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Conservation, the Two Pillars of Ecological Explanation, and the Paradigm of Distance

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ABSTRACT: Ecological explanations of the distributions of living things rest on two general conceptual pillars: the niche difference model and the model of spatial and temporal constraint. Both models suggest the underlying importance of spatial distance as a simple correlate of biological pattern. In this essay we discuss five key, but seemingly disparate, conservation issues that have some correlation with or basis in spatial distance. The realization that the world is, at some level, everywhere unique suggests that optimum nature reserve design must find a balance between protecting grain (habitat integrity) and extent (distance). The distance involved in biotic movements helps us define “exotic” and predict invasive risk. The effect of gene movements also has a strong distance correlate, with fitness potentially declining with distance moved (outbreeding depression). Failure to consider spatial variation in disturbance regimes, community composition, and genetic makeup of populations also may hinder restoration. The relevance of reference site information in general decreases as the distance between these sites and restoration areas increases. The distance paradigm we define suggests that there are two inherent bases to conservation: ecology and geography.

Conservación, los Dos Pilares de la Explicación Ecológica, y el Paradigma de la Distancia

RESUMEN: La explicación ecológica de la distribución de los seres vivos recae en dos pilares conceptuales generales: el modelo de diferencia de nicho y el modelo de restricción espacial y temporal. Ambos modelos sugieren la importancia subyacente de la distancia espacial como una simple correlación de los patrones biológicos. La realización que el mundo es, en un nivel, único en cada aspecto sugiere que el diseño óptimo de reservas naturales debe encontrar un balance entre grado de protección (integridad de hábitat) y extensión (distancia). La distancia involucrada en movimientos bióticos ayuda a definir “exótico” y predecir en riesgo de invasión. El efecto de movimiento de genes también tiene una fuerte componente correlacionada con la distancia, con declinación potencial del fitness con la distancia movida (depresión de outbreeding). La falla de considerar la variación espacial en los regímenes de disturbio, composición de comunidades, y la composición genética de las poblaciones, también puede dificultar la restauración. La relevancia de información del sitio de referencia en general disminuye a medida que la distancia entre esos sitios y las áreas de restauración aumentan. El paradigma de distancia que definimos sugiere que hay dos bases inherentes en la conservación: la ecología y la geografía.

Index terms: biodiversity, conservation strategies, distance decay, exotic species, SLOSS

INTRODUCTION

We propose that explanations for the distribution and abundance of living things rest on two conceptual pillars. The first of these asserts that the physical environment and niche characteristics determine distribution and abundance (MacArthur 1972). We term this first pillar of explanation the niche difference model (White and Nekola 1992). Some have postulated that this is the sole explanation underlying biogeographic pattern at less than continental scales (Krebs 1985). This view has been most succinctly expressed through Beijerinck’s Law (Sauer 1988): everything is everywhere but the environment selects.

The second conceptual pillar asserts that distribution and abundance are a function of the spatial arrangements and histories

of organisms and habitats. For instance, the size and isolation of habitats can act through dispersal to either positively (e.g., mass effect, supply-side ecology) or negatively (e.g., dispersal limitation) influence species distribution (Shmida and Ellner 1984, Roughgarden et al. 1987, Nekola 1999). We term this second pillar the model of spatial and temporal constraint (White and Nekola 1992). At the largest scales, second pillar explanations become equivalent to those of historic biogeography (Ricklefs and Schluter 1993).

Spatial distance can be a critical parameter in both of these conceptual models. Because properties of the environment often exhibit spatial autocorrelation, increasing distance can be correlated with increasing environmental differences and thus species turnover (Palmer 1990). Analysis of

compositional change along environmental gradients has a long ecological history (Curtis 1959, Whittaker 1975). Distance is also important in explanations based on the second pillar, as increasing spatial distances will decrease the effect of dispersal, thereby limiting the mixing of species and genes between areas. At great enough distances, incomplete dispersal will limit rates of competitive exclusion (Shmida and Ellner 1984) and increase the chance for allopatric speciation (Mayr 1963).

Because distance is a common denominator to both conceptual models, we propose it as a useful surrogate variable that cuts through several conundrums and Gordian Knots in conservation biology. In this essay we explore how the distance paradigm clarifies some conservation decisions and practices. We address five areas: identification of priority areas for conservation, optimum reserve design, risks posed by exotic species, issues in conservation genetics, and development of optimum management and restoration policies.

