistance of a landscape to successful dispersal may also be ecological, that is, a function of natural discontinuities in the landscape. The most obvious example is the dispersal of terrestrial species across oceans. The emergence of the Bering Land Bridge during the Ice Age allowed dispersal of *Homo sapiens*

and many other species to the Americas while the emergence of the Panamanian Isthmus allowed North American species to expand their ranges to South America. Large-scale landscape features surrounded by highly contrasting habitat, 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 in the Western US (McCormack et al. 2009). On a smaller scale, some species dependent on moist conditions such as prairie potholes or riparian areas likely find the surrounding dry prairie landscape resistant to dispersal. On the other hand, the pattern of high red maple genetic variation 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, and 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 (Amaral et al. 2016).

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), synthesizing the results of fragmentation experiments spanning multiple biomes, multiple scales, five continents, and 35 years, 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 with greater fragmentation and this decline accumulated over time as a fragmented area became more ecologically isolated (i.e., there was marked resistance to species moving 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) concluded 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 functional dispersal corridor can produce up to 50% more movement (Gilbert-Norton et al. 2005).

A3. Establishment and Colonization

Successful range shifts are also reliant on the conditions found in the unoccupied patches of suitable habitat available for colonization. In addition to the factors influencing the number of dispersers arriving as described in preceding paragraphs, 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.

Ironically, well-established vegetation in mature ecosystems can also pose barriers to colonization. Paleoecological records show many instances of new species making an almost instantaneous transition in ecosystems recently disturbed, as by fire or wind events, but only very slowly becoming more prominent in an established ecosystem, as in the thousand year return of hemlock in the northeast after its sudden disappearance (Jacobson, pers. com. and Jacobson et al.1987),

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 mountain tops are relics of a glacial period when such habitats were much more widespread rather than the products 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.

B. 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, the authors questioned the assumption that taxa disperse seeds 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.

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 Eastern North America and Scots Pine in Europe shifted south, and as the ice sheet receded they moved north again 150 km/century (Davis and 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 Eastern 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 and 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, and 4) locally toward suitable microclimates. The evidence for upslope and northward movements is strong and consistent across many taxa groups and across several continents (Table 2.1, 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, changes in and variability over time of 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 paper we focus on temperate regions.

Table 2.1 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) may be found 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
Invertebrates	554	U/A	20-42 yrs.	37.7	7.4	108.6	12.3	0.62	5
Fish	15	U	25 yrs.	32.7	32.7	32.7	12.7	0.65	1
Herptiles	30	A	10 yrs.	65.3	65.3	65.3	24	0.24	1
Birds	326	A/U	11-25 yrs.	-4.75	-19.3	7.6	9.3	0.795	4
Mammals	37	U/A	25-88 yrs.	50	31	69	71.6	3.05	2
Plants	495	U/A	22-94 yrs.	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
Invertebrates	332	U	8-25 yrs.	59.1	7.9	104.2	15.9	0.6	3
Fish	15	U	25 yrs.	47.2	47.2	47.2	15.4	0.65	1
Birds	361	U/A	12-31 yrs.	24.2	3.6	46	19	0.49	4
Mammals	9	U	25 yrs.	22.4	22.4	22.4	38.4	0.45	1
Algae	37	A	50 yrs.	61.4	61.4	61.4	31.6	0.74	1

Upslope Movement: Chen et al. (2011) recent meta-analysis of over 51 studies detected upslope elevational range shifts for five taxonomic groups with magnitudes ranging from 6.1 m to 11.0 m per decade and this was consistent with other studies (Parmesan and Yohe 2003, Lenoir et al. 2008). Upslope movement appears to be greatest among plants and herptiles, followed by mammals, invertebrates, and fish (Table 2.1). 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. For example, in the tropics there is a 5.2°C to 6.5°C decrease in temperature per 1000 m of elevation, nearly 1000 times as much as the latitudinal rate of decrease (Colwell et al. 2008). Although evidence for upslope movement seems overwhelming (Lenoir et al. 2010) and it may be the dominant way in which most 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, which includes many plants, invertebrates, birds, and mammals, but not for those where a lowland physiographic setting is required for suitable habitat, such as many wetland-associated species or plants that need deep, moist, and nutrient-rich soils. Second, the extent of available upslope habitat is limited in many regions where either the slopes are 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.

Northward Expansions: Northward movements are also well documented for 754 species across five taxa groups, and they appear to be ubiquitous across the northern hemisphere (Table 2.1, Chen et al. 2011). Studies have found latitudinal range shifts from 6.1 km to 16.9 km northward per decade (Chen et al. 2011, Parmesan and 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 and reports that many species will lag behind, 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.

Riparian Climate Corridors: Although the evidence for upslope and northward movements is strong, there is substantial variation in how species respond to climate change, and a third alternative for many species is to move downslope towards the cooler temperatures and moister soils of riparian environments. Riparian areas are the zones along water bodies that serve as interfaces between terrestrial and aquatic ecosystems. Although they comprise a minor proportion of the landscape, they are typically more structurally diverse and more productive in plant and animal biomass than adjacent upland areas, and they supply food, cover, and water for a large diversity of animals (Naiman et al. 1993). Riparian areas sometimes serve as migration routes and connectors between habitats for a variety of wildlife (Manci 1989), particularly within highly modified landscapes (Hilty and Merenlender 2004).

