

Chapter 16

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

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In Brief

- 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 on 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 (Pratt 1994; Hobbs and Norton 1996, 2001; Palmer et al. 1997). Restoring any altered ecosystem comprises a sizeable challenge in that it is critical to determine the appropriate target for restoration, 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; Chen et al. 2015). 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 spatiotemporal scales (Holl and Crone 2004; Jackson and Hobbs 2009; Jackson 2012). Multi-scale ecosystem dynamics 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 his 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 macro-scale 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, metapopulation 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; Brown et al. 2002). It is fairly straightforward to understand the consequences of size variation when examining the properties of individual organisms or groups thereof (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Lee et al. 2014). 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. 1997; West et al. 1999a). These changes can have a number of profound implications for the structure of communities and ecosystems (Enquist et al. 1998; Enquist et al. 1999a; Enquist et al. 1999b; Gillooly et al. 2001; West et al. 1999b). 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 2002; Enquist et al. 2003; McGill et al. 2006). 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 macro-scales 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; Brown 1999; Maurer 1999; 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 (Peters and Lovejoy 1992; 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 macro-scale 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; Falk et al. 2007; 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 macro-scale patterns exert controls on species' distributions. 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. We now outline four areas of active research in macroecology that may offer valuable insights to ecological restoration efforts.

1. 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; Maurer 2009, 2012; Mokany et al. 2012). For restoration ecology, there are numerous distribution-shaping processes which 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 (Maurer 2009, Parnell and Streebman 2010). Examples of distributional constraints include species-specific climatic thresholds (e.g.,

critical temperatures; Lee and Rinne 1980; Chen et al. 2015), changing landscape pattern (e.g., patch/matrix composition and configuration; Prugh et al. 2008; 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 inter-specific 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, and the concept has shaped how ecologists have viewed species' distributions for decades (Hutchinson 1957, 1965; Pulliam 2000; 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; Rehfeldt et al. 2006; Araújo and Peterson 2012). 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.; Figure 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 (Pearson and Dawson 2003; 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.

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 inter-specific 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; Heffernan 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 (Figure 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 (Chaine and Beaubien 2001; Morin et al. 2008), physiology (Buckley

2008; Kearney et al. 2008; Kearney and Porter 2009; Régnière et al. 2012), 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 (Purves et al. 2007; Snäll et al. 2008; Abadi et al. 2010; Merow et al. 2011; Schaub and Abadi 2011; Pagel and Schurr 2012; Fitzpatrick et al. 2012; Garcia-Valdez et al. 2013; Chandler and Clark 2014; Newman et al. 2014; Robinson 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 α - and β -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 non-climatic 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 (Hartig et al. 2012; 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.

2. 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). 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 (Brown 1986; Lomolino 1994, 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 (Horsák et al. 2012). 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 macro-scale 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; Maurer and Taper 2002; 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 (Figure 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 (Figure 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 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; Prugh et al. 2008; Horsák et al. 2012; 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 re-established 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.

3. 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). 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 (Maschinski and Quintana-Ascencio, Ch.7, this volume). 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 (Davis and Glick 1978; 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; Prugh et al. 2008; Horsák et al. 2012; 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 (Figure 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 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 (Figure 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 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 (Figure 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 similar communities likely relies upon the unique ecoregion to which a community belongs as well as influences from human populations and other disturbances.

4. 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 macro-scale 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 (Figure 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 (Kinzig et al. 2001; 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 (Figure 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 ecosystems 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. 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. Macro-scale 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).

Case Study: Offering the Theory in Practice

Inspired by our discussion thus far, we recall that the functional integrity of ecological systems incompletely relies on the fitness and persistence of its units of biological organization (e.g., individuals and populations). While it might be simpler to imagine cases where broad-scale restoration efforts are designed to benefit populations in terrestrial systems, nevertheless, similar considerations may be illustrated for managed aquatic systems as well. Consider the following case in the Marys River watershed (41°33' N, 115°18' W) in the Lahontan Basin of the Great Basin desert, USA. We might envision this 500 km² region as a candidate example for macro-

scale restoration of Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*) populations, a federally-threatened species in the western United States. This species is endemic to the Lahontan basin and is often restricted to small and isolated streams, which makes their population dynamics an important case for restoration considerations on broad spatial scales, especially with respect to spatial structuring of their populations in response to dispersal barriers, habitat quality, and patch connectivity.

