Diversity

Ecological Connectivity for a Changing Climate

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A frequently proposed strategy to reduce the negative effects of climate change on biological diversity is to increase ecological connectivity (Heller & Zavaleta 2009)—the flow of organisms and ecological processes across landscapes (Taylor et al. 1993). Traditionally, conservation professionals have sought to maintain or restore connectivity to ensure gene flow among isolated populations and promote recolonization of vacant patches (Hanski 1998). Given the rapid emergence of connectivity enhancement as a climate-change adaptation strategy, we considered whether connectivity should be emphasized in conservation strategies as global or regional temperatures increase and what principles for connectivity enhancement could be applied to maximize the usefulness of the strategy.

The best historical analogue for the ongoing rise in global temperatures occurred 55 million years ago at the Paleocene and Eocene boundary, when the average global temperature rose 5–6 °C in 10,000–20,000 years (Wing et al. 2005). At that time, species' ranges shifted and subtropical cypress swamps, complete with alligators, existed on Ellesmere Island in the Arctic (Estes & Hutchison 1980). A similar rise in temperature has been projected within the next 100–200 years (IPCC 2007), two orders of magnitude faster than previous warming events. Movements of some species, however, are now restricted by human-caused fragmentation and other barriers.

The primary rationale for increasing connectivity is that if the effects of land-cover fragmentation can be mitigated, this should enhance the ability of species to move into new regions as climate changes (Fig. 1), thereby decreasing the probability of extirpation or extinction. Here, *increasing connectivity* refers to management actions that facilitate dispersal of species among natural areas, for example, through the establishment of landscape corridors or stepping-stone reserves or through actions that increase matrix permeability. Because funds are limited, conservation professionals need to know whether increasing connectivity will be more effective than other management strategies in facilitating range shifts and which types of actions will benefit the greatest number of species.

Connectivity enhancement's greatest strength as an adaptation strategy is that it is spatially explicit and can be extensive, which may facilitate dispersal by many species simultaneously. The pace and pattern of range shifts caused by climate change are expected to vary from species to species (Davis & Shaw 2001), and the ability to model these distinct responses accurately and to prioritize conservation actions for particular species is limited. Although species use corridors at different rates and to differing extents, the majority of mobile species respond positively to corridors (Gilbert-Norton et al. 2010; Haddad et al. 2010). Thus, increasing connectivity may increase the probability of persistence for many organisms as climate changes (Fig. 1).

Anticipated shifts in species' ranges in response to climate change have turned old notions in conservation biology on their heads. Individuals reintroduced in landscape restoration projects are typically drawn from geographically proximate populations, but some foresters are now planting seeds harvested from distant, warmer regions with the goal of establishing populations of trees that will thrive under future climatic conditions (Marris 2009). And although conservation professionals typically avoid moving species beyond their native ranges, some are now calling for assisted migration of dispersal-limited species (Hoegh-Guldberg et al. 2008).

Increasing connectivity can in many cases meet the same objectives as assisted migration, yet we believe it has lower probability of unintended consequences. For example, deliberately introducing individuals from warmer regions with the aim of accelerating genetic adaptation to climate change risks reducing local adaptation (Storfer 1999). In contrast, increasing connectivity along

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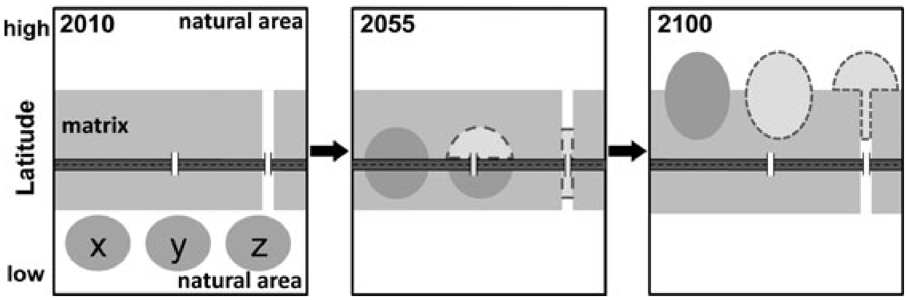

Figure 1. The effect of connectivity on species' range shifts as temperatures increase by 2100 (x, generalist species with high mobility and flexible resource requirements; y, species that can move through a matrix of land uses that do not constitute the species' primary habitat, but cannot cross hard barriers, such as highways, in the absence of corridors; z, species that can move between natural areas only through corridors; green areas, species ranges; gray areas, matrix lands; white areas: natural areas and corridors).

climatic gradients may facilitate the spread of genotypes that can tolerate warmer temperatures (Davis & Shaw 2001). And whereas long-distance assisted migration may introduce species that may become invasive (Ricciardi & Simberloff 2009), no corridor created for restoration or conservation is known to have promoted the spread of invasive species (Haddad et al. 2010).

We do not wish to dichotomize assisted migration and efforts to increase connectivity. Assisted migration and other intensive practices can be useful tools when integrated into comprehensive conservation plans. But we believe many climate-related conservation strategies will be more effective if they are implemented in the context of increasing connectivity. For example, planting trees short distances poleward beyond the edges of their current ranges could increase the probability of range shifts in species that depend on the habitat that those tree species provide (Ellison et al. 2005). By extending the ranges of such habitat-forming species to nearby locations, where they may be most likely to persist, rather than introducing them to distant locations, where they may be less likely to become established or persist, the probability of non-native species invasions associated with assisted migration may be reduced.

