

---

# *Macroecology and the Theory of Island Biogeography: Abundant Utility for Applications in Restoration Ecology*

Andrew J. Dennhardt, Margaret E. K. Evans, Andrea Dechner,  
Lindsay E. F. Hunt, and Brian A. Maurer

## **Theory and Application**

- Ecological systems are dynamic, which poses a number of challenges to restoration efforts because ecosystems can change at multiple spatiotemporal scales.
- With respect to practical application, an ecological restoration project must take into account issues regarding the size, macrogeographic composition, and connectedness of the system being restored.
- When restoring biota to locations in degraded landscapes, the ecosystem may depend on both the quality and quantity of colonists it receives from beyond its borders.
- Through explicit assessment of species' assemblages on broad scales, macroecology promotes insight into the structure of biodiversity and influences the success or failure of restoration efforts.

Restoration ecologists are tasked with the challenge of returning an ecological system to a configuration that approximates its natural state (Hobbs and Norton 1996, 2001). Restoring any altered ecosystem comprises a sizeable challenge in that it is critical to determine the appropriate target for restoration (chap. 1), especially prior to disturbances such as novel anthropogenic impacts as well as the relevant scales thereof. Determining the target for restoration involves four main considerations: (1) the “natural” state of the system might include pre-European human influences (e.g., widespread colonialism); (2) change is normal in ecological systems (i.e., systems exhibit a historical range of variation in disturbance regimes and species composition); (3) some system changes are completely irreversible (e.g., legacy effects), or nearly so (e.g., ecological tipping points); and (4) stochasticity plays a crucial role in shaping ecosystem state (Jackson and Hobbs

2009). Moreover, some historically important steady states may not be attainable because of legacy effects such as the emergence of novel configurations and the spread of invasive species (e.g., establishing new biotic interactions and ecosystems; Hobbs et al. 2014), prevalence of historical contingencies (e.g., immigration of despotic breeders to isolated populations; Hedrick et al. 2014), or altered boundary constraints (e.g., climatic thresholds such as critical thermal maxima; Lee and Rinne 1980). Nevertheless, historical knowledge of ecosystems may still play a critical role in the success of future restoration efforts in the face of modern-day ecological novelties (Higgs et al. 2014).

Ecosystems are dynamic and constantly in flux, which poses a number of difficulties to restoration efforts because ecosystems can change at a variety of spatio-temporal scales (Jackson and Hobbs 2009; Jackson 2012). Multiscale ecosystem dynamics (chap. 2) make it challenging to define the natural conditions that existed prior to novel disturbance of the system. Furthermore, various biotic processes within ecological systems may change at different rates in space and time. For instance, some population-level processes (e.g., immigration) operate at very different scales than processes associated with the geophysical template of the ecosystem (Heffernan et al. 2014). At the root of the aforementioned difficulties is the realization that multiple biotic components (e.g., species with respect to composition) and abiotic processes (e.g., fire, with respect to disturbance) of the original ecosystem may be significantly altered or even entirely absent at present, and thus unavailable to the restored system. Counter to this is the notion that some abiotic and biotic processes may, in fact, be restored to the degraded system; however, to what degree can such processes be restored? It is likely that some impaired processes may never be fully restored. As a consequence of imperfect restoration, the resultant configuration and functional organization of “restored” systems is often attenuated and inadequate to sustain basic ecosystem functions and biodiversity over time (Hooper et al. 2012).

Another difficulty in defining natural system states is that many ecological communities (e.g., tallgrass prairie in central North America) likely occupied larger spatial extents than are presently available to the system designated for restoration. This implies that the current abiotic and biotic context within which the restored system must function may be very different from that of the historic context—which largely depended on ecosystem size and other relevant scales. Although there are many challenges to ecological restoration, the approaches to meet those challenges are also abundant. However, this only begs the question: are the scales and perspectives employed in restoration ecology adequate to meet the challenges of system restoration within complex, evolving contexts?

To answer this question, we begin by considering how ecosystem size affects ecological processes—considerations informed by advancements in ecological

theory. Building upon reflections on system size and intrinsic processes, we then discuss the importance of scale in restoring ecological systems and ultimately propose a macroscale perspective for restoration efforts. We then outline four areas of rapid development in macroecology that offer important tools and insights to restoration ecologists: species distribution models, species-area relationships, meta-population models, and neutral theory. Finally, we conclude this chapter with a discussion of its central themes—considerations of which may lead to improved ecological restoration efforts in the future.

### **System Size, Ecological Processes, and Theoretical Foundations**

Biological systems of all kinds vary functionally with size (Brown and West 2000). It is fairly straightforward to understand the consequences of size variation when examining the properties of individual organisms or groups thereof. As biotic systems grow in size, physiological processes often change in a nonlinear fashion as a consequence of the fractal nature of organismal structure (West et al. 1999). These changes can have a number of profound implications for the structure of communities and ecosystems (Enquist et al. 1999a, b). For example, although much is known about organismal scaling, less is known about the way that populations, communities, and ecosystem functions change with system size (Enquist et al. 2003). The first model to address this problem was the equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967). In subsequent decades, the field of macroecology emerged as a paradigm for evaluating how spatial and temporal processes on macroscales affect the maintenance of species diversity and organization (Brown and Maurer 1987, 1989; Brown 1995; Gaston and Blackburn 2000).

Macroecology began as an attempt to explain patterns in geographical distribution, abundance, and body size among species inhabiting continents (Brown and Maurer 1987, 1989). However, it became evident that mechanistic explanations for such patterns required an expansion of perspective from focus on local ecological processes at smaller scales (e.g., individuals, populations, and ecosystems) to larger continental-scale processes (e.g., species' range distributions; Brown 1995; Maurer 2012; Gaston and Blackburn 2000). These insights were reinforced by advances in other fields, including studies of species diversity (Rosenzweig 1995), community ecology (Ricklefs and Schluter 1993), biogeochemistry (Schlesinger 1997), global ecology (Kareiva et al. 1993), and biogeography (Brown and Lomolino 1998; Hubbell 2001). Essentially, ecologists found that it was necessary to expand the spatiotemporal scales at which they viewed ecological systems in order to understand what processes were important in determining patterns in distribution, abundance, ecosystem function, and species diversity. Today, macroecology

continues to enhance the present understanding of biodiversity conservation and management as well as ecological restoration, as we explore below.

By examining the properties of continental-scale species assemblages, macroecology provides the empirical basis for developing insights into the structure of biodiversity and how that organization influences the success or failure of ecological restoration efforts. Because of its focus on large-scale processes, macroecology explicitly assumes that the spatiotemporal scales of ecological systems extend far beyond political, geographical, and functional boundaries within which these systems are often managed. In this chapter, we examine the implications of a macroscale perspective for biodiversity conservation and management based on tools for ecological restoration.

Macroecology provides a benchmark for understanding the context within which ecological restoration efforts must operate as well as the limitations that are imposed by restricting the extent of restoration efforts because of mechanisms operating across scales. For example, macroecological systems (i.e., called *macrosystems*) consist of complexly interacting biological, geophysical, and sociocultural mechanisms that exhibit variation on spatiotemporal scales relevant to regions and continents such that system-wide restoration efforts now require much broader considerations than ever before (Heffernan et al. 2014; Soranno et al. 2014). Recent conceptual advances of direct relevance to ecological restoration include cross-scale interactions (i.e., how processes at one scale interact with processes at another scale; Soranno et al. 2014) and cross-scale emergence (i.e., how components at local scales interact and accumulate across scales; Peters et al. 2007). Although the importance of scale across general ecological studies is duly noted historically, one of the major questions currently confronting macroecology is the functional extent(s) to which various macroscale patterns exert controls on species' distributions (see also chap. 4 on spatial context). This knowledge gap is a central consideration in restoration ecology, and cumulative results from recent work in macroecology may shed light on how macrogeographic characteristics shape species' distributions.

## Focal Areas of Current Research in Macroecology

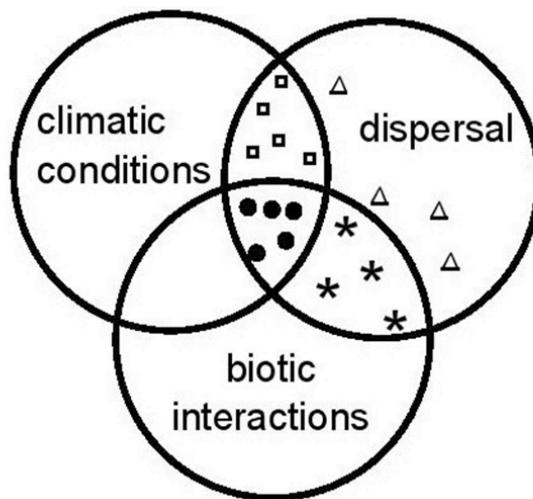
We now outline four areas of active research in macroecology that may offer valuable insights to ecological restoration efforts.

### *Species Distribution Models: Macrogeographic Controls and Realized Distributions*

Macroecology integrates macrogeographic patterns and processes into explanations of local and continental dynamics that control species' distributions (Kerr

et al. 2007; Mokany et al. 2012). For restoration ecology, there are numerous distribution-shaping processes that warrant greater consideration in the development and improvement of new and ongoing restoration efforts. First, understanding how conditions and resources (e.g., the multidimensional niche; Hutchinson 1957, 1965) shape species' distributions is crucial to the success of ecological restoration projects, for they represent boundary constraints for species—constraints mediated via macroevolutionary adaptations (Parnell and Streebman 2010). Examples of distributional constraints include species-specific climatic thresholds (e.g., critical temperatures; Lee and Rinne 1980), changing landscape pattern (e.g., patch/matrix composition and configuration; Koh and Ghazoul 2010; Kennedy et al. 2011), and density-mediated processes (e.g., availability and quality of breeding habitat as well as intra- and interspecific competition for space, mates, and resources). Here, we describe these distribution-shaping factors both in theory and in practice for modeling geographic distributions.

