

From Connect-the-Dots to Dynamic Networks: Maintaining and Enhancing Connectivity to Address Climate Change Impacts on Wildlife

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Little doubt remains among scientists that humans are changing the global climate system, and that these changes will have farreaching and fundamental impacts on ecosystems and biodiversity (Solomon et al. 2007). Even if atmospheric greenhouse gas concentrations were stabilized at year 2000 levels, average global temperature would continue to rise due to lags associated with greenhouse gas absorption by the oceans (Solomon et al. 2007). Therefore, prudence dictates the development of specific conservation and management strategies that help species persist in the face of rapidly changing climate.

During paleoclimatic changes, many plants and animals avoided extinction through a combination of adapting in place through phenotypic plasticity or genetic evolution and dispersing to areas that were more suitable (Graham et al. 1996, Davis and Shaw 2001, Davis et al. 2005). While in situ persistence did occur, paleoecological records indicate that many species' ranges shifted in response to past climatic changes. For example, many plant and animal species in North America and Europe experienced dramatic range shifts during the most recent glacial and interglacial periods (DeChaine and Martin 2004). Since the last glacial period, species have responded to warming largely individualistically rather than as a cohesive community, and movements have varied significantly in rate and direction (Hunter et al. 1988, Graham et al. 1996).

There is a growing body of evidence that 20th-century warming trends are already altering the distribution of species (e.g., see meta-analyses and reviews by Parmesan and Yohe 2003, Root 2003, Parmesan 2006). Range shifts have been detected at both poles and in northern temperate, tropical, marine, and montane regions. Species that have exhibited shifts include mammals, amphibians, birds, fish, marine invertebrates, plants, and pathogens (see Parmesan 2006 and Paremsan 2005 for detailed reviews of evidence of recent range shifts). In the Northern Hemisphere a meta-analysis demonstrated that range boundaries for 99 species of

birds, butterflies, and alpine herbs have moved an average of 6.1 km/decade northward or 6.1 m/decade upward (Parmesan and Yohe 2003).

While paleoecological and recent information suggests some capacity for species to move in response to changing climate, the unprecedented rate of future climate change may mean that the movements and range shifts that occurred during previous climate changes may be more difficult to achieve in the future, especially for species with limited dispersal ability (Malcolm et al. 2002, Pearson and Dawson 2005). The expanding global human footprint will also inhibit species movement by continuing to accelerate habitat loss and fragmentation of the natural world (Sanderson et al. 2002). There is evidence that human land use already deters the movement of some species where they once moved freely (e.g., Berger 2004).

The designation of protected areas (i.e., parks, reserves, and refuges) has historically been the primary approach for conserving species and ecosystems of societal concern. However, the fixed boundaries of these protected areas present a problem as species' ranges shift with climate change. The loss and arrival of species could lead to significant turnover of species diversity and new species combinations (Burns et al. 2003). Reserves designed to protect particular species or communities may no longer serve their intended purpose as the climate changes.

For species that respond to climate change with range shifts, maintaining biodiversity will require conservation strategies that operate on scales much larger than individual parks or preserves. Maintaining and restoring connectivity across landscapes is an existing conservation tool that could reduce species extinction by facilitating range shifts among biota in response to long-term environmental change (Hunter et al. 1988, Halpin 1997, Shafer 1999, Noss 2001, Hannah et al. 2002, Hannah and Hansen 2005, Hulme 2005, Huntley 2007). Increasing connectivity between protected areas is the most commonly cited strategy for long-term biodiversity conservation (Heller and Zavaleta 2009), yet there have been few detailed discussions of exactly what connectivity requirements will look like as climate changes, and how to implement that strategy on the ground (e.g., Halpin 1997). We also lack an examination of the extent to which connectivity needs for responding to climate change are similar to or different from connectivity needs for other purposes.

In this chapter we discuss the definition of connectivity for addressing wildlife (i.e., terrestrial vertebrate) responses to climate change and compare it to connectivity under current conditions. We provide guidance on identifying, prioritizing, and protecting connectivity as a tool for facilitating wildlife conservation in light of climate change. Clarity on how to define and identify these connectivity needs will be important to deter-

mining how on-the-ground conservation practitioners and managers can implement this important strategy.

Defining Connectivity

Connectivity is a widely used term that can take on multiple meanings and serve many purposes. We define it as the measure of the extent to which organisms can move between habitat patches (Taylor et al. 1993). Connectivity is inherently a species-specific concept, and it is determined from the perspective of individual species' vagility and behavior (e.g., Hilty et al. 2006; Taylor et al. 2006). For that reason, a given landscape at a given time might be connected for some species, but not others. Species movement is critical for resource acquisition, seasonal migration, demographic and genetic dispersal, metapopulation dynamics, niche expansion, and predator/competitor avoidance. Connecting habitat fragments has been shown to result in increased species and population persistence, greater functional population sizes, more species diversity, and higher genetic exchange (Hilty et al. 2006). Many species are more prone to extinction in less connected and more isolated habitat fragments, including isolated protected areas (Newmark 1987; Parks and Harcourt 2002).

While there are clearly many benefits to fostering connectivity, there are also concerns about potential disadvantages, including the possibility that corridors might facilitate movement of invasive species or diseases, and increase the risk of predation (e.g., Simberloff et al. 1992; and see box 6.1 in Hilty et al. 2006 and table 1.1 in Crooks and Sanjayan 2006 for more extensive lists of potential disadvantages). It is also true that some degree of isolation is natural, and at times perhaps necessary, for species conservation. For example, intentional isolation of native westslope cutthroat trout (Oncorhynchus clarkii lewisi) populations in the western United States is a conservation tool aimed at preventing competitive displacement by nonnative brook trout (Salvelinus fontinalis; Peterson et al. 2008). While it is important to consider potential pitfalls in the context of connectivity conservation efforts, there is little empirical evidence of any negative effects of corridors on wildlife (Beier and Noss 1998). Conversely, mounting evidence supports their use in conservation, and the benefits of connectivity are likely to outweigh the negatives in the majority of cases (Beier and Noss 1998, Crooks and Sanjayan 2006, Hilty et al. 2006).