In this stream network system, Neville et al. (2006) assessed the genetic characteristics of various subpopulations of cutthroat trout across the Marys River catchment. Though the Marys River has been well studied in terms of conventional ecological methods (e.g., censuses, mark-recapture, etc.), the authors note that complementary genetic approaches provide a new avenue for inferring demographic processes—approaches which may also reveal both past and present influences (e.g., decreased fitness of individuals) on such processes in the system (Slatkin 1985; Davies et al. 1999; Manel et al. 2003). Given the longstanding recognition that landscape, and in this case “riverscape,” patterns have important influences on ecological processes that shape and constrain populations in space and time (*sensu* MacArthur and Wilson 1967), Neville et al. (2006) sought to investigate the potential influence of dispersal barriers on genetic population structure across the study region. They posited that isolated subpopulations of trout would exhibit sedentary behaviors in terms of their life history (i.e. withdrawn migratory behavior); whereas, connected subpopulations would favor individuals with requisite movement behaviors. Under their research design, the authors evaluated the relative diversity and flow of genes between trout subpopulations, particularly in the context of dispersal barriers.

Neville et al. (2006) found that trout populations with low spatial connectivity did, in fact, exhibit a sedentary life history strategy and also occupied habitats of poor quality (e.g.,

smaller-sized habitat), which contributed to lower genetic diversity than subpopulations inhabiting connected, higher quality (e.g., larger) habitats. Consequently, concomitant increases in genetic differentiation were also associated with isolated populations in response to decreased gene flow above one-way dispersal barriers in contrast to more connected populations, which were located below (i.e. able to move to and from the river main stem) or able to traverse passable barriers (i.e. throughout various tributaries; Neville et al. 2006).

Moreover, Neville et al. (2006) found no evidence of differential genetic patterns solely based on the type of dispersal barrier present (e.g., man-made dams or natural waterfall features); however, the authors note that the response of trout to such barriers depends markedly on the habitat in which isolated populations exist. For example, one specific population inhabited broad, high quality habitats above a waterfall yet was also subject to asymmetrical gene flow (i.e. with respect to the waterfall). Despite such 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 genetic constraints (i.e. asymmetrical flow due to dispersal barriers). In addition, researchers found that spatial structure in the region was more important for shaping genetic diversity, rather than temporal structure, in these trout populations.

Collectively, these findings imply that 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. To this point, across the Lahontan basin, 89% of interconnected habitats consistently maintained populations of cutthroat trout; whereas, only 32% of isolated areas supported any populations at all (Dunham et al. 1997). In summary, researchers concluded that population persistence concurrently depends on the life history strategy (i.e. sedentary v. 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.

Now, let us imagine that this catchment were of interest to restoration ecologists. What solution(s) might we offer to managers of such a freshwater basin that is important to the persistence of Lahontan cutthroat trout? Given our discussion up to this point, we should consider several criteria for restoration: (1) the size of the system (e.g., a 500 km² freshwater catchment); (2) the macrogeographic constraints of the system (e.g., multiple subpopulations of migratory trout, which are able to move > 50 km annually and are structured by the spatiotemporal distribution of habitat resources; Neville et al. 2006); (3) the connectedness of the system (e.g., considering the flux of individuals, genes, energy, and resources across barriers or in the absence thereof); and (4) the greater spatiotemporal context of system's landscape (e.g., the proximate influences of individuals, genes, energy, and resources outside of the system targeted for restoration). Solutions relevant to each of these considerations might include continued assessments of individual fish (e.g., via genetic methods) across the restored system, the enhancement of key habitat resources and movement corridors in space and time (e.g., via in-stream manipulations of habitat as well as facilitation around and/or permanent removal or retrofitting of impeding dispersal barriers), and recurrent monitoring surveys within and beyond the restored system (e.g., the Marys River catchment independently considered on the local scale as well as dependently evaluated within the Lahontan basin on the broad scale; Figure 16.8). With such a hypothetical case in mind, we can begin to appreciate how comprehensive and diverse the myriad considerations are for applied efforts in ecological restoration.