Hutchinson's concept of the niche as an "*n*-dimensional hypervolume" of conditions and resources rests at the foundation of niche-distribution theory (chap. 3), and the concept has shaped how ecologists have viewed species' distributions for decades (Hutchinson 1957, 1965; Blonder et al. 2014; Swanson et al. 2015). In terms of organismal distribution, the *fundamental niche* comprises the complete range of resources and environmental conditions a species can use and occupy. Recent decades have witnessed an explosion of efforts aimed at modeling species' distributions with what are termed *bioclimatic envelope models*, or species distribution models, wherein species' occurrence data are predicted solely as a function of climatic variables (Hampe 2004; Araújo and Peterson 2012; chap. 17). While there is no reason, in theory, that other factors could not be included as covariates (e.g., density of competitors or mutualists, time since disturbance, land use classes, etc.), in practice, climate data are the most readily available sources of information for prediction. This contributes to the impression that bioclimatic envelope models estimate climatic boundary constraints for species' ranges on geographic scales. However, models fit to occurrence data are likely to confound climatic boundary constraints with other distribution-limiting factors (e.g., interspecific competition, dispersal limitation, etc.). In fact, to the degree that species distribution models are fit tightly to occurrence data, they model the *realized niche* and not the fundamental niche, where the former is the subset of geographic space a species is actually observed to occupy (i.e., in the presence of competitors, predators, mutualists, facilitators, etc.; fig. 16-1). This has raised concern that such approaches (1) simply model the environmental conditions associated with the presence or abundance of a particular species (Kearney 2006; Morin and Lechowicz 2008); (2) fail to provide any mechanistic understanding of what limits species' ranges (e.g., dispersal constraints; Colwell and Rangel 2009); and (3) may not produce reliable forecasts of how species' distributions might change under future climates.



**Figure 16-1.** Species' niches and geographical distributions are shaped by many factors, of which, three important categories are illustrated here: climatic conditions, biotic interactions, and dispersal. The *upper left* circle indicates the geographical area in which climatic conditions support an intrinsic population growth rate at or above population replacement level. The *bottom* circle designates the geographical area in which the species can persist in the presence of interfering species (e.g., competitors or predators) or beneficial species (e.g., mutualists or facilitators). The *top right* circle signifies the geographical area within the species' capacity to disperse (i.e., over a specified time frame). The open triangles represent sink populations wherein both the climatic and biotic components of the environment are (collectively) insufficient for the population to replace itself, on average. The asterisks and open squares denote sink populations in which the climatic and biotic components of the environment, respectively, are (separately) insufficient for the population to replace itself, on average. Finally, the filled circles specify source populations wherein the climatic and biotic components are sufficient for the population to replace itself on average. This diagram is modeled after the conceptual foundations laid by Soberón (2007).

Factors other than climate that limit species' presence at a given site demand additional attention in restoration efforts. This includes biotic interactions, from competition to mutualism to facilitation; from predation to parasitism to disease, and more; as well as the diversity of spatiotemporal scales at which such interactions operate—from fine to broad. Specifically, intra- and interspecific levels of competition may often be important for explaining species composition and configuration at both localized and geographic scales (e.g., *sensu* emergent or interactive ecological processes that operate across scales in a macrosystem; Hefernan et al. 2014). Species' realized geographic distributions are the result of all of the above processes acting at once, including abiotic conditions, biotic interactions, and landscape-scale ecological processes such as dispersal, succession, disturbance, irruptions of competitors, and outbreaks of disease (fig. 16-1; Soberón 2007).

Given these considerations, the frontier of distribution-modeling research aims to better represent these processes in models of species' distributions. One avenue for doing so is the integration of macrogeographic (occurrence) data into process-based or mechanistic models of species' distributions. Examples of process-based or mechanistic distribution models include those based on phenology (Chuine and Beaubien 2001; Morin et al. 2008), physiology (Kearney and Porter 2009), and demography (Vanderwel et al. 2013; Lynch et al. 2014; Merow et al. 2014). A second avenue is to model distributions in terms of landscape-scale processes using metapopulation models, stochastic patch-occupancy models, integrated population models, or other formulations that treat dispersal explicitly (Pagel and Schurr 2012; García-Valdés et al. 2013; Chandler and Clark 2014; Newman et al. 2014; Yackulic et al. 2015).

Another example of this landscape-scale approach is the use of a spatially explicit dynamic macroecological model. Mokany et al. (2012) projected the future geographic distributions of the native plants in Tasmania (2,051 species) under climate and land use scenarios using dynamic, climate-driven models of  $\alpha$ - and  $\beta$ -diversity. Addition or loss of species in each 250 m grid cell was governed by a species' proximity to a focal cell in geographic and environmental space. Though the number of species modeled and spatial scope are impressive, the explanatory power (i.e.,  $R^2$ ) of the underlying diversity models was poor, and all species were assigned an identical dispersal capacity. The next step would be to account for nonclimatic drivers of species diversity (e.g., biotic interactions or disturbance)—that is, incorporate additional processes into these models along with their relevant data.

Hierarchical and inverse models are promising tools to integrate occurrence data into process-based range models, or add more processes into coarse landscape-scale models. These integrated models have the capacity to fuse data across natural hierarchies of both biological organization and spatiotemporal scales, reflecting the multitude of processes, from fine to broad scales, which shape species' distributions (Marion et al. 2012; Pagel and Schurr 2012; Schurr et al. 2012). Models that more explicitly treat the underlying processes that shape species' distributions should improve understanding of which ecological processes ensure local persistence of species in space and time—which, in turn, should help increase the success of restoration efforts.

### *Species-Area Relationships: Ecosystem Size and Species Diversity*

Ecologists have long sought to understand how ecosystem size determines the number of species inhabiting it (Rosenzweig 1995; chap. 4). MacArthur and Wilson (1963, 1967) first proposed that the number of species in an ecosystem of a given size reflects a dynamic balance between immigration of new species into

the system and local extinction of species already residing in the system. Although capable of predicting some aspects of a *species-area relationship* (SAR), the island biogeographic model proved too simplistic to completely explain how species richness varies with ecosystem size (Lomolino 2000a, b, c; Lomolino et al. 1995). Clearly, mechanisms underlying SARs on continents and island archipelagos must incorporate both dispersal and population viability, as MacArthur and Wilson (1967) envisioned. However, ecological processes that regulate population rates and determine population viability, as well as individual dispersal, depend on a large number of complexly interacting mechanisms. These components include, among other things, the ecological attributes of individual organisms, abundance and variety of resources, spatiotemporal patterns of those resources, and the context in which the ecosystem exists (McGill et al. 2007; Morlon et al. 2009).

A macroscale perspective on the processes that generate SARs provides a different viewpoint that, in some ways, simplifies the problem and may take the place of mechanistic-based explanations. The basic idea is that SARs are generated as a consequence of overlapping distributions of species in geographic space (Maurer 1999; McGill and Collins 2003). However, explaining why each species has a unique geographic distribution is difficult if the focus is solely on the particular mechanisms bounding each species in space and time. If the patterns in demography of species across their ranges are examined, the myriad components underlying SARs may be condensed into simpler models describing population-level mechanisms responsible for SARs (Hubbell 2001; Maurer 1999; McGill and Collins 2003). Consider the following simple model for distributions of species in space (Maurer 1999; McGill and Collins 2003). Suppose species are distributed across space in a unimodal manner (fig. 16-2). Each species has a different-sized geographic range, some with larger ranges and others with smaller ones. At any given point in space, this results in a skewed distribution of abundance. The SAR resulting from this pattern is similar to empirical patterns seen in many collections of species at the level of metacommunities (fig. 16-3). This approach can thus be expanded to examine SARs at different geographic scales, leading to the prediction that SAR exponents will vary with the scale at which they are measured (Rosenzweig 1995).

Of particular relevance to ecological restoration is the observation that the smallest islands often depart from a SAR for an archipelago (MacArthur and Wilson 1967; Brown and Lomolino 1998; Rybicki and Hanski 2013). Many such islands are too small to maintain viable populations of any species, and must therefore be maintained by immigration alone. This observation has important implications for ecological restoration projects. Island biogeographic theory predicts that small or isolated areas may require closer proximity to a source of colonists, or greater connectivity to such source pools if the objective of restoration is to

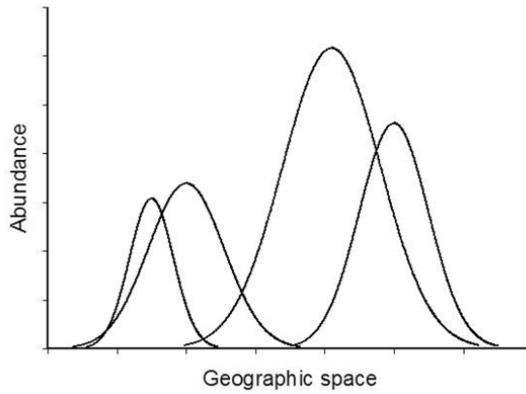


Figure 16-2. Graphical representation of the distribution of species in geographic space hypothesized to be responsible for species-area relationships.