MEETING GROUNDS AND CONSERVATION PRIORITIES

The introductions to floras and faunas often note that the study area in question is a meeting ground of northern, southern, eastern, and western species. Tracing our collective professional careers, we have found such statements made with determined regional pride for New England, Iowa, Missouri, North Carolina, Tennessee, and Wisconsin and at scales ranging from watersheds to counties to physiographic regions to states. On hearing this observation, colleagues elsewhere have readily agreed that their study regions, too, are meeting grounds of eastern and western, northern and southern elements. We don't mean to belittle these claims—rather they paint a picture of a biological world that is, to some degree, made up of unique places. For all these claims to be true, species must have unique distributions, allowing every place to be at the range limit for different suites of taxa.

Both conceptual pillars contribute to this pattern. First, spatial autocorrelation of the environment and the individualistic char-

acteristics of species niches results in continual spatial turnover in the biota—and locally unique biotas. Second, distance itself can contribute to this pattern, as movement probability is inversely correlated with distance and the strength of dispersal barriers (Okubo and Levin 1989). Thus, compositional similarity should decrease with increasing distance simply due to differences in the opportunity for migration and gene flow.

The decrease in similarity with distance has been codified by geographers as distance decay, or the “first law of geography” (Tobler 1970). Such a pattern is clearly evident among boreal and Appalachian spruce-fir forest floras, where similarity falls between 25% and 75% per 1000 km (Nekola and White 1999). The variation in distance decay rate is related to a number of factors. For instance, the similarity of

boreal forest herbs decreases at a 33% greater rate than for trees in the same landscape. In this same region, the composition of large-seeded plants decreases at an 87% greater rate as compared to microscopic-seeded and spore-bearing species. The floristic similarity within the contiguous boreal spruce-fir forest decreases at 25% of the rate experienced in isolated Appalachian communities. Such relationships between compositional similarity and distance can be found in biological systems ranging from temperate terrestrial land snail faunas (Nekola, unpubl. data) to birds and mammals in Baja California (Kratler 1992) to tropical canopy tree floras (Condit et al. 2002).

Distance decay rate can be used to determine conservation priorities. Consider a hypothetical landscape with 20 total species and a constant alpha diversity of 3