Connectivity can occur across a diverse range of landscape patterns that facilitate organism movement—from narrowly defined linear pathways to more diffuse landscape permeability. These ecological patterns can range from contiguous patches of landscape to discontinuous "stepping stones" (e.g., stopover points along bird migratory routes). Corridors (sometimes

called linkages) are natural or human-designed linear features (e.g, a greenway, a mountain range, strips of riparian vegetation), and they represent one way of facilitating connectivity. There is likely to be connectivity value to many terrestrial and aquatic areas, although at any given moment some areas will have higher connectivity values than others. Connectivity areas do not necessarily preclude land from providing livelihoods to people (Knight et al. 1995). Traditional "working landscapes," such as large ranches in western North America and the seminomadic grazing systems of east Africa, have proven to be functional in maintaining biodiversity and connectivity (Reid et al. 2003, DeFries et al. 2005).

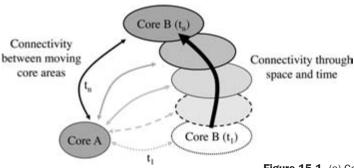
A challenge for conservation practitioners is determining how patterns that appear geospatially connected to human observers ("structural connectivity") represent actual species use ("functional connectivity"; Taylor et al. 2006). The goal of connectivity conservation efforts is to facilitate functional connectivity, but often there is limited knowledge of exactly why and how species move across the landscape. Therefore, it is difficult to pin-point where to focus connectivity conservation efforts, and what type of connectivity (e.g., corridors, linkages, stepping stones, or landscape permeability) would be most effective.

Connectivity for Climate Change

Enhancing connectivity in light of climate change requires designing landscapes that allow species to track shifting climate and habitat conditions through time. This differs from the traditional purpose of connectivity in three key ways. First, from a species-specific perspective, promoting range shifts requires connecting targets that are moving and changing. Areas of current habitat for a given species need to be connected with areas that are not currently habitat, but that likely will be in the future. The connectivity value of particular lands may also change as habitats change and species ranges shift. Second, enhancing connectivity to facilitate wildlife response to climate change requires considering the needs of a much wider array of species than is traditionally considered, since they all need to move in response to climate change and other wildlife depends on them. Finally, connecting landscapes to address climate change will often require consideration of broader spatial and temporal scales than does connectivity for other purposes.

Connecting Moving and Changing Targets

Connectivity is often conceived of as static lines connecting static core habitat areas. Identifying connectivity needs as climate changes will require anticipating how optimal climate and habitat conditions for spe-



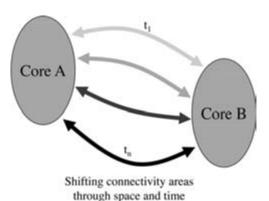


Figure 15.1. (a) Core habitat area B shifts as climate changes, creating the need for connectivity through space and time between the original location of core area B at time t = 1 and its future location at t = n. Connectivity may also be needed between core areas B and A as core area B shifts through time. (b) Conditions that define an existing connectivity area may shift across the landscape through time t = 1 to time t = n, resulting in new routes for connectivity between two core habitat areas.

cies will shift and change across the landscape through time. While this dynamic concept of connectivity is acknowledged under current conditions due to human impact on the landscape as well as processes like hydrology and wildfire (e.g., Crooks and Sanjayan 2006, Taylor et al. 2006), climate change is likely to further increase this dynamism.

As core habitat areas shift in response to changing climate, the land in between the current and future locations of a core habitat area will become important to the survival of species because they will need to be able to track the movement of optimal climate and habitat conditions through space and time (figure 15.1a). For example, coastal marsh species will need to be able to migrate inland as sea level rise inundates areas along the current coastline. At each incremental time step into the future, coastal marsh species will need to be able to move into and inhabit new areas. For some species and habitats, these changes might entail gradual movement across the landscape, whereas other species may experience abrupt or discontinuous shifts.

Climate change will also shape other forms of connectivity, such as migrations and dispersal. New connections between shifting core habitat areas and other core areas (which may or may not be shifting themselves) might become important at different times (figure 15.1a). For example, core A in figure 15.1a might represent a particular species' winter habitat and core B its summer habitat, with annual migrations that occur along fairly regular paths between them. If vegetation and other factors that make up the species' summer habitat are sensitive to climate change and shift across the landscape, it may alter the distance and direction of that species' annual migration route.

Even if climate change does not affect the location of core habitat areas, it could alter the suitability of certain corridors or linkages for species that require particular conditions (e.g., vegetation structure or food resources) for connectivity. Those shifts may result in newly identified connectivity areas within a region that is not currently deemed important (figure 15.1b). It also may increase the suitability of some corridors for particular species (e.g., generalists, invasives, or drought-tolerant organisms). An increase in the ability of these species to move across the land-scape could have significant consequences for individual species and for ecosystems more broadly.

Climate change may increase the need for or importance of connectivity in some areas. While there is a general premise that species and ecosystem distributions will shift poleward and/or up in elevation as climate changes, there is also evidence that the spatial extent of some systems will contract rather than shift (Lawler et al. 2010). The survival of some species could be threatened as a core habitat area large enough to support a viable population shrinks to a size that is no longer sufficient. In that case, species may need to disperse to or establish genetic exchange with other core areas, thereby creating a necessity for connectivity where it previously has not existed (figure 15.2). For species that now persist through meta-population dynamics, connectivity is already a requirement for species survival, and shrinkage of core habitat areas will only make that connectivity more important. A related concern involves contiguous patches of habitat that become fragmented, leading to isolated smaller patches of habitat that require connectivity between them to sustain viable populations (figure 15.2).

Climate-induced changes in ecological processes may also modify connectivity. For example, as climate change increases wildfire frequency and severity, large swaths of forest may transition to a more permanent early successional stage, characterized by a high density of short, young saplings (figure 15.3a). Those new conditions may render those forested

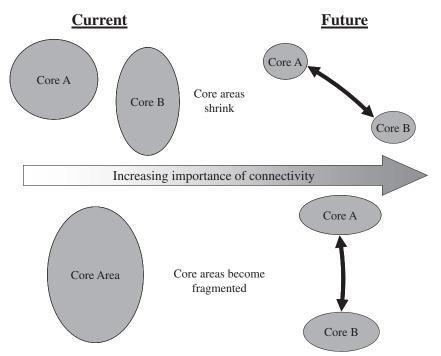


Figure 15.2. Climate change may increase the importance of connectivity between smaller core habitat areas as they shrink (*top*) or become fragmented (*bottom*).