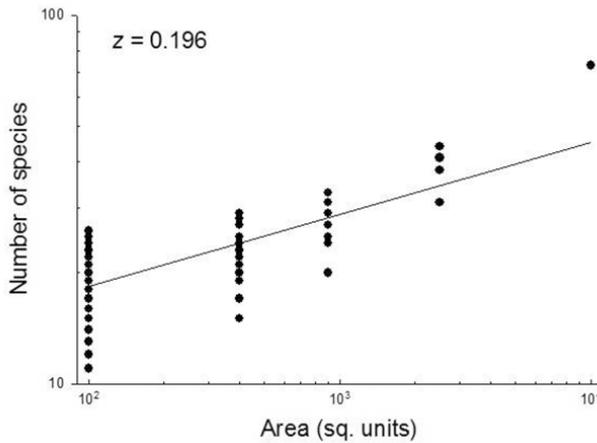


Figure 16-3. An example species-area relationship derived from a simulation of a two-dimensional version of the model represented in figure 16-2.

maintain the species diversity of a larger ecosystem. Many local populations persist as parts of larger metapopulations (Hanski 1998a, b, 1999); therefore, if the size of the area to be restored is too small, or too isolated from colonist source pools, then the likelihood of maintaining the original species richness and diversity of the restored ecosystem may be relatively small (Haddad et al. 2015; Jarzyna et al. 2015; but see also Sabatino et al. 2010).

Such consequences regarding species diversity have been debated for many years (Brown and Lomolino 1998; Whittaker 1998). What is less clear is whether there are additional properties of ecosystems that are affected by ecosystem size, patch composition, and configuration. Some unknown properties might involve

ecosystem stability, functional redundancy (or equivalence) between species, and spatiotemporally autocorrelated system states. One system property that is likely to be important is the unique characteristics of the landscape matrix in which habitat islands are embedded and the degree to which the matrix is inhospitable to dispersers (Debinski 2006; Nowicki et al. 2014). In some situations, altered portions of the matrix may even facilitate connections between habitat islands. For example, Barnes et al. (2014) demonstrated that restored matrix habitat mediated responses of dung beetle (i.e., family Scarabaeidae and subfamily Scarabaeinae) communities to edge effects in Nigerian tropical rainforests. Beetle community responses were so striking, in fact, that formerly extirpated species reestablished themselves in the restored matrix habitat, which led to improved capture rates of individual beetles in the matrix as well as more abundant populations in areas adjacent to it (Barnes et al. 2014). In similar cases where the landscape is manipulated and restored in some functional manner, the once hostile matrix may act as a networked conduit for colonists, helping to sustain crucial ecological processes at the level of populations and communities.

### *Metapopulation Models: The Matrix and Connectivity between Habitat Islands*

Metapopulation dynamics comprise a fundamental ecological process that operates across scales and is relevant to the long-term success of any restoration project (Hanski 1998a, b, 1999; see also chaps. 4 and 7). How metapopulations operate emphasizes the importance of external transport processes in maintaining a viable ecological system. A *metapopulation* is simply an aggregate of local populations connected via dispersal. The metapopulation can only persist if there is sufficient exchange of individuals among local populations to offset extinctions with colonization of new local populations—a type of ecological restoration that is organism-driven (Zhang et al. 2012). Although local populations may experience negative growth rates (e.g., “sink” populations), a metapopulation may persist indefinitely as a consequence of the external transport of colonists between subpopulations (chap. 7). Metapopulation dynamics are essential to buffering population size against demographic and environmental stochasticity as well as maintaining gene flow across populations.

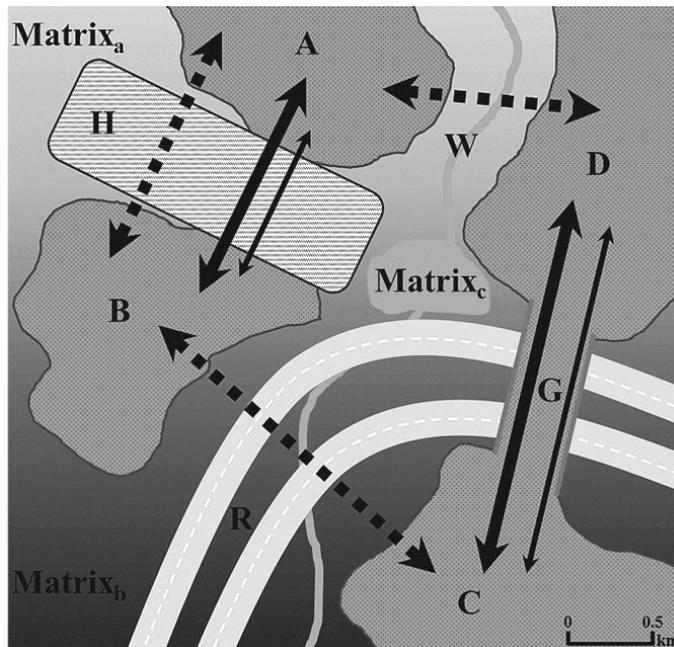
For ecological restoration, this means that the species diversity of a restored ecosystem may depend heavily on the quality and quantity of colonists the ecosystem receives from beyond its borders. In the face of degraded and fragmented landscapes, subpopulations are coerced into colonizing remaining areas of suitable habitat, which often have complex shapes, greater amounts of edge habitat, and reduced connectivity between disparate and isolated fragments. Such patch

fragments have been termed *habitat islands*—ecological units readily conducive to island biogeographic theory and its applications (Fernández-Juricic and Jokimäki 2001; Kennedy et al. 2011; Szlavecz et al. 2011). Moreover, the concept of habitat islands allows for direct integration with ideas about ecosystem size and species diversity as well as restoration efforts that help recover connectivity between species-specific habitat patches in a frequently inhospitable matrix on landscape-scales.

Facilitation of colonist dispersal through the landscape matrix is a relatively new idea. For decades, the landscape matrix was assumed in practice to be wholly inhospitable to species moving between disparate patches of habitat, and to some extent, the matrix does affect several species in this manner (Debinski 2006; Nowicki et al. 2014). For example, Nowicki et al. (2014) found that forest-dominated matrix was an inhospitable environment to focal grassland butterflies such that dispersal mortality was highest in forested matrix compared to other areas of open matrix, which suggested that forests impose strong selection against colonist dispersal in their study system. Though examples such as these exist, recent data suggest that for some systems the landscape matrix may, in fact, aid colonist dispersal to new population patches when the matrix is managed and improved for dispersers (Barnes et al. 2014; Kang et al. 2015). Such findings are clearly relevant to ecological restoration efforts in that managing landscape matrices to produce gradients of hospitability for various species may facilitate colonist dispersal by connecting isolated habitat islands (fig. 16-4; Blaum and Wichmann 2007; Szlavecz et al. 2011; Kang et al. 2015). These conceptual advancements may thus allow for improved mitigation of the effects of fragmentation by ensuring demographic and genetic exchange between separated subpopulations via landscape connectivity (Fernández-Juricic and Jokimäki 2001; Blaum and Wichmann 2007; Storfer et al. 2007; Hedrick et al. 2014; Wang et al. 2014) as well as in the context of connected stream networks (Dunham et al. 1997; Neville et al. 2006).

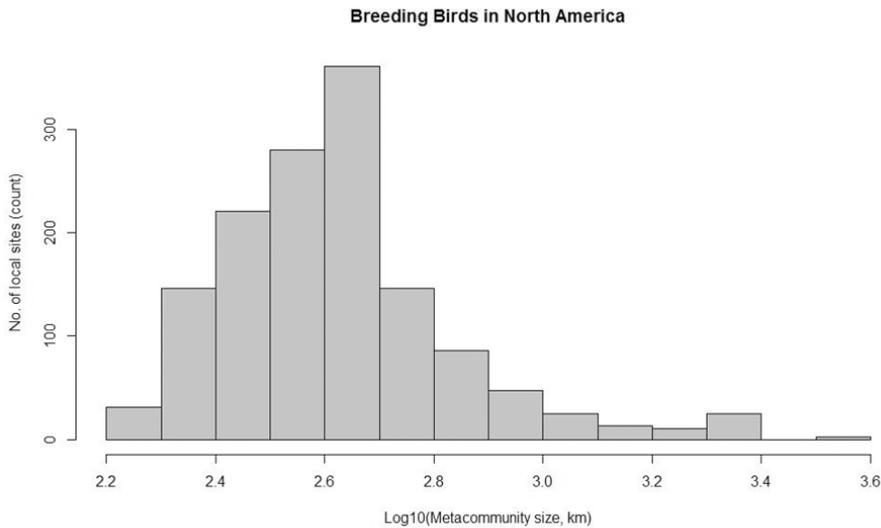
Macroecology contributes to this conceptual understanding by promoting management of population connectivity across the landscape matrix. Findings from fragmentation experiments worldwide indicate that landscapes deficient in connectivity between habitat islands lead to more broad and accelerated extinctions on localized scales over time and may exacerbate ecosystem changes (Hooper et al. 2012) on broad scales via biodiversity loss in the face of increased landscape fragmentation (Haddad et al. 2015; Jarzyna et al. 2015). Properties of metacommunities (e.g., the size, shape, composition, configuration, and connectivity between like communities) are also of great interest to restoration projects that intend to alter characteristics of the matrix to improve landscape connectivity and dispersal conditions (Kang et al. 2015).