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 (Brawn et al. 2001; 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; Lathrop et al. 2007). 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 multi-scaled 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 non-stationary climate regimes. 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). Distribution models or bioclimatic envelope models have been used extensively to project future species' distributions (Thomas et al. 2004; Thuiller et al. 2005; Jetz et al. 2007), 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, neo-native translocations (e.g., assisted migration), and enhancing genetic diversity in managed populations (Millar et al. 2007; Storfer 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 macro-scales—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, macro-scale 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; Clement et al. 2014; Hobbs et al. 2014; United States Council on Climate Preparedness and Resilience 2014; Shafer 2015). 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).

Summary: the Macroecological Perspective and Restoration Ecology

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 macro-scale 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 (i.e. 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. 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, macroecology 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. 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 (Temperton et al. 2004). 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 (Falk and Millar, Ch.17, this volume). 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 non-stationary and ever-challenged world.

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Figures and Captions

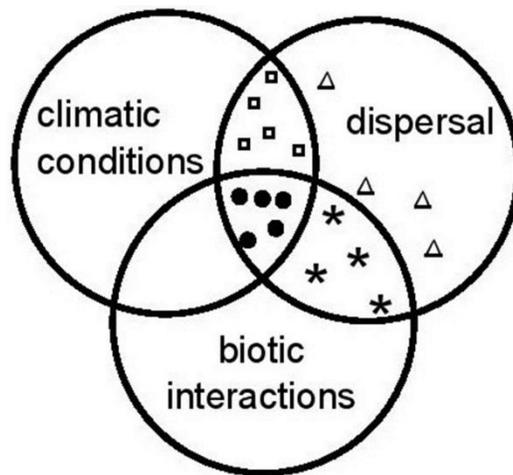


Figure 16.1 Species' niches and geographical distributions are shaped by many factors—of which, three important categories are illustrated here: climatic conditions, biotic interactions, and dispersal. The upper left circle indicates the geographical area in which climatic conditions support an intrinsic 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).