Some argue that efforts to increase connectivity should be made only after attempting to increase the size, quality, and number of protected areas. Hodgson et al. (2009) suggest that the effectiveness of connectivity enhancement for species persistence in a changing climate is less certain than the effectiveness of increasing the size of protected areas. Yet the distances many species are expected to move are too great to be accommodated by simply expanding reserve boundaries. Temperature isoclines are expected to shift more than 1 km/year in many systems (Loarie et al. 2009). In the 1900s, when temperatures increased by less than one-third of increases projected by 2100 (IPCC 2007), the ranges of diverse taxa advanced poleward by an average of 61 km (Parmesan & Yohe 2003). This distance is an order of magnitude larger than the average north–south extent of protected areas in North America (Fig. 2). Enlarging protected areas to the sizes necessary to accommodate these range shifts within their boundaries is unrealistic, as are assumptions that conditions within existing protected areas will

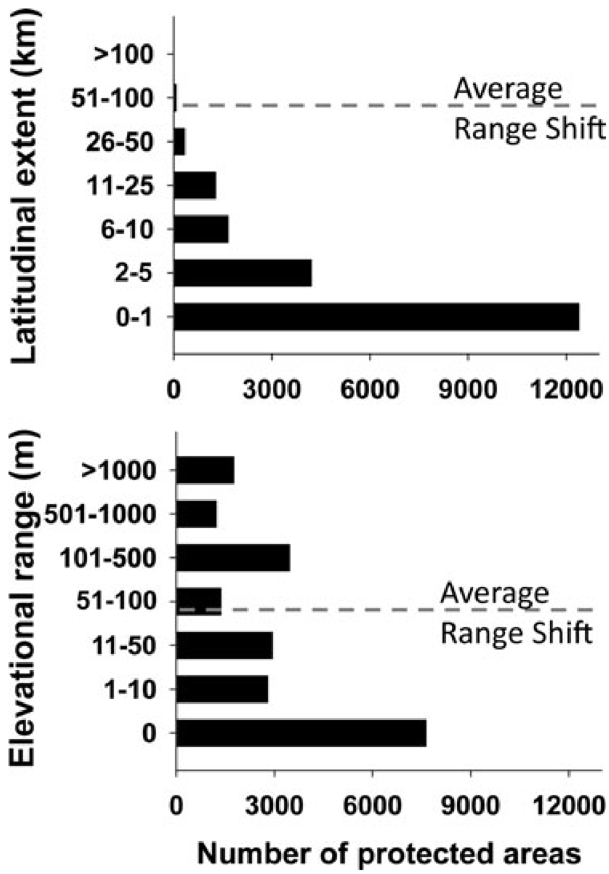

Figure 2. The average latitudinal extent and elevational range of protected areas within the continental United States (CBI 2007, GAP status < 3). The average shift (line) in species' range of 61 km/100 years northward and 61 m/100 years higher in elevation is derived from a meta-analysis of 1700 species (Parmesan & Yohe 2003).

remain suitable for resident species as climate changes. We believe future land acquisitions for the protection of species' habitats will be most effective if they increase connectivity among isolated protected areas along climatic gradients (Hunter et al. 1988).

Some also argue that actions to protect habitat should be directed toward areas with high degrees of environmental heterogeneity before they are directed toward increasing connectivity (Hodgson et al. 2009). Species can track a 3 °C increase in temperature by moving upward in elevation <500 m. Tracking a 3 °C rise along a latitudinal gradient, by comparison, would require poleward movement of almost 400 km. Mountainous terrain already comprises a large fraction of protected areas (Fig. 1). Yet the elevation of more than half of the world's terrain (excluding Antarctica) is <300 m, and even in mountainous regions the area of high-elevation land is limited (Harrison et al. 1983). The short-term persistence that a species may gain by shifting its range upward in elevation may isolate it over the long term if the climate zone simultaneously is decreasing in size, and the species may disappear entirely at the mountaintop (Peters & Darling 1985). Furthermore, values of other environmental variables, such as soil moisture and solar radiation, may be correlated with elevation but may not shift as climate changes. Changes in these other values could impose additional limitations on the quantity or quality of habitat at higher elevations (Meentemeyer et al. 2001).

To restore ecological connectivity at extents required for climate change, policies will be needed that encourage private landowners to reduce barriers to species movement on their lands (Da Fonseca et al. 2005), which would increase connectivity among protected areas. One such mechanism is financial incentives offered by governments and world financial institutions (IUCN and Conservation Measures Partnership 2006). Such incentives are not unprecedented. For instance, the U.S. Farm Bill and similar initiatives in Europe allocate billions of dollars per year toward incentives for agricultural practices that are consistent with conservation objectives (Donald & Evans 2006). Furthermore, some community-based efforts aimed at promoting connectivity are underway (Bennett 2004). For example, the Yellowstone to Yukon Conservation Initiative in the United States and Canada works with stakeholders to reconnect natural areas across a 3200-km, north–south oriented corridor in the Rocky Mountains.

Not all species will be conserved as climate changes simply because connectivity is increased. But spatially extensive efforts to enhance connectivity along major environmental gradients and rigorous monitoring of species' responses to inform future management actions will provide a stronger foundation for biological conservation as temperatures increase.

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