Consider the following example, which highlights the importance of avian



**Figure 16-4.** Schematic of a hypothetical landscape where habitat islands (A–D; i.e., supporting disparate local populations) are separated by a gradient of matrix. This gradient represents changing matrix habitat that is either (a) conducive, (b) semiconductive (e.g., an agricultural field), or (c) unconductive (e.g., a lake) to dispersal between patches for two hypothetical organisms, a mammal (i.e., high vagility; thick black arrows) and an insect (i.e., low vagility; thin black arrows). Dispersal events are assumed low risk (e.g., to mortality (solid lines), high risk (dashed lines), or impossible (e.g., for the insect between B and C; no lines) between habitat islands for each organism across the matrix. Obstacles to dispersal include an open agricultural hayfield (H), a fast-moving waterway (W), and a highly trafficked roadway (R); while one corridor is a green-way (G) bridge constructed for wildlife. In all cases, local population persistence across the landscape is mediated by immigration and colonization, influenced by the dispersal limitations of the organism and connectedness of patches as well as subsets of a connected and permeable matrix.

metacommunity properties on a broad spatial scale. Maurer et al. (2013) developed methods for describing spatial properties of metacommunities based on avian species' sampled during 1996–2000 from the North American Breeding Bird Survey (Pardieck et al. 2014). Maurer et al. (2013) used information on species' abundances, local environmental variation, and avian phylogenetic relationships to estimate the extent of metacommunities for breeding bird assemblages across 1,393 survey routes (fig. 16-5). Metacommunity extent (i.e., distance, in km) was estimated as a function of ecological similarity between survey sites. By plotting the similarity among sites as a function of the distance between them, Maurer et

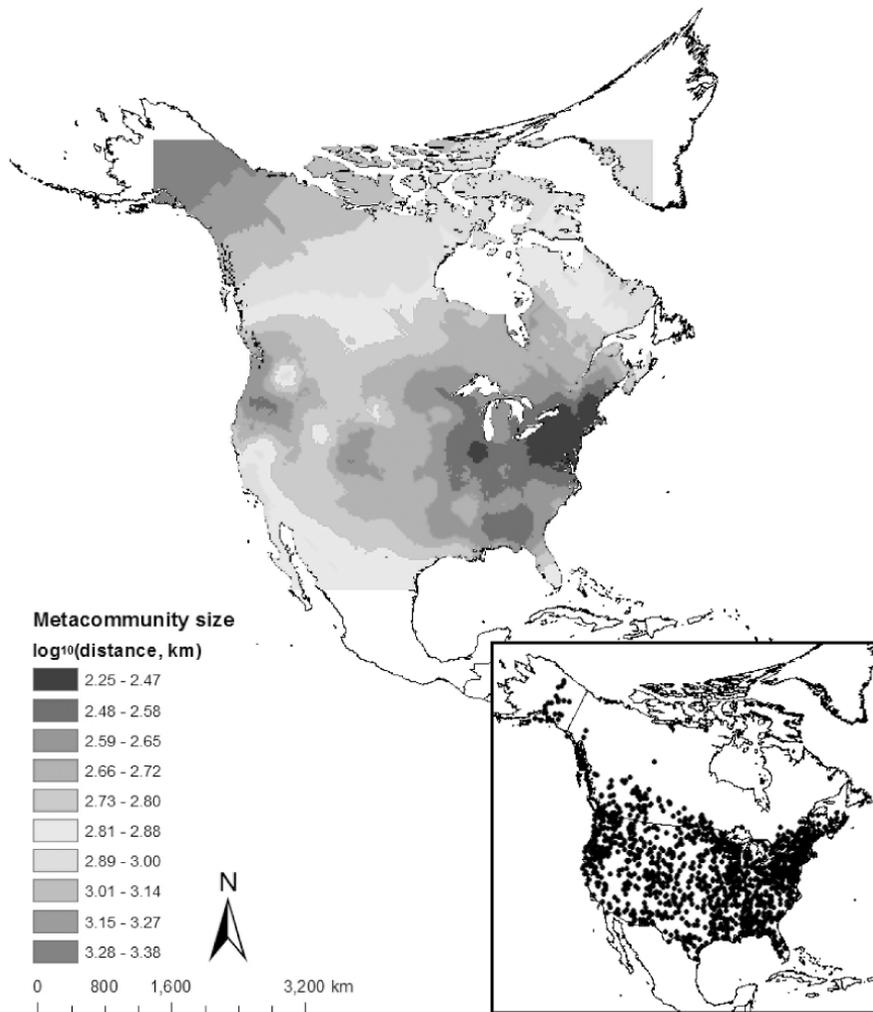


**Figure 16-5.** Distribution of metacommunity size (i.e., distance, units of  $\log_{10}$  km) for 1,393 avian assemblages sampled by the North American Breeding Bird Survey (Maurer et al. 2013).

al. (2013) were able to estimate a maximum distance beyond which the similarity decreased as more sites were added to the pool of metacommunity-eligible sites. Interpreting this maximum distance as a measure of metacommunity extent thus facilitates understanding of spatial patterns of metacommunity size.

Applying this method to data on North American terrestrial birds during the breeding season, the size of metacommunities (in terms of geographic distance) reveals that breeding bird assemblages are diverse in the spatial extent from which local communities draw colonists from other communities. Interestingly, patterns of metacommunity size reflect the underlying structure of important ecoregions in North America. For instance, metacommunity sizes tend to be much smaller in the eastern temperate forests than in the northwestern forested mountains and southwestern deserts (fig. 16-6). In contrast, metacommunity size tends to be larger in the Great Plains and northern boreal forests.

These patterns imply that the region from which a restoration project might draw colonists will likely be smaller in the eastern temperate forests than in the Great Plains, for example. Metacommunity extents illustrate the importance of macroecological context in restoring ecological systems. Analyses such as these demonstrate that no ecological community is entirely isolated, and sites vary in the degree to which they are able to draw upon colonists. This suggests that spatial connectivity *among* habitat patches must play an important role in local community persistence over time. Furthermore, connectivity between ecologically simi-



**Figure 16-6.** Geographic variation in metacommunity size (i.e., distance) for avian assemblages across 1,393 Breeding Bird Survey routes in North America—produced via an ordinary kriged interpolation. Metacommunity distances are measured as a function of site similarity based on species relative abundance, local environmental variation, and phylogenetic relationships between species (Maurer et al. 2013). The inset displays the spatial distribution of routes ( $n = 1,393$ ) sampled during 1996–2000. The geographic patterns in metacommunity size suggest the immediate significance of spatial context in system restoration efforts—settings which likely depend on ecoregion type, connectivity between ecological communities, and relative anthropogenic influences, among other potential factors.

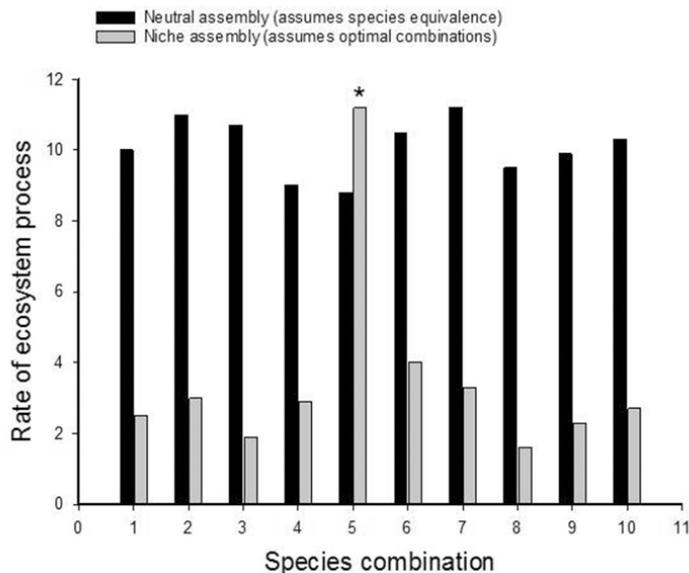
lar communities likely relies upon the unique ecoregion to which a community belongs as well as influences from human populations and other disturbances.

### *Neutral Theory: Species Equivalence and the Maintenance of Biodiversity*

In attempting to understand the underlying causes for patterns such as SARs, the neutral theory of biodiversity (Hubbell 2001) posits a specific population mechanism responsible for macroscale diversity patterns is based on the assumption of functional equivalence among species. From the perspective of restoration ecology, neutral theory implies that a complete, functional ecosystem can be constituted from an arbitrary set of species from the pool of available organisms that could occupy a given site. Because one species is substitutable for another in this model, the relative abundances and identities of species in a community should have little impact on the final structure and function of the ecosystem (fig. 16-7). Contrast this with an ecosystem where species differences were important and where an “optimal” set of species best adapted to local conditions existed. In such a context, maximal ecosystem functioning would only exist for a few (or even just one) set of species best adapted for the local conditions. As such, restoration would require identification of the best set of species necessary to meet functional goals of the restoration endeavor.

To what degree are the assumptions of the neutral theory met in nature? The initial response to this question by many ecologists would be that differences among species are ecologically important. However, demonstrating that differences among species have a cumulative impact on the structure and function of ecosystems has not been straightforward (Loreau et al. 2001). Furthermore, successful ecological restoration may often depend on bringing together the right combination of species to generate and maintain a functional ecosystem. If this is generally true, then restoration projects can be viewed as experiments that can provide tests for the assumption of functional equivalence among species. If functional equivalence is true, then there may be a relatively large number of species combinations that might produce a persistent, functional ecosystem. If functional equivalence is false, then there would only be a few appropriate combinations of species that will produce an ecosystem that can persist and function appropriately over time (fig. 16-7). There are a number of ways that these hypotheses might be tested. In fact, a survey of restoration activities that were evaluated based on whether or not they led to an appropriately functioning ecosystem might provide a test of functional equivalence if it was found that species composition was an important factor in determining the success of the restoration attempt.