With respect to climate change, riparian areas feature microclimates that are significantly cooler and more humid than immediately surrounding areas (Olsen et al. 2007), and are expected to provide refugia from warming and drought for many species, particularly wetland species (Seavy et al. 2009). Species showing downslope shifts have been well documented (Archaux 2004, Popy et al. 2010), and an illustrative, non-comprehensive survey of such 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 and 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). A spatially-explicit climate resilience analysis based on microclimates and connectedness identified many riparian corridors as key landscape features because of the many climate options they provide, especially in relatively flat landscapes (Anderson et al. 2014).

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 US; however, the modeled temperature gradients within most riparian or floodplain corridors is extremely small, ranging from an average 0.14 C on the coastal plain to an average of 1.3 C in the Central Appalachian Mountains, suggesting little temperature relief for species moving along a riparian corridor except in the mountains where the gradients are steep (Anderson et al. 2015). This is in contrast to the temperature and moisture differences between riparian corridors and their surrounding landscapes, which are much larger (5-20^oC cooler and 10-15% higher in soil moisture, Yeakley et al. 2008, Bennie et al 2008), and provide ample incentives for species to move into riparian areas even if there is less reason to move in a directional way along the corridor. Temperature gradients and directionality aside, riparian areas are cooler and moister than the surrounding landscape, and they naturally connect many landscape features. These unique attributes 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 riparian connectivity network has been proposed as a strategy for maintaining climate resilience (Fremier et al. 2015).

The numerous studies documenting preferential use of naturally vegetated riparian zones by a wide range of species of terrestrial wildlife (e.g. Hilty and 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 because of 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 riparian plants whose propagules survive inundation periods (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 for rivers that flow north, which are much less common in the Eastern US.

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 preferential use of strips of natural vegetation in altered landscapes. In the Southeast Coastal Plain, for example, extensive and 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 very likely that many wildlife species would use a riparian corridor for dispersal if that is the only safe natural cover in the larger 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 conserving riparian corridors right up to their headwaters can provide critical over-the-ridge links for dispersal across watersheds (Olson and Burnett 2013). It is less clear in a landscape where 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. Finally, in planning for riparian areas as climate corridors it is well to remember that during major climatic shifts the moisture balance is likely to shift significantly, leading to either or both much higher and wider flood zones or much lower normal lake or river levels.

Microclimates and Rates of Change: The fourth and perhaps most common alternative is for species and populations to find suitable habitat nearby, moving a small distance to take advantage of a local microclimate. Organisms experience climate at extremely local scales (cm to m) 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° 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 and 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 and Lister 2001). Mapping the distribution of microclimates has been the basis of a study by The Nature Conservancy to identify climate resilient sites (Anderson et al. 2014), and some of the areas identified as microclimate concentrations (e.g., the Piedmont-Coastal Plain fall line), correspond to areas from which plant species ranges have expanded and contracted in historic periods of climate change (Weakley pers. com. 2015).

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. At least 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 eastern coast of Maine where the maritime influence allowed spruce to survive even when the relatively dry and warm climate of the early Holocene and the consequent frequency of fires prevented spruce survival inland (Schauffler and Jacobson, 2002). These populations were likely the primary source of the rapid expansion and dominance of spruce throughout the rest of the state about 1000 years ago during a region-wide shift to cooler and moister conditions. Note, however, that a few spruce did persist in Big Reed forest, well inland, throughout this period when spruce was not otherwise widespread.

The localized movement of populations to utilize microclimates is so restricted that it probably doesn't 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 come close to the estimated rate of range shifts that would be necessary to keep up with predicted climate changes (e.g., 300-500 km/century as per Davis and Shaw 2001, or one to two orders of magnitude faster 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. What is surprising, however, is that this example seems to be singular.

The evidence for contemporary range shifts provides 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 (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 postglacial recolonization of northern areas was characterized by long-distance dispersal beyond the plant's apparent capabilities. 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 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 mediation.

C. 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 cited a 35-year synthesis of the world's largest and longest running fragmentation experiments by Haddad et al. (2014), which clearly demonstrated 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 and 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.

III. 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. The latter 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, leading instead to range constrictions.

The conservation implications of this review can guide conservation aimed at maintaining diversity in a changing climate. Some of the findings reinforce well-known conservation design principles while other call for new mapping and integration methods to identify the spatial implications of climate-driven range shifts. These are organized below under the headings of facilitating dispersal and facilitating dispersal under climate change, and where possible linked to the resilience analysis (Anderson et al. 2016) completed for the Eastern US.

Facilitating Dispersal

1. It all starts with dispersal pressure. It is essential that there are source areas for all species that 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 such 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 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.

Facilitating Dispersal in Response to Climate Change

4. Upslope range shifts in response to climate change 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 in the Eastern US should highlight areas for explicit conservation focus. This may include pinch points that play a disproportionately 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. 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 riparian corridors 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 than their surroundings (e.g., bottomland forests in the Southeastern Coastal Plain).
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 rock and soil type that holds more or less moisture. Such opportunities are more likely in areas identified as having higher landscape diversity, as defined by the resilience analysis.
8. Over time, some geographies are likely to play an essential role as longer term refugia. Some of these can be predicted based on geology, topography or attributes that make their climates intrinsically more stable, such as the eastern coast of Maine cooled by cold ocean currents. 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, 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, and especially if they are source areas 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.

This document also serves as the literature review for the project “Resilient and Connected Landscapes for Terrestrial Conservation” (Anderson et al. 2016). Please see the full document for information on how landscape permeability and riparian climate corridors were mapped and integrated with resilient geophysical sites in the Eastern United States and Maritime Canada.

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