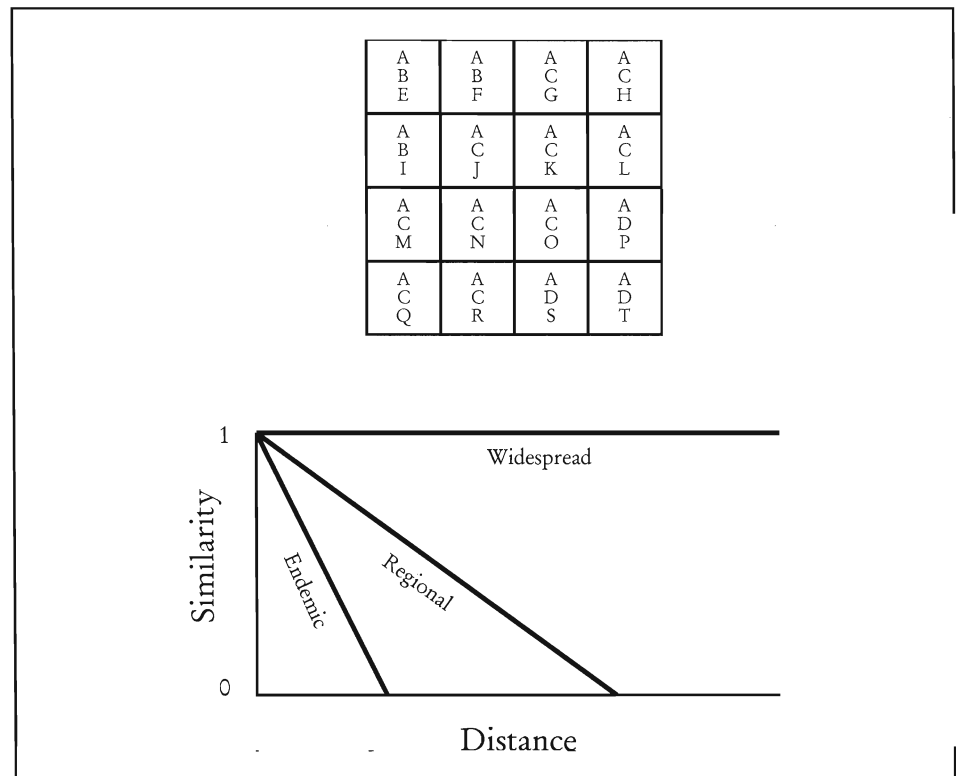


Figure 1. Effect of differential distance decay rates on community composition and conservation strategies within a hypothetical 16-grid-cell landscape. Each cell in this landscape supports 3 co-occurring species, with a total of 20 species occurring over the entire area. These species exist in three different distribution patterns. The single widespread species (A) occurs in every cell. The 3 regional species (B,C,D) occur over 20%–60% of the landscape, arrayed along an environmental gradient running from the upper left to lower right. The remaining 16 endemic species (E–T) occur only within single cells. Distance decay rates based on these distributions range from none in the widespread species, to intermediate levels for the regional species, to very high levels in the endemic species.

species per cell (Figure 1): 1 species is cosmopolitan (found throughout the landscape), 3 are regional (restricted to a portion of the landscape), and the remaining 16 are endemic (restricted to a single cell). Let us assume that all species are stable at the scale of the landscape cell. Based upon the cosmopolitan species, the world is everywhere the same (low distance decay rates) so that the conservation of only one cell is necessary. However, from the perspective of the endemic species, the world is everywhere unique (high distance decay rates) so that loss of species scales directly with the loss of cells. In this landscape, the conservation of the wide-ranging species occurs with the conservation of only one cell. Conservation of regional or endemic species will require additional reserves to be spread across the landscape. Identification of such missing species is presently addressed through gap analysis (Kiestler et al. 1996).

Conservation of multiple sites will be important even when they are environmentally identical, as different migration histories may cause such sites to be dissimilar in species composition. Different migration histories may mean that the biotas of smaller areas will not necessarily be nested subsamples of the biota of larger sites. In such cases, simply protecting the most species-rich sites will not capture all taxa. For instance, only the most species-rich fens in Iowa have been selected for protection by conservation organizations. In the process, many less rich sites have been ignored, even though they support taxa not found on the species-rich sites. To fully protect the biodiversity of this habitat, sites across the entire landscape must be protected, independent of their individual richness (Nekola 1994).

THE SLOSS DEBATE

Conservation design is initially a sampling problem, as protected sites can be seen as remnants of an original, larger whole. Since the early 1970s, the issue of optimum sampling design for biological diversity has been represented by the Single Large Or Several Small (SLOSS) reserve debate: For a given financial investment (translated to the area of land to be protected), will

a single large area or several smaller locations that sum to the same total size protect more species (Diamond 1975, Simberloff and Abele 1976)? The SLOSS debate has been laid to rest and resurrected many times; we believe that this is inevitable for the simple reason that the size and number of reserves protect fundamentally different aspects of how biological diversity is distributed and maintained. Because of this, the debate can never be resolved (see also discussion in Nekola and White 1999).

To understand this argument, the influence of two components of scale (grain and extent) on biodiversity must be separately considered (Weins 1989). Maximization of reserve size (grain) is important in protecting ecological integrity (e.g., hydrologic and disturbance regimes) and in maintaining viable populations of area-sensitive species such as top-level predators. However, maximization of the geographic spread of reserves (extent or distance encompassed) is also critical because species richness often accumulates more rapidly with increasing extent as compared to increasing grain (Palmer and White 1993). Given a fixed amount of area to be conserved, the price of maximizing reserve size will be the minimization of reserve extent, which will likely decrease the total number of species initially "captured" within the reserve system. Similarly, the price of maximizing reserve extent will be smaller individual reserves, placing into question reserve integrity and populations of area-sensitive species.

Whether a Single Large area will capture and protect more species than Several Small ones is contingent on the relative contribution of grain and extent to diversity. Higgs (1981; see also Bell et al. 1990, Shafer 1990) suggested that optimization of reserve design in the SLOSS context will be based on the slope of the species-area relation and the similarity among the Several Small areas. As similarity between potential reserves is described by distance decay, this rate can be used to determine optimal reserve number. The greater the distance decay, the more reserves will be needed to initially capture species richness.