Adaptive management of restored ecosystems might also provide opportunities to design experiments to test the degree to which degraded habitats and eco-



**Figure 16-7.** Graphical representation of the differences between the neutral assembly and niche assembly hypotheses. The vertical axis is the rate of some ecosystem process of interest to restoration efforts. Suppose that there are ten different combinations of species that could occupy the local ecosystem. In this hypothetical system, the neutral theory would predict that all ten species combinations would generate roughly the same rate of the process because each species was composed of the same kind of ecologically equivalent individuals. Under the niche assembly hypothesis, there is a combination of species ( $x = 5$ , asterisked) that maximizes the rate of the ecosystem process. This combination contains the species that are best adapted to the local conditions in the ecosystem. As illustrated, it is apparent that restoration efforts for a particular system would necessitate different goals, given these two hypotheses of community assembly.

systems are restored (Millar et al. 2007; Theiling et al. 2015). Because of the importance of understanding how species composition of an ecosystem affects its structure and function, it is imperative that restoration projects be monitored carefully and thoroughly after they are completed (Heer et al. 2013; Theiling et al. 2015). Such monitoring will serve the dual purpose of establishing criteria to judge the degree to which restoration objectives are met via decision support tools (e.g., Optimal Restoration of Altered Habitats; Lethbridge et al. 2010) and provide data to test models of community assembly that make assumptions about the functional equivalence of species (chap. 9). In this way, ecological restoration can become not only a practical field that deals with the *what* of restoring ecosystems, but it can also provide a fertile field to test scientific theories that provide answers to *why* and *how* degraded ecosystems should be restored in order to maintain their

integrity in space and time. Macroscale concepts thus provide restoration ecology with a conceptual framework for long-term management on landscape scales with the goal of maintaining biodiversity and the functional integrity of restored ecosystems (Hooper et al. 2012).

### **Thematic Considerations for Applied Developments in Restoration Ecology**

A comprehensive discussion of how large and connected specific restored ecosystems must be in order to preserve target species and ecosystem functions is beyond the scope of this chapter. For the present purpose, we can say confidently, as a basic principle, that any restoration project needs to take into account practical issues regarding the size, macrogeographic composition, and connectedness of the ecosystem being restored (Aronson and Le Floch 1996; White and Walker 1997). Since ecosystem functions often require input from processes not physically contained within the boundary of the ecosystem, a fundamental principle of ecosystem restoration should be to ensure that the restored ecosystem resides within a comprehensive landscape context (Weinstein et al. 2014). Such a setting must be conducive to providing adequate flux of individual organisms, energy, and resources between populations inhabiting patch islands in order to maintain ecosystem viability over long-term temporal scales. To understand the importance of the aforementioned concepts to restoration ecology, we briefly consider management challenges that the planet faces today.

Although global societies foster a well-connected landscape for human populations, the same cannot be said for numerous floral and faunal populations. While landscape fragmentation is an important issue today, increasing trends in land use change that are detrimental to wildlife are likely to continue (Sala et al. 2000). Moreover, landscape changes in composition and configuration will likely produce harmful synergistic effects with future climate scenarios as species begin to track their climatic constraints. The emergence of species' range shifts poses a great challenge to biodiversity management and conservation (Morin and Lechowicz 2008; Chambert et al. 2015). However, analytical tools exist now that can help managers address multiscaled environmental drivers of range shifts. For example, once again, species distribution models may provide valuable capacity for anticipating conservation concerns such as forecasting species' range shifts (Pagel and Schurr 2012; Schurr et al. 2012).

One of the emerging challenges to restoration ecology is managing ecological systems in the face of nonstationary climate regimes (chap. 17). Such climatic shifts suggest that the targets for restoration are moving targets, including the composition and functionality of ecological communities (García-Valdés et al. 2013).

### Case Study Box 16-1

#### Hypothetical Restoration of Wild Populations Facing Demographic Consequences Mediated by Landscape Structure on Broad Spatiotemporal Scales

**Marys River watershed, Great Basin Desert, US:** The Marys River (41°33' N, 115°18' W) is a 500 km<sup>2</sup> watershed located in the Lahontan Basin of the Great Basin Desert, US, and the area supports federally threatened populations of the Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*). These trout are endemic to the region and often restricted to small isolated streams. This makes investigation of demographic consequences from landscape structure on their populations a model case for restoration considerations on broad scales. In this stream network system, Neville et al. (2006), hereafter *researchers*, assessed the genetic characteristics of trout populations with respect to attributes of the local landscape, research that we now summarize and discuss with respect to macroecological considerations for ecological restoration.

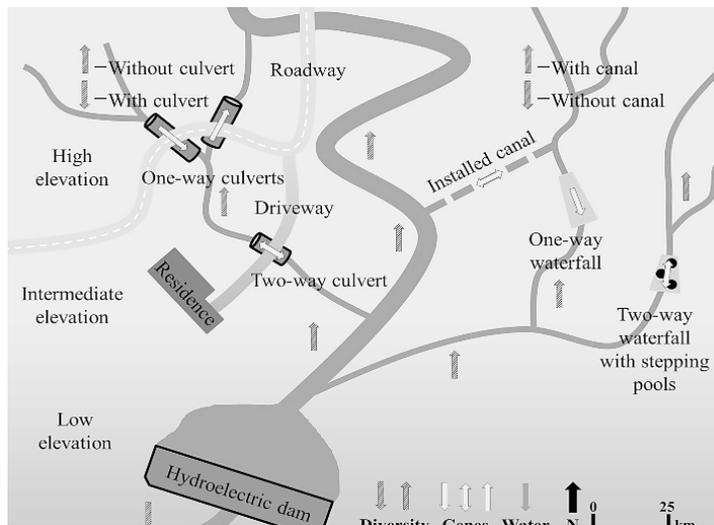
**Expectations informed by island biogeographic and metapopulation theory:** Given the long-standing recognition that landscape patterns have important influences on ecological processes that shape and constrain populations, researchers sought to investigate the influence of dispersal barriers on genetic population structure in this stream network.

**Results of the population-level assessment:** Trout populations facing low spatial connectivity exhibited sedentism and also occupied habitats of poor quality, which contributed to lower genetic diversity than subpopulations inhabiting connected, higher quality habitats. Concomitant increases in genetic differentiation were also associated with isolated populations in response to decreased gene flow across one-way dispersal barriers in contrast to more connected populations, which were able to move to and from the river main stem or were able to traverse more passable barriers throughout the stream network. Researchers found no evidence that genetic differences arose solely based on the type of dispersal barrier present (e.g., man-made dams or natural waterfall features); however, the response of trout to such barriers depended markedly on the habitat that isolated populations occupied. For example, one subpopulation inhabited broad, high quality habitats above a waterfall yet was also subject to asymmetrical gene flow across that same barrier. Despite deficiencies in gene flow, over time, these areas still supported larger and more stable populations than did areas with fine, poor quality habitats in the face of similar constraints with respect to gene flow. Finally, researchers found that spatial structure, rather than temporal structure, was more important for shaping population genetic diversity in the system.

**Research implications:** Spatial aspects such as habitat connectivity and quality, as well as concomitant genetic effects on dispersal behavior or individual fitness, may be important factors for limiting population productivity, recruitment, and persistence over time. Researchers concluded that population persistence concurrently depends on the life history strategy (i.e., sedentary versus migratory behavior), the connectedness of habitat patches (i.e., whether symmetric or asymmetric gene flow across barriers), and general habitat complexity (i.e., in both quantity and quality) in order to sustain the greater metapopulation of cutthroat trout.

**Considerations for ecological restoration and management objectives:** If we imagine that this region was of interest to restoration ecologists, then what solutions might we offer to managers of this region with respect to conservation of Lahontan cutthroat trout? Our discussion suggests that we should consider several criteria for restoration: (1) the size of the system (e.g., a 500 km<sup>2</sup> freshwater catchment); (2) the macrogeographic constraints

on the system (e.g., multiple subpopulations of migratory trout capable of moving >50 km annually and also constrained by the distribution of quality habitats); (3) the connectedness of the system (e.g., the variable flux of genes, energy, and resources throughout the stream network); and (4) the broader context of the system's landscape (e.g., the proximate influences of genes, energy, and resources beyond the stream network). Management solutions relevant to each of these considerations might include regular long-term assessments of individual trout (e.g., via genetic methods), macroscale enhancement of key habitat resources and movement corridors (e.g., via in-stream manipulations of habitat or via facilitation across dispersal barriers, whether by permanent removal or retrofitting thereof), and recurrent monitoring surveys beyond the stream network in order to improve conditions for the species' metapopulation to persist across the system (fig. 16-8).



**Figure 16-8.** Schematic of a hypothetical riverscape where water predominantly flows southward and fish populations are either connected or isolated across tributary waters that contain both natural (i.e., waterfalls) and man-made barriers (i.e., dams and culverts) to individual dispersal. If this area were unmanaged for fish, then we might imagine that movement barriers would remain in place and meet their intended purposes. However, these barriers might also produce various unintended consequences (e.g., changes in gene flow [white arrows] and genetic diversity [gray arrows]). For example, inhibited dispersal could lead to decreased genetic diversity in isolated fish populations, and thus produce increased probabilities of local extinction. Despite these conditions and their associated demographic consequences (e.g., hindered productivity, recruitment, and persistence), restoration efforts could provide solutions through management intervention (e.g., barrier removal, retrofitting, or facilitation measures, such as installing movement corridors) intended to promote spatial (genetic) connectivity throughout the watershed and ensure greater probability of metapopulation persistence for the target species over time.