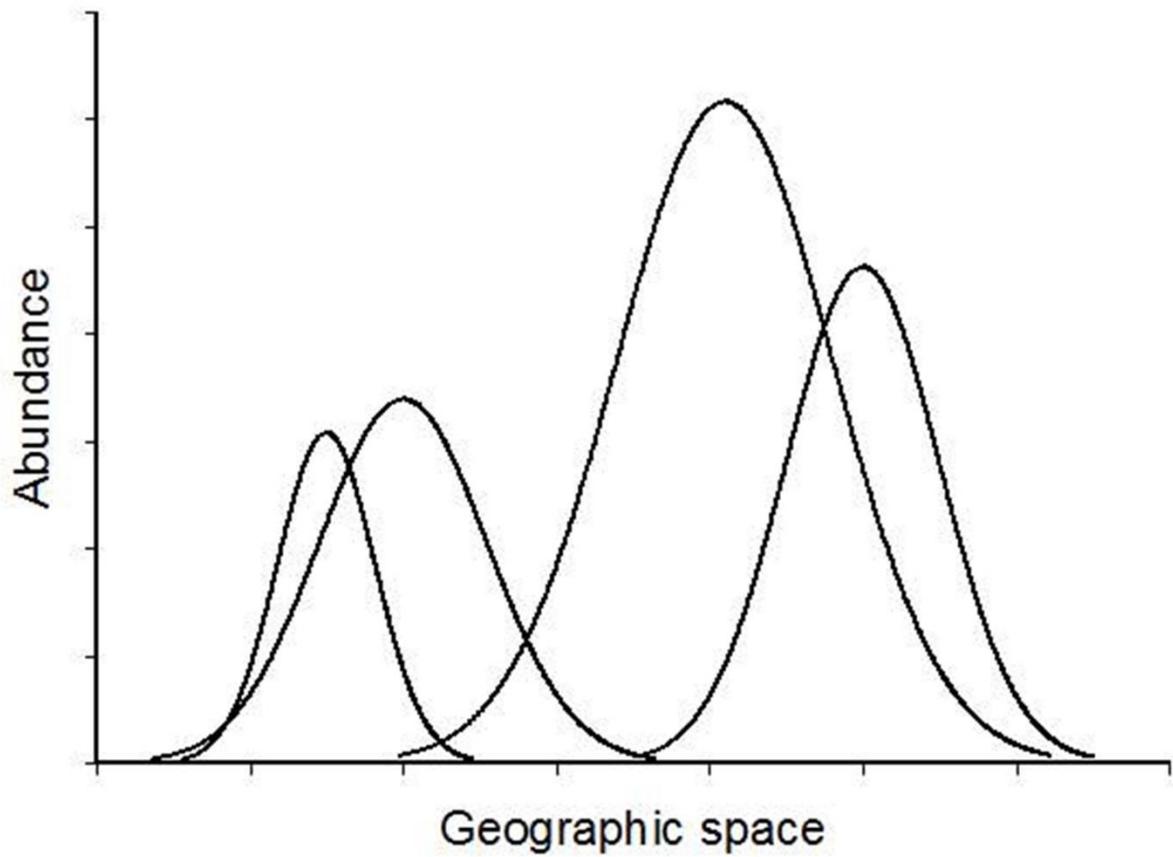


Figure 16.2 Graphical representation of the distribution of species in geographic space hypothesized to be responsible for species-area relationships.