If the distance decay rate for more poorly dispersed or smaller-bodied species is higher than for better dispersed and larger-bodied ones (Oliver et al. 1998), no single optimum reserve design exists. Thus, while many small reserves will be required to capture the richness of poorly dispersing or small taxa, only a few large reserves will be needed to protect mobile or large species. These differential contributions of extent and grain to biodiversity underlie ongoing debates between those advocating large reserves and those advocating many small reserves, and they suggest why dispersed smaller reserves often contain more species than fewer larger ones (McNeill and Fairweather 1993, McCoy and Mushinsky 1994). The separate contributions of grain and extent explain why California state parks have more plant and bird species (small home-range taxa) than Sequoia-Kings Canyon National Park (which is much larger than the summed area of the state parks; Stohlgren and Quinn 1991), while at the same time small national parks have lost more large mammal species since settlement than larger ones (Newmark 1987). In fact, Sequoia-Kings Canyon is only marginally large enough for its most area-sensitive large (Schoenwald-Cox 1983). Protecting all species will thus require a spatially dispersed network of reserves covering a spectrum of sizes, ranging from a relatively few megareserves (>10⁶ ha) to many mini-reserves (0.1–10 ha) dispersed throughout a landscape. Such a regional network will also provide migrational stepping stones (Schultz 1998), which will become useful in the advent of global climate change.

EXOTIC SPECIES

Humans serve as dispersal vectors for a wide range of plant, vertebrate, invertebrate, and disease organisms. The movement of taxa has created serious environmental problems on all continents (Forgs and Allen 1999). One of the dilemmas that arises for managers is the definition of the term "exotic": exotic species represent introductions of organisms not "originally" "here." The problem is that "originally" and "here" require specification of spatial and temporal scale. Over what spatial scale should we judge nativeness: one

square kilometer, a county, a state, a biogeographic province, or a continent? As species ranges have repeatedly changed over hundreds to thousands of years, over what time period do we claim "original" presence: 50 years, 500 years (i.e., pre-Columbian), or more? A further complication is the continual change of environments, which may result in unrealistic conservation goals when definitions of "native" remain static. Biotic movers often justify further introductions because of the vagueness of these terms. This vagueness can be partially dealt with by a consideration of the distances crossed in a given anthropogenic movement. The larger the spatial extent (and the smaller the time period) covered by a given movement, the more agreement will likely exist among conservationists as to whether the resulting species is "exotic" in that particular setting.

The existence of the exotic species problem indicates that processes related to the second pillar of ecology are important for biodiversity at a global scale: if species were simply limited by the physical environment, the introduction of exotic species would be impossible—all species would occur across their complete potential range. However limits on dispersal have created a world in which places with similar environments on different continents (or different parts of continents) are often inhabited by different species. The biotic world thus represents a loaded gun of exotic species problems waiting to happen. To assess which species movements may pose the greatest risks will require assessing not only the physical and biological similarities between sources and destinations, but also the magnitude of previous biotic interactions between them. As the rate of biotic interaction should be negatively correlated with distance, the ecological risks of biotic movements should be positively correlated with the distances involved. The greater the distances moved, the greater the likelihood that the natural migration barriers of a species (and its coevolved friends or enemies) will be exceeded.

CONSERVATION OF GENETIC DIVERSITY

Like species diversity, genetic processes and diversity are also strongly influenced by distance. Not only does genetic similarity often decrease with increasing distance (McKechnie et al. 1975, Peterson and Denno 1998, Evans et al. 2000, Petit et al. 2001), but the gene flow rate is also often negatively correlated with interpopulation distance (Aguirre-Planter et al. 2000). Even in *Betula occidentalis* Hook., which demonstrates no spatial genetic structuring across all elevational zones along the eastern Rocky Mountain front, a strong genetic-spatial distance relationship exists when comparisons are limited to populations of similar altitude (Williams and Arnold 2001).

As gene flow rates are largely a function of dispersal rate, genetic similarity between populations is often correlated by dispersal ability, spatial distance, and dispersal barriers. Peterson and Denno (1998) showed that isolation by distance increased with decreases in the mobility of different insect species. Decreased between-population genetic variation has been noted for plants in areas with fewer dispersal barriers (Nassar et al. 2001, Williams and Arnold 2001), whereas a lessened rate of genetic divergence has been noted for prairie dogs (*Cynomys ludovicianus* [Ord]) along migration corridors (Roach et al. 2001). Conversely, populations that are isolated can be genetically dissimilar as a function of distance and isolation (Wolf et al. 2000). Thus, like species diversity, conservation of genetic diversity will require an explicit consideration of distance and its effect on other processes such as gene flow and migration.