(A) Increased wildfire frequency and severity



(B) Decreased stream flows

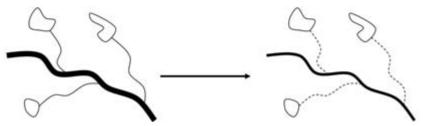


Figure 15.3. Climate-induced changes in ecological processes such as wildfire (A) or stream flows (B) may modify connectivity or conditions within connectivity areas.

areas unusable by species that depend on mature forest conditions (e.g., for food resources or physical protection from aerial predators), or impassable by species that have trouble physically moving through dense post-fire, early-succession forests. Climate change impacts on stream flows represent another example, whereby decreased flows may diminish or completely cut off connectivity between lakes, tributary streams, and a river's main stem (figure 15.3b).

Anticipating future habitat or ecosystem conditions and species distributions can be done using a variety of techniques, from statistically based climate envelope models for specific species (e.g., Pearson and Dawson 200,; Thuiller 2004, Lawler et al. 2006) to dynamic models depicting the distribution of broad vegetation categories (e.g., Cramer et al. 2001, Bachelet et al. 2003) and models of ecological processes such as wildfire (e.g., Arora and Boer 2005) and hydrology (e.g., Liang et al. 1994). Determining appropriate methodologies will depend on the extent to which a species uses particular core habitat areas and connectivity zones because of physical features (e.g., topography, geology, the distance between core habitats), biological characteristics (e.g., presence of a particular plant or animal food source, vegetation community type, vegetation structure), and/or human land use (e.g., avoidance of human population centers or infrastructure). Climate change will impact biological factors more directly than most physical features, whereas human land use may be either independent of or related to changes in climate (e.g., agricultural patterns or practices that shift in response to altered climate conditions).

Connectivity for a Broader Suite of Species

While some connectivity conservation efforts have focused on facilitating connectivity for less vagile organisms (e.g., amphibians), connectivity is mostly considered necessary for relatively wide-ranging wildlife species that require more space than is typically found within single protected areas to persist. As climate conditions shift across the landscape in the future, more organisms will need to move in ways that are not deemed necessary under current conditions. A challenge is how to accommodate the movements of so many species, each of which may have differing, or even conflicting, temporal and spatial connectivity needs.

The location and importance of connectivity for many wildlife species will depend on how other organisms on which they depend (e.g., plants, invertebrates, other vertebrates) respond to climate change. Some wildlife movements are determined by the presence or absence of other species (e.g., forage, prey, predators, competitors, or pollinators), so understanding how climate change could affect species interactions and behaviors

will be crucial to determining overall impacts on some wildlife species' connectivity needs. One way in which species interactions may be altered is through climate-induced changes in the timing of seasonal events (e.g., bud burst, migrations, and emergence from hibernation; Inouye et al. 2000, Root et al. 2005, Parmesan 2006). These phenological shifts could create species interaction mismatches and modify connectivity needs. For example, as individuals are forced to search outside of their current range for food that is not available at traditional places and points in time, the timing and location of seasonal migration routes currently seen as static may be altered.

Wildlife and the species on which they depend can have very different movement abilities, and therefore different connectivity requirements. Species vary significantly in their ability to disperse (e.g., some can travel long distances through wind-dispersed seeds or fly over nonhabitat patches, while others are relatively or completely sessile) and their ability to tolerate different types of land use and levels of fragmentation. Modeled estimates of the distance between current and future optimal climate conditions also vary for different species (figure 15.4). Combining information on species' movement abilities with estimates of distances between current and future optimal conditions can help in estimating which species are more likely to benefit from connectivity as a conservation strategy.

An additional consideration is not just how far wildlife species will have to move, but whether they will have suitable habitat to colonize once they get there. Even if suitable climate conditions can be found in places relatively near a species' current range, appropriate vegetation, soils, or other habitat factors may be unavailable in those new areas. Many animal distributions and movements are driven by interactions with vegetation, so understanding plant responses to climate change may be a key limiting factor in determining how those species will respond to changing climate, and what role connectivity might play. The ability of plant populations to adapt and move in response to past and future changes in climate is complicated and remains uncertain (Clark et al. 1998, Davis and Shaw 2001, Malcolm et al. 2002, Jump and Peñuelas 2005, McLachlan et al. 2005, Pearson 2006), thus making it difficult for us to predict subsequent impacts on vegetation-dependent wildlife.

Temporal and Spatial Scales

What constitutes a connected landscape for a given species in a changing climate will depend on the spatial and temporal scale considered. For example, over the next 30 to 50 years, the location and condition of

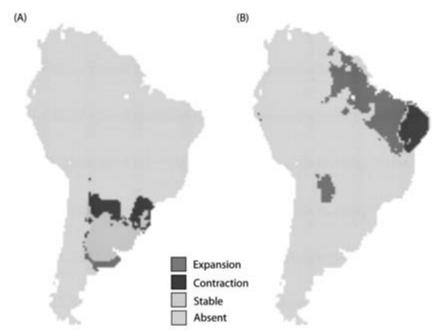


Figure 15.4. Projected climate-driven range shifts for two amphibians, *Leptodactylus gracilis* (A) and *Proceratophrys cristiceps* (B), illustrating how the distance between current and future optimal climate conditions may vary across species. The projected shifts are for an averaged time period between 2071 and 2099, and are based on climate simulated by the Hadley Centre UKMO-HadCM3 model run for the SRES A2 emissions scenario for the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (adapted from Lawler et al. 2009).

habitats for particular species may be only slightly shifted or altered. By 2100, however, the magnitude of climate change may lead to a species or its habitat moving entirely out of a region such that increasing connectivity is no longer a viable solution for maintaining that species in that location (Hannah and Hansen 2005). The greater uncertainty associated with longer-term projections of future climate conditions, along with the emergence of novel climate conditions and species assemblages (Williams et al. 2007), will make connectivity needs over the next century especially difficult to predict.