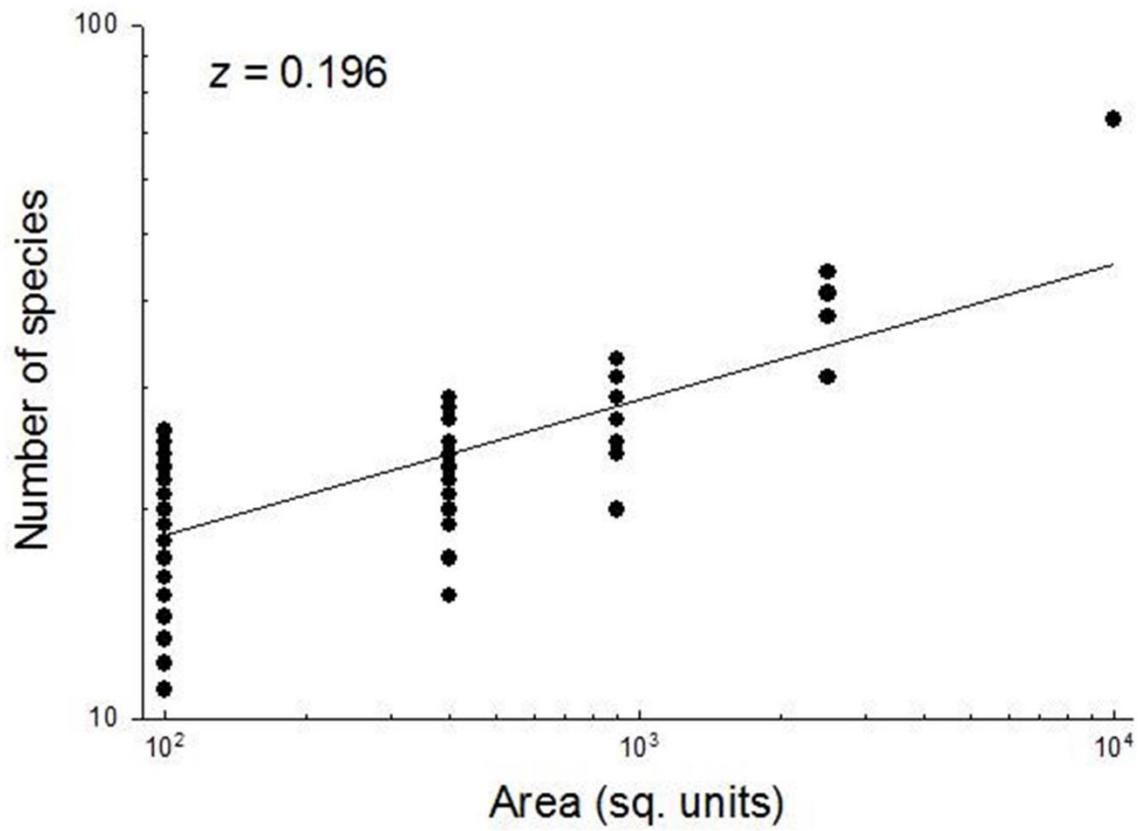


Figure 16.3 An example species-area relationship derived from a simulation of a two-dimensional version of the model represented in Figure 16.2.

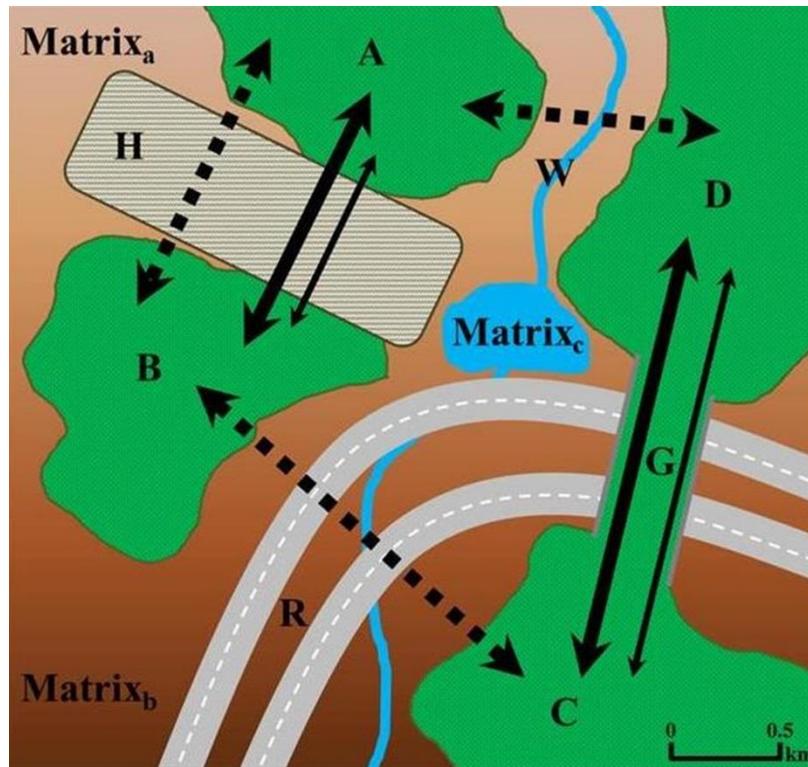


Figure 16.4 Schematic of a hypothetical landscape where habitat islands (A-D; i.e. supporting disparate local populations) are separated by a gradient of matrix (a) conducive, (b) semi-conductive (e.g., an agricultural field), or (c) unconductive (e.g., a lake) to dispersal between patches for two hypothetical 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.