**References:** MacArthur and Wilson 1967; Slatkin 1985; Dunham et al. 1997; Davies et al. 1999; Manel et al. 2003; Neville et al. 2006.

Distribution models or bioclimatic envelope models have been used extensively to project future species' distributions (Thuiller et al. 2005; Jetz et al. 2007; chap. 17), and these projections may offer key guidance to restoration ecologists in terms of anticipating appropriate targets of species composition and associated ecosystem function at a given location. For example, adaptive strategies aimed at managing forests in the face of climate change include mixed species plantings, neontative translocations (e.g., assisted migration), and enhancing genetic diversity in managed populations (Millar et al. 2007; Storer et al. 2007), which can be informed by forecasts of the distributions of species, subspecies, varieties, or haplotypes.

Management actions such as assisted migration and the use of future climate-adapted genotypes have thus far been discussed more in theory than attempted in practice (McLachlan et al. 2007; Vitt et al. 2010; Maschinski and Haskins 2012). Nonetheless, it seems likely that restoration ecology is poised to use macroecological distribution models in such ways. Reconstructions of species' past distributions, as well as past ecological communities, indicate consistently that organismal distributions can change dramatically over time and often lead to the realization that some local communities in the past have no analogues in the present (Jackson and Hobbs 2009). Furthermore, individualistic trajectories of species' past distributions (*sensu* Gleason 1926) suggest that species-level prediction, as opposed to community-level forecasting, is most appropriate for coordinated conservation and management. Pairing species distribution models and other conservation tools with innovative ideas, such as efficient theories (Marquet et al. 2014), may also provide unique insights into ecological patterns and processes on macroscales—insights useful to applied management and restoration efforts.

Moreover, species distribution models and similar tools may provide guidance for establishing new, and managing existing, set-aside areas for conservation (e.g., national reserves, parks, and local easements). What is certain from our review of current literature is that connectivity between habitat islands is an *essential* component for dispersing organisms, genetic flow, and persistent metapopulations (Cushman et al. 2011). Additionally, macroscale management of wild populations across landscapes is also important for the maintenance of such crucial ecosystem properties (i.e., populations that are connected, genetically diverse, and stable; McKinney et al. 2010; Hobbs et al. 2014). In addition, set-aside areas and reserves should incorporate management procedures that enhance landscape connectivity between habitat islands, especially those areas confronted with increased isolation as well as shifting rates of local population growth and genetic diversity (Rybicki and Hanski 2013; Wang et al. 2014). Such management practices will enable ecological restoration to advance beyond efforts at localized scales (e.g., individuals, populations, and ecosystems) to conservation of the properties of single ecosystems and their connections to other systems at broader scales, such as those of

continents, biomes, and the biosphere—coarse scales that structure and interact with ecological patterns and processes at finer scales (Cattarino et al. 2014).

## **Closing Remarks**

Ecological systems are dynamic and constantly in flux, and systems in need of restoration are certainly no exception to such fundamental characteristics. Restoration of degraded ecosystems thus requires special consideration of features such as the target system's former natural state, its alternative steady states, inherent legacy effects and ecological tipping points, and the role of stochasticity in shaping the target system's state. These requirements underscore the numerous difficulties facing ecological restoration efforts. Such complications include issues with (1) identifying ecosystem size and restoration scales; (2) analyzing macrogeographic controls and selecting tools to forecast or hindcast species' distributions based on those controls; and (3) applying mechanistic or process-based (e.g., metapopulation) tools versus species-area or neutral system relationships to inform restoration objectives. Despite these challenges, macroecological perspectives may provide guidance to restoration efforts moving forward, especially with respect to accounting for historic and current ecosystem factors, both abiotic and biotic, in space and time.

The macroscale perspective we have described strongly suggests that ecosystem restoration cannot be successfully carried out without thoughtful consideration of the spatiotemporal context within which the restored system will exist. Ecosystems are composed of numerous collections of species, each of which are shaped by unique macrogeographic controls (e.g., abiotic and biotic factors) on their distributions and abundance in space and time. Consequently, ecological restoration should not lose sight of these species-specific controls that partly assemble ecological systems. An ecosystem is not only defined by the species composition, edaphic conditions, and interaction networks that exist within its boundaries, but also by the ebbs and flows across its boundaries that connect its internal processes with broader external systems and their processes, for example, nutrient, energy, and hydrological (chaps. 12–14). Accordingly, restoration efforts must acknowledge the emergent novel dynamics of habitat islands for populations that exist in modified landscapes. This also necessitates focused recognition and management of landscape-scale factors, such as habitat matrices for increased hospitability, to connect and facilitate flows of colonists between distinct habitat islands and ecological communities—factors well-grounded in island biogeographic and metapopulation theory.

Through explicit incorporation of established theory to assess the properties of species assemblages and distributions on broad spatiotemporal scales, macro-

ecology provides an empirical basis that can generate insight into the structure of biodiversity and how that organization influences the success or failure of ecological restoration efforts. Because of its focus on regional- and continental-scale processes, macroecology readily identifies the importance of landscape connectivity between, as well as the relative isolation of, ecological communities, because ecosystems extend far beyond political, geographical, and functional boundaries — even though such systems are frequently managed at these scales. Therefore, a restoration project that fails to consider external transport processes (e.g., species dispersal across project boundaries) over managed landscapes may be unable to meet crucial project objectives, because the restored system may be governed (e.g., limited or enhanced) by flows across its borders such as from neighboring landscapes (chaps. 4, 7). One important way to maintain the integrity of a restored ecosystem is to replace external transport processes with intensive management activities that serve or enhance the same function, but such approaches represent a more or less permanent commitment that may not be logistically or fiscally viable.

Furthermore, data on the relationship between species composition and the success of restoration activities can be used to test the functional equivalence of species, an assumption that underlies neutral models of macroecological patterns. In particular, carefully planned restoration projects can be used as active experiments in adaptive management to test this (and other) important assumption(s) about the assembly, functionality, and persistence of disparate ecological communities and systems, especially on landscape-level scales. Restoration ecology must become increasingly able to anticipate and address species' range shifts, novel system configurations, and accelerated extinction rates in response to complex synergies amidst changing land use practices, expanding human populations, and future climate dynamics (chap. 17). In the face of these substantial interacting processes, macroecology thus provides a foundational framework to enhance endeavors in restoration ecology on vast spatiotemporal scales as well as aid the future of biodiversity conservation and management in a nonstationary and ever-challenged world.

## References

- Araújo, M. B., and A. T. Peterson. 2012. "Uses and Misuses of Bioclimatic Envelope Modeling." *Ecology* 93:1527–1539.
- Aronson, J., and E. Le Floch. 1996. "Vital Landscape Attributes: Missing Tools for Restoration Ecology." *Restoration Ecology* 4:377–387.
- Barnes, A. D., R. M. Emberson, H. M. Chapman, F.-T. Krell, and R. K. Didham. 2014. "Matrix Habitat Restoration Alters Dung Beetle Species Responses Across Tropical Forest Edges." *Biological Conservation* 170:28–37.

- Blaum, N., and M. C. Wichmann. 2007. "Short-Term Transformation of Matrix into Hospitable Habitat Facilitates Gene Flow and Mitigates Fragmentation." *Journal of Animal Ecology* 76:1116–1127.
- Blonder, B., C. Lamanna, C. Violle, and B. J. Enquist. 2014. "The  $n$ -Dimensional Hypervolume." *Global Ecology and Biogeography* 23:595–609.
- Brown, J. H. 1995. *Macroecology*. Chicago: University of Chicago Press.
- Brown, J. H., and M. V. Lomolino. 1998. *Biogeography*. Sunderland: Sinauer Associates.
- Brown, J. H., and B. A. Maurer. 1987. "Evolution of Species Assemblages: Effects of Energetic Constraints and Species Dynamics on the Diversification of the North American Avifauna." *American Naturalist* 130:1–17.
- Brown, J. H., and B. A. Maurer. 1989. "Macroecology: The Division of Food and Space Among Species on Continents." *Science* 243:1145–1150.
- Brown, J. H., and G. B. West. 2000. *Scaling in Biology*. New York: Oxford University Press.
- Cattarino, L., C. A. McAlpine, and J. R. Rhodes. 2014. "Land-Use Drivers of Forest Fragmentation Vary with Spatial Scale." *Global Ecology and Biogeography* 23:1215–1224.
- Chambert, T., W. L. Kendall, J. E. Hines, J. D. Nichols, P. Pedrini, J. H. Waddle, G. Tavecchia, et al. 2015. "Testing Hypotheses on Distribution Shifts and Changes in Phenology of Imperfectly Detectable Species." *Methods in Ecology and Evolution* 6: 638–647.
- Chandler, R. B., and J. D. Clark. 2014. "Spatially Explicit Integrated Population Models." *Methods in Ecology and Evolution* 5:1351–1360.
- Chuine, I., and E. G. Beaubien. 2001. "Phenology is a Major Determinant of Tree Species Range." *Ecology Letters* 4:500–510.
- Colwell, R. K., and T. F. Rangel. 2009. "Hutchinson's Duality: The Once and Future Niche." *Proceedings of the National Academy of Sciences, USA* 106:19651–19658.
- Cushman, S. A., T. N. Wasserman, and K. McGarigal. 2011. "Modeling Landscape Fire and Wildlife Habitat." In *The Landscape Ecology of Fire*, edited by D. McKenzie, C. Miller, and D. A. Falk, 223–245. Dordrecht: Springer-Verlag.
- Debinski, D. M. 2006. "Forest Fragmentation and Matrix Effects: The Matrix Does Matter." *Journal of Biogeography* 33:1791–1792.
- Dunham, J. B., G. L. Vinyard, and B. E. Rieman. 1997. "Habitat Fragmentation and Extinction Risk of Lahontan Cutthroat Trout." *North American Journal of Fisheries Management* 17:1126–1133.
- Enquist, B. J., J. H. Brown, and G. B. West. 1999a. "Plant Energetics and Population Density." *Nature* 398:573.
- Enquist, B. J., E. P. Economo, T. E. Huxman, A. P. Allen, D. D. Ignace, and J. F. Gillooly. 2003. "Scaling Metabolism from Organisms to Ecosystems." *Nature* 423:639–642.
- Enquist, B. J., G. B. West, E. L. Charnov, and J. H. Brown. 1999b. "Allometric Scaling of Production and Life-History Variation in Vascular Plants." *Nature* 401:907–911.
- Fernández-Juricic, E., and J. Jokimäki. 2001. "A Habitat Island Approach to Conserving Birds in Urban Landscapes: Case Studies from Southern and Northern Europe." *Biodiversity and Conservation* 10:2023–2043.
- García-Valdés, R., M. A. Zavala, M. B. Araújo, and D. W. Purves. 2013. "Chasing a Mov-