Spatial scale also needs to be explicitly considered when discussing species' connectivity needs under changing climate. Our understanding of how a species' range might shift at a coarse scale and across large geographic areas may be different from how that species moves across the landscape at a finer resolution. This could be due to the relative importance of various factors (e.g., climate, topography, land cover, human

land use) in determining species ranges at different spatial scales, or due to fine-scale idiosyncrasies in how climate will change or species will move.

Connectivity at a fine spatial scale may be especially important in the near term, whereas coarse-scale connectivity over large areas may be more important over longer timeframes. For example, as climate change negatively impacts boreal forest isolates at the southern extent of the boreal ecotone in the northeastern United States, like the Adirondack State Park, the near-term focus (e.g., over the next few decades) may be on how to facilitate movements of boreal species over several kilometers between their current locations and those places within the park where boreal forests are most likely to persist. In the long term (over the next 50 to 100 years), boreal forests may move completely out of the Adirondack State Park and the focus of connectivity efforts for those boreal species will be on how to help them move several hundreds of kilometers north into the boreal forests of Canada. Connectivity conservation efforts within the park in the longer term are likely to be less about maintaining boreal species, and more about allowing the in-migration of new species to form new assemblages and ecological communities.

Another spatial consideration is how connectivity needed to help species move in mountainous areas may differ from connectivity needs in flatter areas. Predicted velocities of temperature change (the pace at which temperature is expected to change in km per year) are lowest for topographically diverse landscapes like mountainous biomes, and fastest for flatter biomes such as flooded grasslands, mangroves, and deserts (Loarie et al. 2009). Heterogeneous mountain systems are also more likely than relatively flat regions to house potential climatic refugia, due to diverse combinations of slope, aspect, and other topographic features. Therefore, species in mountainous biomes may not have to move as far as species in more flat biomes to encounter suitable climate conditions in the future. The challenge facing species in mountainous areas is that while elevation shifts may allow them to reach more suitable climates more quickly, upslope shifts are limited since the amount of available areas decreases and eventually disappears at the tops of mountains.

Identifying Areas for Connectivity in a Changing Climate

Designing connected landscapes to address climate change involves understanding how connectivity facilitates movement. Recognizing the potential for, and location of, future connectivity is important for conserving biodiversity as climate changes. Connectivity needs may be fully captured by current conceptualizations, or there may be new needs as

climate changes in the future. While many current aspects of connectivity will continue to be important as climate changes, if we focus only on them, we might miss other important future needs.

Strategies for identifying connectivity priorities in light of changing climate are likely to rely on species-specific approaches as well as relatively coarse approaches that consider wildlife species or biodiversity in the aggregate. These approaches have tradeoffs in terms of the nature and scale of connectivity being addressed, the amount of information they require, and their ability to address climate change. Ideally, a combination of these approaches will be applied whenever possible.

Species-Specific Approaches

The inherently species-specific nature of connectivity suggests that identifying specific corridors or broader areas for allowing wildlife movement will require some consideration of the changing needs of particular species. Figure 15.5 outlines a series of broad steps towards identifying priority areas for species-specific connectivity conservation efforts in response to climate change. Many researchers recommend that these efforts concentrate on a suite of focal species that together represent the connectivity and habitat needs of a larger number of native species and ecological processes (e.g., Beier et al. 2008; also see box 1 in figure 15.5). These focal species could be selected on the basis of factors including their current importance for connectivity conservation, the sensitivity of their current

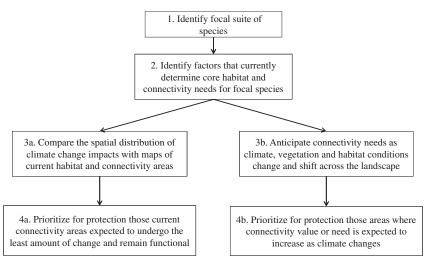


Figure 15.5. A species-specific approach to identifying connectivity areas important for facilitating wildlife responses to climate change

habitat and connectivity areas to climate change, or a general understanding of their current or future dispersal or other movement needs.

There are two important components of identifying and promoting the type and location of connectivity needed to facilitate focal species movements in light of climate change, both of which will be important. The first component involves understanding the potential impact of climate change on currently identified zones of connectivity, and highlighting the ones expected to change the least and which are therefore most likely to remain functional (box 4a in figure 15.5). The other component anticipates how climate and vegetation or ecosystem conditions will shift in the future, and identifies the areas in which connectivity will be necessary for species to relocate (box 4b in figure 15.5). Together, these approaches will ensure that current connectivity is valued and maintained without ignoring the need for new connectivity in less obvious areas.

The primary challenge in implementing the first component is that we lack a strong understanding of current connectivity priorities for wildlife in most places (box 2 in figure 15.5), and the priority connectivity areas that have been identified often are not formally protected. Several empirical and modeling approaches can help identify the location of important connectivity areas for particular species and ecological systems (e.g., Beier and Noss 1998, Bunn et al. 2000, Moilanen and Nieminen 2002, Tewksbury et al. 2002, Williams et al. 2005, Chetkiewicz et al. 2006, Beier et al. 2008, McRae et al. 2008, Phillips et al. 2008, Cushman et al. 2009, Schwartz et al. 2009, Carroll et al. 2010). But while connectivity needs have been studied extensively for some species in some places (e.g., the South Coast Missing Linkages project described in Beier et al. 2006), many areas lack any such identification. State fish and wildlife agencies in the western United States are currently working to compile priority connectivity maps (Western Governors' Association 2008). Additional efforts to understand the factors that determine current connectivity needs will improve our ability to project how climate change may alter those needs.