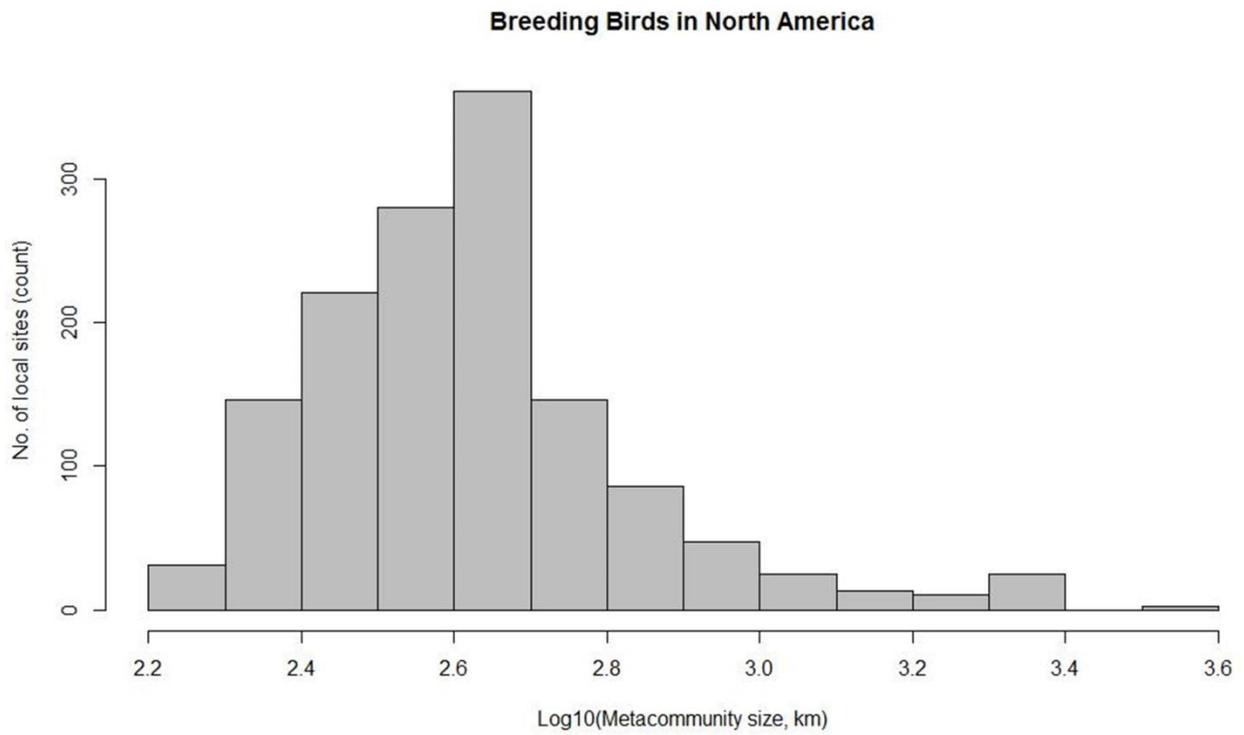


Figure 16.5 Distribution of metacommunity size (i.e. distance, units of \log_{10} km) for 1,393 avian assemblages sampled by the North American Breeding Bird Survey (Maurer et al. 2013).