An example of how genetic conservation is intricately tied to distance is the consideration of inbreeding and outbreeding depression. Limitation of breeding to the nearest individuals often results in inbreeding depression, as these individuals are often genetically related. However, if breeding occurs between genetically distant individuals, decreased fitness may also result due to the introduction of traits not adapted to local conditions (Ellstrand and

Elam 1993). Such outbreeding depression appears to occur in as much as 75% of plant species (Waser 1993). As genetic similarity is a function of spatial distance, the risk of outbreeding depression increases as individuals from distant populations are brought into close proximity (Fenster and Galloway 2000, Keller et al. 2000, Montalvo and Ellstrand 2001). Because behavioral barriers to outbreeding may be rare (Palmer and Edmands 2000), it is essential that the reintroduction, augmentation, and restoration of native species limit the contact between individuals from distant sources (Storfor 1998). Distance thresholds for outbreeding depression may even occur at extents contained within some rare plant populations (Quilichini et al. 2001). Thus, at a minimum, the movement of species for conservation purposes should not exceed more than a small fraction of the native range (White 1996).

MANAGEMENT AND RESTORATION ACTIVITIES

Because compositional and environmental similarity decreases with distance, even within the same habitat type, no single management strategy will be appropriate for all areas, and no single mix of species should be used for restoration. For instance, native prairies in the U.S. Midwest are typically managed with 3- to 4-year fire rotations throughout the region. However, a strong compositional gradient was originally present, with southern prairies being dominated by C₄ plants, and northern sites being dominated by C₃ plants (Stowe and Teeri 1978). As fire shifts the competitive balance in favor of C₄ taxa (Hill and Platt 1975), frequent fire intervals lead to an expansion of C₄ prairie plants at the expense of C₃ plants (Collins et al. 1998). Use of similar fire rotation rates throughout the Midwest may thus have the unintended consequence of homogenizing prairie composition by causing all prairies in the region to become dominated by similar proportions of C₄ taxa.

Restoration requires the selection of appropriate reference areas so that we can construct the restoration goal. One approach to selection of reference areas is to realize that relevance may decrease with

distance and that only nearby, undisturbed reference sites of similar habitat should be studied (White and Walker 1997). The farther such reference areas are from a given reserve, the less meaningful comparisons between them and managed or restored habitats are likely to be.

It has also become common for prairie seed retailers to create seed mixes of native taxa that have been tailored to specific environmental conditions (e.g., wet, mesic, and xeric prairie) based on principles of the first pillar of ecology, but not to geographic location. These mixes are subsequently marketed to public and private restoration projects over wide areas. By using the same seed mixes for sites over a broad geographic extent, restored prairies will ultimately be made more homogeneous in species composition and genetic structure than was originally true in the landscape. Standardized seed mixes may also promote the introduction of taxa beyond their normal range. For instance, the large purple coneflower (*Echinacea purpurea* [L.] Moench) is commonly included in prairie restoration projects throughout Wisconsin, even though the less showy pale purple coneflower (*Echinacea pallida* [Nutt.] Nutt.) is the only native member of that genus in the state. Keller et al. (2000) documented outbreeding depression caused by the use of commercial seed mixes of native plants over wide areas of Europe. We derive from this a general principle: species and genotypes used in restoration should be both ecologically appropriate (fit for the site, with site physical environment restored) and geographically appropriate (native, unlikely to cause outbreeding depression).

CONCLUSION

In this essay, we address conservation issues through a simple distance paradigm. We do so knowing that such surrogates are ideally replaced by empirical data. We realize that not all species are identical in their reaction to a given distance—indeed, the differences between species and landscapes are fascinating areas in studies of biological diversity. We also realize that what we have described consists of spatial pattern and that conservation is equally

concerned with long-term survival of diversity. Nonetheless, we suggest that biological processes and environmental patterns are constrained by distance and that distance matters, whether one is considering reserve design, organism movement, genetic conservation, or the relevance of given management or restoration activities.

Although both of ecology's pillars predict a correlation between similarity and distance, these sources of variation have different conservation implications. The first pillar suggests that composition varies with changes in the physical environment. In this context, the major challenge of conservation is the protection of sites that encompass a variety of environments. The implications of the second pillar are quite different. As limits on dispersal can lead to different species compositions in areas with identical physical conditions, focusing solely on the protection of environmental variation will not lead to the conservation of all species. Rather, the geographic context of habitats and populations must also be conserved. Formal consideration of distance-constrained processes and the patterns they cause thus will make conservation biologists better protectors of the Earth's natural heritage.

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