As mentioned above, there are many techniques for anticipating the impact of climate change on habitat and connectivity areas (boxes 3a and 3b in figure 15.5). Comparisons of the spatial distribution of climate changes and associated impacts with maps of current habitat and connectivity areas can help us identify areas expected to undergo the least change, which are therefore likely to provide connectivity benefits under both current and future climate conditions (boxes 3a and 4a in figure 15.5). Rose and Burton (2009) propose a method for mapping the persistence of climate space through time as a way of prioritizing areas

for protection given the temporal connectivity needs of species. Climate change impact information can also be used to identify any additional areas whose connectivity value may increase (boxes 3b and 4b in figure 15.5). Identifying such areas requires anticipating how climate, vegetation, and other habitat conditions may change and shift across the landscape, and understanding the other connectivity needs of a species or group (box 3b in figure 15.5). This challenge is largely being addressed in two ways: (1) by relying on general rules of thumb about how species will move in response to climate change (e.g., poleward or upslope in elevation), and (2) by using spatial models to project future climate, habitat, and species distributions.

Using models to predict where species and their habitats may be distributed in the future is appealing, because we anticipate that not all species will adhere to the generalized rules of thumb. For example, increasing drought will likely cause species to move toward relatively cool or moist microclimate refugia, or to seek out areas with persistent water availability. Movement to these areas may or may not be in line with poleward and elevational movements, so focusing on the rules of thumb may not be sufficient.

Spatial models that attempt to project future climate, habitat, and species distributions have recently been used to identify areas of connectivity for facilitating species shifts in response to climate change (Williams et al. 2005, Phillips et al. 2008, Vos et al. 2008, Carroll et al. 2010). But while model projections can be used to consider more complicated consequences of climate change, they all have uncertainties associated with both the climate projections they take as inputs and the biotic models themselves (Pearson et al. 2006, Beier and Brost 2010). The challenge is to determine how to integrate spatial models into connectivity conservation efforts in a way that increases the chance of effectively allowing species movements as climate changes, even given model uncertainties.

For areas where uncertainty about the future consequences of climate change is fairly high, one strategy could be to identify priority connectivity zones under current conditions and see how well they would allow for wildlife movement poleward and upward in elevation, or towards more well-watered sites. If currently identified connectivity cannot adequately capture those movements, then areas that augment the movements could be added as conservation priorities. This would provide a good first approximation of connectivity needs under climate change. Because not all species will follow those general rules, another strategy would be to look at the best available research and expert opinion on wildlife responses to climate change in a region, and broadly outline the type and location of

connectivity that would be needed to facilitate those responses. A third strategy would be to apply more complex modeling approaches that explicitly link climate change and connectivity models to project potential future needs (e.g., Williams et al. 2005, Phillips et al. 2008, Vos et al. 2008, Carroll et al. 2010).

Focusing on Wildlife and Biodiversity in the Aggregate

In some cases it may be preferable or necessary to take a coarser approach to targeting connectivity conservation. If there is not sufficient information about the current or future habitat or connectivity needs for a species, it may not be possible to take a species-specific approach. There also may be a preference for strategies that aim to capture a wide range of potential connectivity needs, given the uncertainties involved in knowing exactly how species and their habitats will be affected by climate change. Some of these coarser strategies might include protecting landscape features that encompass latitudinal gradients, elevation, or other physical gradients, and managing the matrix to promote permeability of movement for wildlife and other species.

Although not all species will adhere to general rules of thumb about species distributions shifting poleward and up in elevation, the fact that many species are already following those patterns suggests that protecting areas that encompass north-south gradients and elevation gradients may be reasonable for increasing connectivity. As mentioned earlier, it might be appropriate in situations where uncertainty about future climate change is fairly high. Another coarse-filter approach involves protecting and connecting areas that encompass diverse physical environments (Hunter et al. 1988). For example, Beier and Brost (2010) recommend protecting landscape units that include diverse "land facets" (recurring land units that represent similar topographic and soil conditions). They argue that wildlife corridors that contain continuous areas of different land facets should also contain continuous areas of vegetation, even though the specific species assemblages may change through time. Therefore, protecting a diversity of land facets should facilitate the persistence of diverse vegetation and wildlife species, and complement conservation strategies that are based on species-specific responses to climate change (Beier and Brost 2010).

Yet another way to maxime the number of species that can move in response to climate change is to think beyond corridors and stepping stones, and to consider managing the matrix of lands between protected areas in ways that promote permeability and species movement (Da Fonseca et al. 2005, Franklin and Lindenmayer 2009). Because 83% of the earth's

land surface (excluding Antarctica) is directly affected by human infrastructure and land use activities (Sanderson et al. 2002), and because we cannot predict exactly how future vegetation and ecosystem conditions may shift and change, these human-dominated matrix lands (e.g., agricultural areas, private forested lands, ranchlands) present an important opportunity for securing the kind of landscape-scale connectivity that will be necessary for future movements of plant and animal species.

One Tool in the Conservation Toolbox

While connectivity will obviously help some species respond to climate change, it will not be a panacea. Relatively immobile or poorly dispersed species may not benefit as much as relatively vagile species, and may require more aggressive management interventions, such as translocation to future suitable areas (Hoegh-Guldberg et al. 2008, Richardson et al. 2009, Willis et al. 2009). Climate change may present less of a threat to generalist species that are broadly distributed in a diverse array of habitat patches. However, species that are more limited by climate or are isolated in relatively few patches will be less able to rapidly relocate to survive climate change, especially if landscape fragmentation prevents their movement (Opdam and Wascher 2004).

The rate and magnitude of shifts in climate and ecosystems and the future existence of suitable climate and habitat somewhere on the land-scape will ultimately determine the usefulness of maintaining or enhancing connectivity for wildlife conservation. Such efforts will also be futile unless sufficient investments are made in establishing core habitat areas towards which species can move. Some argue that focusing conservation on increasing the size, quality, and number of protected areas is better than attempting to identify and protect connectivity, which is fraught with uncertainties (Hodgson et al. 2009). Others point out that the distances that species will need to move in response to climate change are likely to be much greater than what can be accommodated within individual protected areas (Krosby et al. 2010). For these reasons, connectivity conservation efforts need to be applied in the context of broader landscape conservation work in which protected areas, connectivity, and land management approaches are considered simultaneously.