- ing Target: Projecting Climate Change-Induced Shifts in Non-Equilibrium Tree Species Distributions." *Journal of Ecology* 101:441–453.
- Gaston, K. J., and T. M. Blackburn. 2000. *Pattern and Process in Macroecology*. Malden: Oxford-Blackwell Science.
- Gleason, H. A. 1926. "The Individualistic Concept of the Plant Association." *Bulletin of the Torrey Botanical Club* 53:7–26.
- Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, et al. 2015. "Habitat Fragmentation and its Lasting Impacts on Earth's Ecosystems." *Science Advances* 1:e1500052.
- Hampe, A. 2004. "Bioclimate Envelope Models: What they Detect and What they Hide." *Global Ecology and Biogeography* 13:469–476.
- Hanski, I. 1998a. "Connecting the Parameters of Local Extinction and Metapopulation Dynamics." *Oikos* 83:390–396.
- Hanski, I. 1998b. "Metapopulation Dynamics." *Nature* 396:41–49.
- Hanski, I. 1999. "Habitat Connectivity, Habitat Continuity, and Metapopulations in Dynamic Landscapes." *Oikos* 87:209–219.
- Hedrick, P. W., R. O. Peterson, L. M. Vucetich, J. R. Adams, and J. A. Vucetich. 2014. "Genetic Rescue in Isle Royale Wolves: Genetic Analysis and the Collapse of the Population." *Conservation Genetics* 15:1111–1121.
- Heer, P., J. Pellet, A. Sierro, and R. Arlettaz. 2013. "Evidence-Based Assessment of Butterfly Habitat Restoration to Enhance Management Practices." *Biodiversity Conservation* 22:239–252.
- Heffernan, J. B., P. A. Soranno, M. J. Angilleta, Jr., L. B. Buckley, D. S. Gruner, T. H. Keitt, J. R. Kellner, et al. 2014. "Macrosystems Ecology: Understanding Ecological Patterns and Processes at Continental Scales." *Frontiers in Ecology and the Environment* 12:5–14.
- Higgs E., D. A. Falk, A. Guerrini, M. Hall, J. Harris, R. J. Hobbs, S. T. Jackson, et al. 2014. "The Changing Role of History in Restoration Ecology." *Frontiers in Ecology and the Environment* 12:499–506.
- Hobbs, R. J., E. Higgs, C. M. Hall, P. Bridgewater, F. S. Chapin III, E. C. Ellis, J. J. Ewel, et al. 2014. "Managing the Whole Landscape: Historical, Hybrid, and Novel Ecosystems." *Frontiers in Ecology and the Environment* 12:557–564.
- Hobbs, R. J., and D. A. Norton. 1996. "Towards a Conceptual Framework for Restoration Ecology." *Restoration Ecology* 4:93–110.
- Hobbs, R. J., and D. A. Norton. 2001. "Restoration Ecology: Repairing the Earth's Ecosystems in the New Millennium." *Restoration Ecology* 9:239–246.
- Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, et al. 2012. "A Global Synthesis Reveals Biodiversity Loss as a Major Driver of Ecosystem Change." *Nature* 486:105–108.
- Hubbell, S. P. 2001. "The Unified Neutral Theory of Biodiversity and Biogeography." *Monographs in Population Biology*. Volume 32. Princeton: Princeton University Press.
- Hutchinson, G. E. 1957. "Concluding Remarks." *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–427.

- Hutchinson, G. E. 1965. *The Ecological Theater and the Evolutionary Play*. New Haven: Yale University Press.
- Jackson, S. T. 2012. "Conservation and Resource Management in a Changing World: Extending Historical Range of Variation Beyond the Baseline." In *Historical Environmental Variation in Conservation and Natural Resource Management*, edited by J. A. Wiens, G. D. Hayward, H. D. Safford, and C. M. Giffen, 92–109. London: John Wiley and Sons, Inc.
- Jackson, S. T., and R. J. Hobbs. 2009. "Ecological Restoration in the Light of Ecological History." *Science* 325:567–568.
- Jarzyna, M. A., W. F. Porter, B. A. Maurer, B. Zuckerberg, and A. O. Finley. 2015. "Landscape Fragmentation Affects Responses of Avian Communities to Climate Change." *Global Change Biology* 21:2942–2953.
- Jetz, W., D. S. Wilcove, and A. P. Dobson. 2007. "Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds." *PLoS Biology* 5:1211–1219.
- Kang, W., E. S. Minor, C.-R. Park, and D. Lee. 2015. "Effects of Habitat Structure, Human Disturbance, and Habitat Connectivity on Urban Forest Bird Communities." *Urban Ecosystems* 18:857–870.
- Kareiva, P. M., J. G. Kingsolver, and R. B. Huey. 1993. *Biotic Interactions and Global Change*. Sunderland: Sinauer Associates.
- Kearney, M. 2006. "Habitat, Environment, and Niche: What are we Modeling?" *Oikos* 115:186–191.
- Kearney, M., and W. Porter. 2009. "Mechanistic Niche Modelling: Combining Physiological and Spatial Data to Predict Species' Ranges." *Ecology Letters* 12:334–350.
- Kennedy, C. M., E. H. Campbell Grant, M. C. Neel, W. F. Fagan, and P. P. Marra. 2011. "Landscape Matrix Mediates Occupancy Dynamics of Neotropical Avian Insectivores." *Ecological Applications* 21:1837–1850.
- Kerr, J. T., H. M. Kharouba, and D. J. Currie. 2007. "The Macroecological Contribution to Global Change Solutions." *Science* 316:1581–1584.
- Koh, L. P., and J. Ghazoul. 2010. "A Matrix-Calibrated Species-Area Model for Predicting Biodiversity Losses Due to Land-Use Change." *Conservation Biology* 24:994–1001.
- Lee, R. M., and J. N. Rinne. 1980. "Critical Thermal Maxima of Five Trout Species in the Southwestern United States." *Transaction of the American Fisheries Society* 109: 632–635.
- Lethbridge, M. R., M. I. Westphal, H. P. Possingham, M. L. Harper, N. J. Souter, and N. Anderson. 2010. "Optimal Restoration of Altered Habitats." *Environmental Modelling & Software* 25:737–746.
- Lomolino, M. V. 2000a. "A Call for a New Paradigm of Island Biogeography." *Global Ecology and Biogeography* 9:1–6.
- Lomolino, M. V. 2000b. "Ecology's Most General, Yet Protean Pattern: The Species-Area Relationship." *Journal of Biogeography* 27:17–26.
- Lomolino, M. V. 2000c. "A Species-Based Theory of Insular Zoogeography." *Global Ecology and Biogeography* 9:39–58.
- Lomolino, M. V., J. H. Brown, and R. Davis. 1995. "Analyzing Insular Distribution Pat-

- terns: Statistical Approaches and Biological Inferences." *Annales Zoologici Fennici* 32:435–437.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, et al. 2001. "Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges." *Science* 294:804–808.
- Lynch, H. J., M. Rhainds, J. M. Calabrese, S. Cantrell, C. Cosner, and W. F. Fagan. 2014. "How Climate Extremes—Not Means—Define a Species' Geographic Range Boundary via a Demographic Tipping Point." *Ecological Monographs* 84:131–149.
- MacArthur, R. H., and E. O. Wilson. 1963. "An Equilibrium Theory of Insular Zoogeography." *Evolution* 17:373–387.
- MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. *Monographs in Population Biology*. Volume 1. Princeton: Princeton University Press.
- Manel, S., M. K. Schwartz, G. Luikart, and P. Taberlet. 2003. "Landscape Genetics: Combining Landscape Ecology and Population Genetics." *Trends in Ecology and Evolution* 18:189–197.
- Marion, G., G. J. McInerny, J. Pagel, S. Catterall, A. R. Cook, F. Hartig, and R. B. O'Hara. 2012. "Parameter and Uncertainty Estimation for Process-Oriented Population and Distribution Models: Data, Statistics, and the Niche." *Journal of Biogeography* 39: 2225–2239.
- Marquet, P. A., A. P. Allen, J. H. Brown, J. A. Dunne, B. J. Enquist, J. F. Gillooly, P. A. Gowaty, et al. 2014. "On Theory in Ecology." *BioScience* 64:701–710.
- Maschinski, J., and K. E. Haskins, (Eds.). 2012. *Plant Reintroductions in a Changing Climate: Promises and Perils*. Washington, DC: Island Press.
- Maurer, B. A. 1999. *Untangling Ecological Complexity: The Macroscopic Perspective*. Chicago: University of Chicago Press.
- Maurer, B. A. 2012. "Continental Scale Patterns." In *Encyclopedia of Theoretical Ecology*, edited by A. Hastings and L. J. Gross, 152–155. Berkeley: University of California Press.
- Maurer, B. A., S. W. Kembel, A. J. Rominger, and B. J. McGill. 2013. "Estimating Metacommunity Extent Using Data on Species Abundances, Environmental Variation, and Phylogenetic Relationships Across Geographic Scales." *Ecological Informatics* 13:114–122.
- McGill, B., and C. Collins. 2003. "A Unified Theory for Macroecology Based on Spatial Patterns of Abundance." *Evolutionary Ecology Research* 5:469–492.
- McGill, B. J., R. S. Etienne, J. S. Gray, D. Alonso, M. J. Anderson, H. Kassa Benecha, M. Dormelas, et al. 2007. "Species Abundance Distributions: Moving Beyond Single Prediction Theories to Integration Within an Ecological Framework." *Ecology Letters* 10:995–1015.
- McKinney, M., L. Scarlett, and D. Kemmis. 2010. *Large Landscape Conservation: A Strategic Framework for Policy and Action*. Cambridge: Lincoln Institute of Land Policy.
- McLachlan, J. S., J. J. Hellmann, and M. W. Schwartz. 2007. "A Framework for Debate of Assisted Migration in an Era of Climate Change." *Conservation Biology* 21:297–302.
- Merow, C., A. M. Latimer, A. M. Wilson, S. M. McMahon, A. G. Rebelo, and J. A. Silander, Jr. 2014. "On Using Integral Projection Models to Generate Demographically-