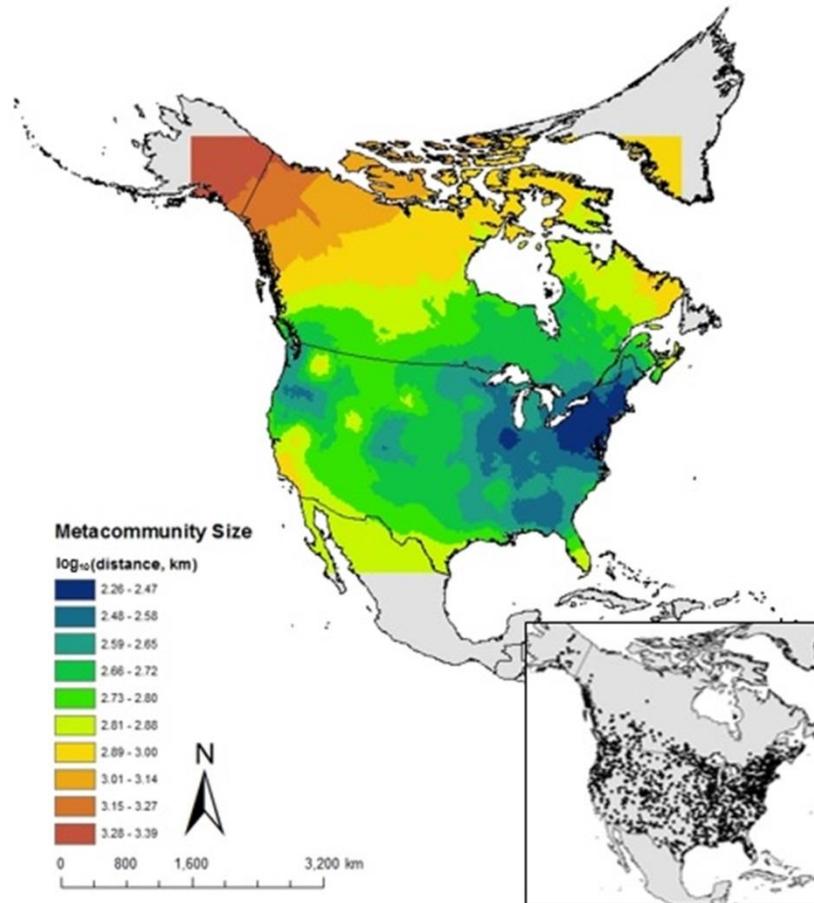


Figure 16.6 Geographic variation in metacommunity size (i.e. distance) for avian assemblages across 1,393 Breeding Bird Survey routes in North America—produced via an ordinary kriged interpolation. Metacommunity distances are measured as a function of site similarity based on species relative abundance, 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.