A Way Forward

Climate change underscores the importance of rethinking the old paradigm of connectivity as "connecting the dots" between disjunct core habitats or protected areas, where both the dots and connecting lines are static concepts in space and time. We need to consider connectivity

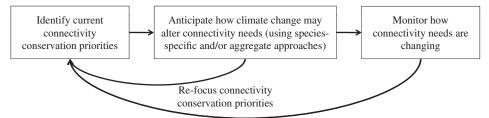


Figure 15.6. An iterative process for setting connectivity conservation priorities that anticipates how climate change may alter connectivity needs and incorporates monitoring information on how connectivity needs actually change through time

to be dynamic and in some cases transitory. This paradigm shift challenges us to design monitoring and modeling efforts that anticipate when and where current connectivity may fail, and when and where new connectivity may form over short (e.g., the next few decades) and long (e.g., the next century) time scales. One answer to this challenge likely lies in an iterative process of identifying current connectivity needs, anticipating how those needs may change in the future, monitoring how those needs are changing, and refocusing conservation attentions as necessary (figure 15.6).

Although the available tools for modeling future conditions have limitations, they are useful for visualizing future scenarios that can form the basis for anticipating future connectivity needs using the best available science. Coupling those modeling efforts with strategic monitoring of species' habitat conditions, distributions, and connectivity needs will allow us to track changes happening on the ground, and to compare and test model projections. Monitoring and research targeted at improving our understanding of functional connectivity under current conditions will elucidate where the most important connections are, and why they are important. This information will in turn strengthen the accuracy and applicability of connectivity models. An iterative process would allow for increasing levels of sophistication in the use of general rules of thumb, expert opinion, and efforts that explicitly link climate change impact and connectivity models. It would also allow for the inclusion of updated ecological information, climate projections, and modeling techniques as they become available.

The good news is that by building a more dynamic paradigm for how we think about connectivity needs as climate changes, we can focus on developing creative, dynamic solutions. Land trusts may be able to devise conservation plans that reflect transitory stages and therefore do not necessarily require conservation in perpetuity. Restoration projects on

currently disturbed or degraded land could be managed specifically to maximize the land's value for connectivity, both now and in the future. For example, the removal of human infrastructure and some restriction of human access to a critical wildlife corridor in Banff National Park in Canada resulted in a significant increase in that corridor's use by wolves (Duke et al. 2001). Low-intensity land uses may also be managed to augment connectivity of undisturbed natural ecosystems in order to provide broader landscape permeability (Hannah and Hansen 2005).

Wildlife species are increasingly challenged to adapt and move in response to changing climatic conditions. As humans, we also need to adapt by designing conservation strategies that allow species to cope with this challenge. Restoring and maintaining connectivity between core protected areas in space and through time will undoubtedly be an important tool. Implementing this strategy through an iterative process whereby the best available science is used to examine both current and changing connectivity needs will increase the likelihood of benefit for as many species as possible. If we do not act quickly to develop and implement a dynamic approach to connectivity, the rapid encroachment of the human footprint will preclude many conservation options.

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LITERATURE CITED

- Arora, V. K. and G. J. Boer. 2005. Fire as an interactive component of dynamic vegetation models. *Journal of Geophysical Research* 110:G02008.1–G02008.20.
- Bachelet, D., R. P. Neilson, T. Hickler, R. J. Drapek, J. M. Lenihan, M. T. Sykes, B. Smith, S. Sitch, and K. Thonicke. 2003. Simulating past and future dynamics of natural ecosystems in the United States. *Global Biogeochemical Cycles* 17: 14.1–14.21.
- Beier, P. and B. Brost. 2010. Use of land facets to plan for climate change: Conserving the arenas, not the actors. *Conservation Biology* 24:701–10.
- Beier, P., D. R. Majka, and W. D. Spencer. 2008. Forks in the road: Choices in procedures for designing wildland linkages. *Conservation Biology* 22:836–51.
- Beier, P. and R. F. Noss. 1998. Do habitat corridors provide connectivity? *Conservation Biology* 12:1241–52.
- Beier, P., K. L. Penrod, C. Luke, W. D. Spencer, and C. Cabanero. 2006. South Coast Missing Linkages: Restoring connectivity to wildlands in the largest metropolitan area in the USA. In K. R. Crooks and M. Sanjayan, eds., Connectivity Conservation. Cambridge University Press, Cambridge.
- Berger, J. 2004. The last mile: How to sustain long-distance migration in mammals. *Conservation Biology* 18:320–31.
- Bunn, A. G., D. L. Urban, and T. H. Keitt. 2000. Landscape connectivity: A