- Driven Predictions of Species' Distributions: Development and Validation Using Sparse Data." *Ecography* 37:1167–1183.
- Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. "Climate Change and Forests of the Future: Managing in the Face of Uncertainty." *Ecological Applications* 17:2145–2151.
- Mokany, K., T. D. Harwood, K. J. Williams, and S. Ferrier. 2012. "Dynamic Macroecology and the Future for Biodiversity." *Global Change Biology* 18:3149–3159.
- Morin, X., and M. J. Lechowicz. 2008. "Contemporary Perspectives on the Niche that can Improve Models of Species Range Shifts Under Climate Change." *Biology Letters* 4:573–576.
- Morin, X., D. Viner, and I. Chuine. 2008. "Tree Species Range Shifts at a Continental Scale: New Predictive Insights from a Process-Based Model." *Journal of Ecology* 96:784–794.
- Morlon, H., E. P. White, R. S. Etienne, J. L. Green, A. Ostling, D. Alonso, B. J. Enquist, et al. 2009. "Taking Species Abundance Distributions Beyond Individuals." *Ecology Letters* 12:488–501.
- Neville, H. M., J. B. Dunham, and M. M. Peacock. 2006. "Landscape Attributes and Life History Variability Shape Genetic Structure of Trout Populations in a Stream Network." *Landscape Ecology* 21:901–916.
- Newman, K. B., S. T. Buckland, B. J. T. Morgan, R. King, D. L. Borchers, D. J. Cole, P. Besbeas, et al. 2014. "Integrated Population Modelling." In *Modelling Population Dynamics. Methods in Statistical Ecology Series*, 169–195. New York: Springer-Verlag.
- Nowicki, P., V. Vrabec, B. Binzenhöfer, J. Feil, B. Zakšek, T. Hovestadt, and J. Settele. 2014. "Butterfly Dispersal in Inhospitable Matrix: Rare, Risky, but Long-Distance." *Landscape Ecology* 29:401–412.
- Pagel, J., and F. M. Schurr. 2012. "Forecasting Species Ranges by Statistical Estimation of Ecological Niches and Spatial Population Dynamics." *Global Ecology and Biogeography* 21:293–304.
- Pardieck, K. L., D. J. Ziolkowski, Jr., and M.-A. R. Hudson. 2014. "North American Breeding Bird Survey Dataset 1966–2013, version 2013.0." Laurel: U.S. Geological Survey, Patuxent Wildlife Research Center. Accessed April 15, 2015. <http://www.pwrc.usgs.gov/BBS/>.
- Parnell, N. F., and J. T. Streebman. 2010. "The Macroecology of Rapid Evolutionary Radiation." *Proceedings of the Royal Society B: Biological Sciences* 278:2486–2494.
- Peters, D. P. C., B. T. Bestelmeyer, and M. G. Turner. 2007. "Cross-Scale Interactions and Changing Pattern-Process Relationships: Consequences for System Dynamics." *Ecosystems* 10:790–796.
- Ricklefs, R. E., and D. Schluter. 1993. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. Chicago: University of Chicago Press.
- Rosenzweig, M. L. 1995. *Species Diversity in Space and Time*. Cambridge: Cambridge University Press.
- Rybicki, J., and I. Hanski. 2013. "Species-Area Relationships and Extinctions Caused by Habitat Loss and Fragmentation." *Ecology Letters* 16:27–38.

- Sabatino, M., N. Maceira, and M. A. Aizen. 2010. "Direct Effects of Habitat Area on Interaction Diversity in Pollination Webs." *Ecological Applications* 20:1491–1497.
- Sala, O. E., F. S. Chapin, III, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, et al. 2000. "Global Biodiversity Scenarios for the Year 2100." *Science* 287: 1770–1774.
- Schlesinger, W. H. 1997. *Biogeochemistry: An Analysis of Global Change*. San Diego: Academic Press.
- Schurr, F. M., J. Pagel, J. Sarmiento Cabral, J. Groeneveld, O. Bykova, R. B. O'Hara, F. Hartig, et al. 2012. "How to Understand Species' Niches and Range Dynamics: A Demographic Research Agenda for Biogeography." *Journal of Biogeography* 39:2146–2162.
- Slatkin, M. 1985. "Gene Flow in Natural Populations." *Annual Review of Ecology, Evolution, and Systematics* 16:393–430.
- Soberón, J. 2007. "Grinnellian and Eltonian Niches and Geographic Distributions of Species." *Ecology Letters* 10:1115–1123.
- Soranno, P. A., K. S. Cheruvilil, E. G. Bissell, M. T. Bremigan, J. A. Downing, C. E. Fergus, C. T. Filstrup, et al. 2014. "Cross-Scale Interactions: Quantifying Multi-Scaled Cause-Effect Relationships in Macrosystems." *Frontiers in Ecology and the Environment* 12:65–73.
- Storfer, A., M. A. Murphy, J. S. Evans, C. S. Goldberg, S. Robinson, S. F. Spear, R. Dezzani, et al. 2007. "Putting the 'Landscape' in Landscape Genetics." *Heredity* 98:128–142.
- Swanson, H. K., M. Lysy, M. Power, A. D. Stasko, J. D. Johnson, and J. D. Reist. 2015. "A New Probabilistic Method for Quantifying  $n$ -Dimensional Ecological Niches and Niche Overlap." *Ecology* 96:318–324.
- Szlavec, K., P. Warren, and S. Pickett. 2011. "Biodiversity on the Urban Landscape." In *Human Population: Its Influences on Biological Diversity*, edited by R. P. Cincotta and L. J. Gorenflo, 75–101. *Ecological Studies Series*. Volume 214. Berlin: Springer-Verlag.
- Theiling, C. H., J. A. Janvrin, and J. Hendrickson. 2015. "Upper Mississippi River Restoration: Implementation, Monitoring, and Learning Since 1986." *Restoration Ecology* 23:157–166.
- Thuiller, W., S. Lavorel, M. B. Araújo, M. T. Sykes, and I. C. Prentice. 2005. "Climate Change Threats to Plant Diversity in Europe." *Proceedings of the National Academy of Sciences, USA* 102:8245–8250.
- Vanderwel, M. C., V. S. Lyutsarev, and D. W. Purves. 2013. "Climate-Related Variation in Mortality and Recruitment Determine Regional Forest-Type Distributions." *Global Ecology and Biogeography* 22:1192–1203.
- Vitt, P., K. Havens, A. T. Kramer, D. Sollenberger, and E. Yates. 2010. "Assisted Migration of Plants: Changes in Latitudes, Changes in Attitudes." *Biological Conservation* 143:18–27.
- Wang, S., W. Zhu, X. Gao, X. Li, S. Yan, X. Liu, J. Yang, et al. 2014. "Population Size and Time Since Island Isolation Determine Genetic Diversity Loss in Insular Frog Populations." *Molecular Ecology* 23:637–648.

- Weinstein, M. P., S. Y. Litvin, and J. M. Krebs. 2014. "Restoration Ecology: Ecological Fidelity, Restoration Metrics, and a Systems Perspective." *Ecological Engineering* 65:71–87.
- West, G. B., J. H. Brown, and B. J. Enquist. 1999. "The Fourth Dimension of Life: Fractal Geometry and Allometric Scaling of Organisms." *Science* 284:1677–1679.
- White, P. S., and J. L. Walker. 1997. "Approximating Nature's Variation: Selecting and Using Reference Information in Restoration Ecology." *Restoration Ecology* 5:338–349.
- Whittaker, R. J. 1998. *Island Biogeography: Ecology, Evolution, and Conservation*. Oxford: Oxford University Press.
- Yackulic, C. B., J. D. Nichols, J. Reid, and R. Der. 2015. "To Predict the Niche, Model Colonization and Extinction." *Ecology* 96:16–23.
- Zhang, F., Y. Tao, and C. Hui. 2012. "Organism-Induced Habitat Restoration Leads to Bi-Stability in Metapopulations." *Mathematical BioSciences* 240:260–266.