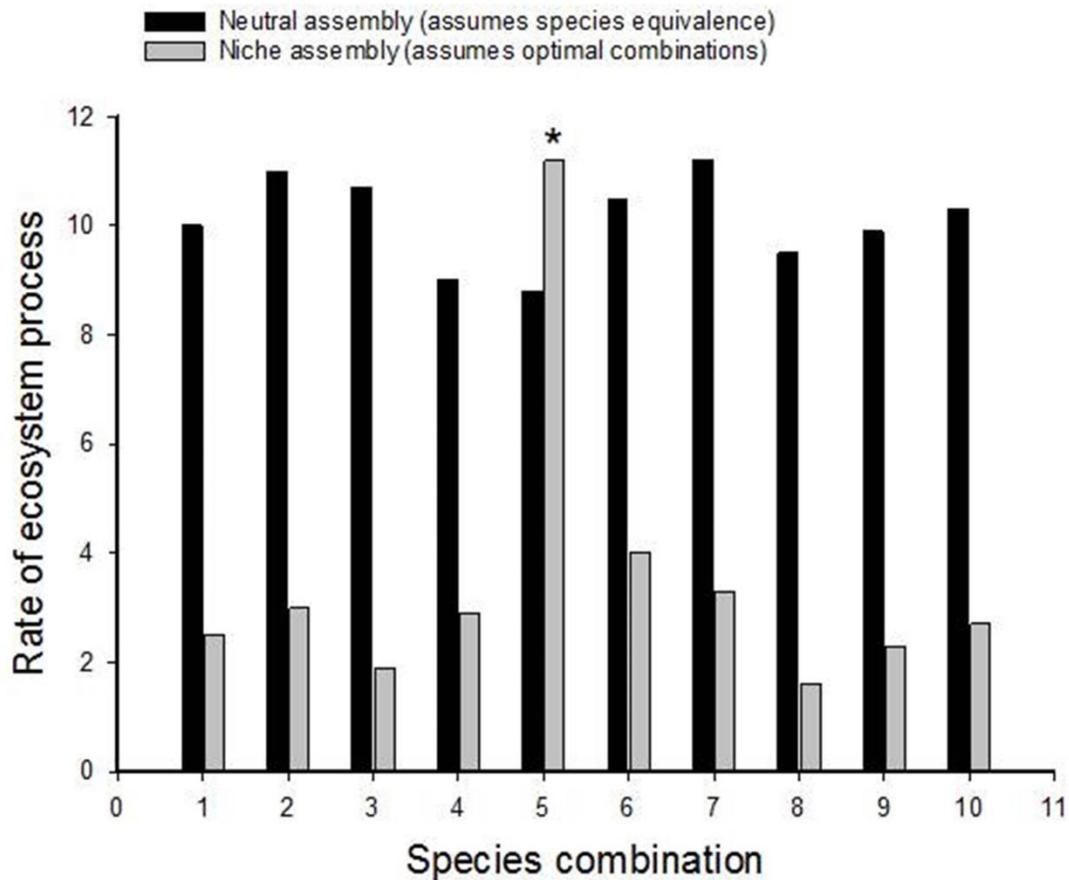


Figure 16.7 Graphical representation of the differences between the neutral assembly and niche assembly hypotheses. The vertical axis is the rate of some ecosystem process of interest to restoration efforts. Suppose that there are 10 different combinations of species that could occupy the local ecosystem. In this hypothetical system, the neutral theory would predict that all 10 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.

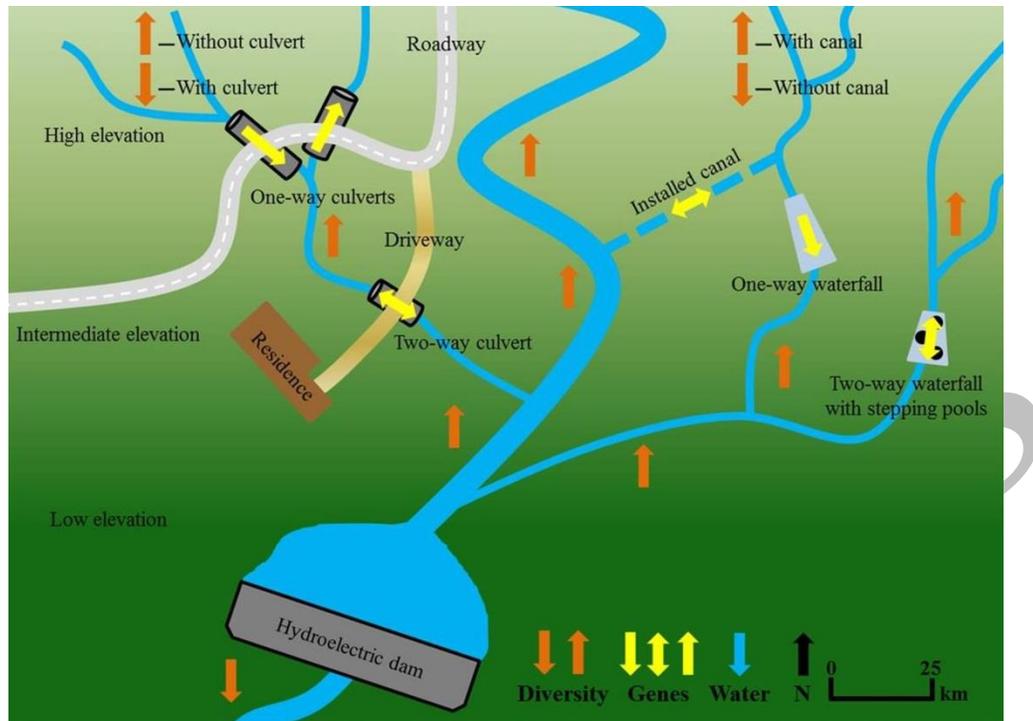


Figure 16.8 Schematic of a hypothetical riverscape where fish populations are either connected or isolated across tributary waters that contain both natural (i.e. waterfalls) and man-made barriers (i.e. dams and culverts) to individual dispersal. If this area were unmanaged for fish, then we might imagine 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 [yellow arrows] and genetic diversity [orange 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.