- conservation application of graph theory. *Journal of Environmental Management* 59:265–78.
- Burns, C. E., K. M. Johnston, and O. J. Schmitz. 2003. Global climate change and mammalian species diversity in US national parks. *Proceedings of the National Academy of Sciences, USA* 100:11474–77.
- Carroll, C., J. R. Dunk, and A. Moilanen. 2010. Optimizing resiliency of reserve networks to climate change: Multispecies conservation planning in the Pacific Northwest, USA. *Global Change Biology* 16:891–904.
- Chetkiewicz, C.-L. B., C. C. St. Clair, and M. S. Boyce. 2006. Corridors for conservation: Integrating pattern and process. *Annual Review of Ecology, Evolution, and Systematics* 37:317–42.
- Clark, J. S., C. Fastie, G. Hurtt, S. T. Jackson, C. Johnson, G. A. King, M. Lewis, J. Lynch, S. Pacala, C. Prentice, E. W. Schupp, T. Webb, III, and P. Wyckoff. 1998. Reid's paradox of rapid plant migration. *BioScience* 48:13–24.
- Cramer, W., A. Bondeau, F. I. Woodward, I. C. Prentice, R. A. Betts, V. Brovkin, P. M. Cox, V. Fisher, J. A. Foley, A. D. Friend, C. Kucharik, M. R. Lomas, N. Ramankutty, S. Sitch, B. Smith, A. White, and C. Young-Molling. 2001. Global response of terrestrial ecosystem structure and function to CO₂ and climate change: Results from six dynamic global vegetation models. *Global Change Biology* 7:357–73.
- Crooks, K. R. and M. Sanjayan. 2006. Connectivity conservation: Maintaining connections for nature. In *Connectivity Conservation*, edited by K. R. Crooks and M. Sanjayan. Cambridge: Cambridge University Press.
- Cushman, S. A., K. S. McKelvey, and M. K. Schwartz. 2009. Use of empirically derived source-destination models to map regional conservation corridors. *Conservation Biology* 23:368–76.
- Da Fonseca, G. A. B., W. Sechrest, and J. Oglethorpe. 2005. Managing the matrix. In *Climate Change and Biodiversity*, edited by T. E. Lovejoy and L. Hannah. New Haven: Yale University Press.
- Davis, M. B. and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* 292:673–79.
- Davis, M. B., R. G. Shaw, and J. R. Etterson. 2005. Evolutionary responses to changing climate. *Ecology* 86:1704–14.
- DeChaine, E. G. and A. P. Martin. 2004. Historic cycles of fragmentation and expansion in *Parnassius smintheus* (Papilionidae) inferred using mitochondrial DNA. *Evolution* 58:113–27.
- DeFries, R., A. Hansen, A. C. Newton, and M. C. Hansen. 2005. Increasing isolation of protected areas in tropical forests over the past twenty years. *Ecological Applications* 15:19–26.
- Duke, D. L., M. Hebblewhite, P. C. Paquet, C. Callaghan, and M. Percy. 2001.
 Restoration of a large carnivore corridor in Banff National Park, Alberta. In *Large Mammal Restoration: Ecological and Sociological Challenges in the 21st Century*, edited by D. S. Maehr, R. F. Noss, and J. F. Larkin. New York: Island Press.
- Franklin, J. F. and D. Lindenmayer. 2009. Importance of matrix habitats in maintaining biological diversity. *Proceedings of the National Academy of Science of the United States of America* 106:349–50.
- Graham, R. W., E. L. Lundelius, M. A. Graham, E. K. Schroeder, R. S. Toomey, E. Anderson, A. D. Barnosky, J. A. Burns, C. S. Churcher, D. K. Grayson, R. D. Guthrie, C. R. Harington, G. T. Jefferson, L. D. Martin, H. G. McDonald,

- R. E. Morlan, H. A. Semken, S. D. Webb, L. Werdelin, and M. C. Wilson. 1996. Spatial response of mammals to late quaternary environmental fluctuations. *Science* 272:1601–6.
- Halpin, P. N. 1997. Global climate change and natural-area protection: Management responses and research directions. *Ecological Applications* 7:828–43.
- Hannah, L. and L. Hansen. 2005. Designing landscapes and seascapes for change. In Climate Change and Biodiversity, edited by T. E. Lovejoy and L. Hannah. New Haven: Yale University Press.
- Hannah, L., G. F. Midgley, T. Lovejoy, W. J. Bond, M. Bush, J. C. Lovett, D. Scott, and F. I. Woodward. 2002. Conservation of biodiversity in a changing climate. *Conservation Biology* 16:264–68.
- 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., W. Lidicker Jr., and A. Merenlender. 2006. *Corridor Ecology: The Science and Practice of Linking Landscapes for Biodiversity Conservation*. Washington: Island Press.
- Hodgson, J. A., C. D. Thomas, B. A. Wintle, and A. Moilanen. 2009. Climate change, connectivity and conservation decision making: Back to basics. *Journal of Applied Ecology* 46:964–69.
- Hoegh-Guldberg, O., L. Hughes, S. McIntyre, D. B. Lindenmayer, C. Parmesan, H. P. Possingham, and C. D. Thomas. 2008. Assisted colonization and rapid climate change. *Science* 321:345–46.
- Hulme, P. E. 2005. Adapting to climate change: Is there scope for ecological management in the face of a global threat? *Journal of Applied Ecology* 42:784–94.
- Hunter, M. L., Jr., G. L. Jacobson, Jr., and T. Webb, III. 1988. Paleoecology and the coarse-filter approach to maintaining biological diversity. *Conservation Biology* 2:375–85.
- Huntley, B. 2007. Climatic change and the conservation of European biodiversity: Towards the development of adaptation strategies. Discussion paper prepared for the 27th meeting of the Standing Committee, Convention on the Conservation of European Wildlife and Natural Habitats, Council of Europe, Strasbourg, 26–29 November 2007.
- Inouye, D. W., B. Barr, K. B. Armitage, and B. D. Inouye. 2000. Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Sciences, USA* 97:1630–33.
- Jump, A. S. and J. Peñuelas. 2005. Running to stand still: Adaptation and the response of plants to rapid climate change. *Ecology Letters* 8:1010–20.
- Knight, R. L., G. N. Wallace, and W. E. Riebsame. 1995. Ranching the view: Subdivisions versus agriculture. *Conservation Biology* 9:459–61.
- Krosby, M., J. Tewksbury, N.M. Haddad, and J. Hoekstra. 2010. Ecological connectivity for a changing climate. *Conservation Biology* 24:1686–89.
- Lawler, J. J., S. L. Shafer, B. A. Bancroft, and A. R. Blaustein. 2010. Projected climate impacts for the amphibians of the western hemisphere. *Conservation Biology* 24: 38–50.
- Lawler, J. J., S. L. Shafer, D. White, P. Kareiva, E. P. Maurer, A. R. Blaustein, and P. J. Bartlein. 2009. Projected climate-induced faunal change in the Western Hemisphere. *Ecology* 90:588–97.
- 326 | Chapter Fifteen

- Lawler, J. J., D. White, R. P. Neilson, and A. R. Blaustein. 2006. Predicting climateinduced range shifts: model differences and model reliability. *Global Change Biology* 12:1568–84.
- Liang, X., D. P. Lettenmaier, E. F. Wood, and S. J. Burges. 1994. A simple hydrologically based model of land surface water and energy fluxes for general circulation models. *Journal of Geophysical Research* 99:14415–28.
- 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* 462:1052–55.
- Malcolm, J. R., A. Markham, R. P. Neilson, and M. Garaci. 2002. Estimated migration rates under scenarios of global climate change. *Journal of Biogeography* 29:835–49.
- McLachlan, J. S., J. S. Clark, and P. S. Manos. 2005. Molecular indicators of tree migration capacity under rapid climate change. *Ecology* 86:2088–98.
- 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* 89:2712–24.
- Moilanen, A. and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. *Ecology* 83:1131–45.
- Newmark, W. D. 1987. A land-bridge island perspective on mammalian extinctions in western North American parks. *Nature* 325:430–32.
- Noss, R. F. 2001. Beyond Kyoto: Forest management in a time of rapid climate change. *Conservation Biology* 15:578–90.
- Opdam, P. and D. Wascher. 2004. Climate change meets habitat fragmentation: Linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation* 117:285–97.
- Parks, S. A. and A. H. Harcourt. 2002. Reserve size, local human density, and mammalian extinctions in US protected areas. *Conservation Biology* 16:800–808.
- Parmesan, C. 2005. Biotic responses: Range and abundance changes. In *Climate Change and Biodiversity*, edited by T. E. Lovejoy and L. Hannah. New Haven: Yale University Press.
- ——. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–69.
- Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Pearson, R. G. 2006. Climate change and the migration capacity of species. *Trends in Ecology & Evolution* 21:111–13.
- Pearson, R. G. and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography* 12:361–71.
- . 2005. Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. Biological Conservation 123:389–401.
- Pearson, R. G., W. Thuiller, M. B. Araujo, E. Martinez-Meyer, L. Brotons, C.McClean, L. Miles, P. Segurado, T. P. Dawson, and D. C. Lees. 2006. Model-based uncertainty in species range prediction. *Journal of Biogeography* 33:1704–11.
- Peterson, D. P., B. E. Rieman, J. B. Dunham, K. D. Fausch, and M. K. Young. 2008. Analysis of trade-offs between threats of invasion by nonnative brook trout (*Salvelinus fontinalis*) and intentional isolation for native westslope cutthroat

- trout (Oncorhynchus clarkii lewisi). Canadian Journal of Fisheries and Aquatic Sciences 65:557–73.
- Phillips, S. J., P. Williams, G. Midgley, and A. Archer. 2008. Optimizing dispersal corridors for the Cape Proteaceae using network flow. *Ecological Applications* 18:1200–1211.
- Reid, R. S., M. Rainy, J. Ogutu, R. L. Kruska, K. Kimani, M. Nyabenge, M. McCartney, M. Kshatriya, J. Worden, L. Ng'ang'a, J. Owuor, J. Kinoti, E. Njuguna, C. J. Wilson, and R. Lamprey. 2003. People, Wildlife and Livestock in the Mara Ecosystem. Report, Mara Count 2002, International Livestock Research Institute, Nairobi.
- Richardson, D. M., J. J. Hellmann, J. S. McLachlan, D. F. Sax, M. W. Schwartz,
 P. Gonzalez, E. J. Brennan, A. Camacho, T. L. Root, O. E. Sala, S. H. Schneider,
 D. M. Ashe, J. R. Clark, R. Early, J. R. Etterson, E. D. Fielder, J. L. Gill, B. A.
 Minteer, S. Polasky, H. D. Safford, A. R. Thompson, and M. Vellend. 2009.
 Multidimensional evaluation of managed relocation. *Proceedings of the National Academy of Science of the United States of America* 106:9721–24.
- Root, T. L., D. P. MacMynowski, M. D. Mastrandrea, and S. H. Schneider. 2005. Human-modified temperatures induce species changes: Joint attribution. Proceedings of the National Academy of Science of the United States of America 102:7465–69.
- Root, T. P., K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60.
- Sanderson, E. W., M. Jaiteh, M. A. Levy, K. H. Redford, A. V. Wannebo, and G. Woolmer. 2002. The human footprint and the last of the wild. *BioScience* 52:891–904.
- Schwartz, M. K., J. P. Copeland, N. J. Anderson, J. R. Squires, R. M. Inman, K. S. McKelvey, K. L. Pilgrim, L. P. Waits, and S. A. Cushman. 2009. Wolverine gene flow across a narrow climatic niche. *Ecology* 90:3222–32.
- Shafer, C. L. 1999. National park and reserve planning to protect biological diversity: Some basic elements. *Landscape and Urban Planning* 44:123–53.
- Simberloff, D., J. A. Farr, J. Cox, and D. W. Mehlman. 1992. Movement corridors: Conservation bargains or poor investments? *Conservation Biology* 6:493–504.
- Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, eds. 2007. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge and New York: Cambridge University Press.
- Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity Is a vital element of landscape structure. *Oikos* 68:571–73.
- Taylor, P. D., L. Fahrig, and K. A. With. 2006. Landscape connectivity: A return to basics. In *Connectivity Conservation*, edited by K. R. Crooks and M. Sanjayan. Cambridge: Cambridge University Press.
- Tewksbury, J. J., D. J. Levey, N. M. Haddad, S. Sargent, J. L. Orrock, A. Weldon, B. J. Danielson, J. Brinkerhoff, E. I. Damschen, and P. Townsend. 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences of the United States of America* 99:12923–26.
- Thuiller, W. 2004. Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology* 10:2020–27.
- 328 | Chapter Fifteen

- Vos, C.C., P. Berry, P. Opdam, H. Baveco, B. Nijhof, J. O'Hanley, C. Bell, and H. Kuipers. 2008. Adapting landscapes to climate change: Examples of climateproof ecosystem networks and priority adaptation zones. *Journal of Applied Ecology* 45:1722–31.
- Western Governors' Association. 2008. Wildlife corridors initiative report. Accessed at www.westgov.org/wga/meetings/am2008/wildlife08.pdf.
- Williams, J. W., S. T. Jackson, and J. E. Kutzbacht. 2007. Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences of the United States of America 104:5738–42.
- Williams, P., L. Hannah, S. Andelman, G. Midgley, M. Araujo, G. Hughes, L. Manne, E. Martinez-Meyer, and R. Pearson. 2005. Planning for climate change: Identifying minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology* 19:1063–74.
- Willis, S. G., J. K. Hill, C. D. Thomas, D. B. Roy, R. Fox, D. S. Blakeley, and B. Huntley. 2009. Assisted colonization in a changing climate: A test-study using two U.K. butterflies. *Conservation Letters* 2:46–52.