Importance of matrix habitats in maintaining biological diversity

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The theory of island biogeography has been the central tenet of conservation biology for several decades, a tenet in which continental landscapes are viewed islands of suitable habitat patches embedded in a matrix (i.e., surrounded by a sea) of unsuitable habitat. Patch size and isolation are predicted to be the critical variables in determining the efficacy of these habitat patches in preserving biological diversity, but this paradigm has never been broadly evaluated. In a recent issue of PNAS, Prugh *et al.* (1) analyze a large body of available data and make the unexpected discovery that the patch size and isolation are poor predictors of patch occupancy for the majority of species reviewed. This is an important result given the centrality of the patch size-isolation tenet to much of academic conservation biology and its wide application in conservation planning and resource management. In fact, the findings of Prugh *et al.* (1) are largely congruent with other analyses, such as the extensive assessment of fragmentation experiments by Debinski and Holt (2). Collectively these analyses raise significant questions about the merits of island biogeographic theory as a basis for conservation biology.

Issues with Island Biogeography

The weak relationship between patch occupancy and patch area and isolation should, perhaps, not be a surprise given two fundamental views that are basic to the island biogeography: the patch-matrix landscape paradigm and a black-and-white view of habitat suitability. In the classic patch-matrix (or island) model of landscape cover, habitat patches are defined from a human perspective and the matrix is considered nonhabitat. In fact, different elements of the biota are likely to differ in their perception of the same landscape (3). There are alternative conceptual models of landscapes available that are often better at predicting species responses to landscape change than the island model (4) and, also, in identifying what constitutes suitable habitat. Examples are the hierarchical patch dynamics model (5), the landscape variegation model (6), and species-specific gradient models (7, 8). Unfortunately, few ecologists and conservation biologists are aware of the richness of alternative conceptual landscape models (9).

Recognition of different models of, and perspectives on, landscapes is critically important because what humans define as a patch may differ significantly from the pattern that is perceived by another species. This will often blur the distinction between "habitat patches" and the surrounding "matrix" [*sensu* Forman (10)]; this, in turn, weakens the effect of patch size and isolation effects. Hence, it is not surprising that Prugh *et al.* (1) found that the type of land cover separating habitat patches most strongly affected sensitivity of species to patch area and isolation. Many of these species may be responding to the overall suitability of landscapes because the landscape matrix surrounding the habitat patches is actually functioning as breeding or foraging habitat or both, rather than simply defining and isolating the patches.

Matrix management matters because formal reserve systems will never cover more than a small fraction of the globe.

The preceding comments segue to the second, significantly limiting view of island biogeography—a dichotomous division of the world into habitat and not-habitat, regardless of the specific landscape model (11, 12). In fact, critical habitat for many species does not come at the level of the landscape but at the level of individual habitat features, which are not necessarily confined to any single patch type or landscape-level condition. Hence, conservation of biological diversity has to involve maintenance of habitat at multiple spatial scales, from the scale of centimeters to that of thousands of hectares. For example, critical habitat for some species may be the provision of an individual structure, such as a standing dead tree or a log on the forest floor, in an otherwise human-modified environment. For other species it may be the provision of a large natural reserve, with a diversity of habitat conditions.

Importance of the Matrix

We strongly agree with Prugh *et al.* (1) that resource management practices that maintain or improve the suitability of the matrix are fundamental to the conservation of biodiversity. Many studies have highlighted the importance of the matrix in agricultural areas (13), temperate forests (11), and tropical forests (e.g., 14 and 15), such as through work on countryside biogeography (16).

Many conservation biologists have largely overlooked the pivotal importance of the matrix and the habitat that it provides for enhanced biodiversity conservation—or could provide, if it were managed differently (11, 12). Rather, most conservation biologists have focused on such topics as retention of large patches of undisturbed habitat as reserves and intact habitat corridors as the primary strategy for providing for connectivity. Indeed, some biologists still assert that reserves are the only way to conserve biological diversity. In fact, approaches to matrix management have major implications for such fundamental tenets of conservation biology as reserve design, metapopulation processes (17), extinction proneness (15), and connectivity and species persistence in human-modified landscapes (11).

Matrix management matters because formal reserve systems will never cover more than a small fraction of the globe; human-modified land—the matrix—overwhelmingly dominates not just forests (11) but all of the world's terrestrial ecosystems (18). Of course, our freshwater ecosystems are also embedded in this same terrestrial landscape along with their constituent biodiversity (11).

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Hence, the future of the vast majority of the earth's species will depend on how the matrix is managed—including not only the human-perceived habitat patches, but also the extensive areas that surround them.

The analysis of effects of matrix type by Prugh *et al.* (1) underlines the importance of the matrix in conservation; we would have liked for she and her colleagues to report further on this analysis. As stated they ". . . did not expect to find consistent effects of matrix type across species" but they most certainly did. As forest ecologists, we were particularly interested in their finding that clearcutting had the strongest isolating effect among the 4 categories of matrix types, including urban matrices. It provides confirmation of the extremely hostile and unnatural state created by clearcutting. This strongly supports the need for timber harvesting practices that provide more favorable environments for survival and movement of biota, a movement that is well underway in modern forest management (19, 20).

Conclusion

We agree strongly with the conclusion of Prugh *et al.* (1) that the ". . . patch/nonpatch dichotomy appears to be a gross oversimplification for many species in fragmented landscapes." Conservation biologists and resource managers need to give major attention to the matrix if programs to conserve the world's biological diversity are to succeed. This includes recognizing and facilitating the multiple roles of the matrix in management programs, including provision of habitat and facilitation of movement. As Prugh and her colleagues conclude in their abstract (1), "Improving matrix quality may lead to higher conservation returns than manipulating the size and configuration of remnant patches for many of the species that persist in the aftermath of habitat destruction." We agree.

Conservation research and management programs must seriously reflect on the implications of this important analysis (1). Managers must realize that conservation of biological diversity is *not* primarily a set-aside issue that can be dealt with by reserving or modifying management on 10 or 20% of their landscape; rather, it is a pervasive issue that must be considered on every acre of land that they manage. Similarly, conservation scientists must reconsider the focus of their scientific endeavors if their goal is, truly, to retain the majority of the world's biodiversity. For example, what key questions need to be empirically addressed to flesh out the matrix-based conservation biology paradigm? We also think some introspection by conservation scientists may be in order about why it has taken so long for academic conservation biology to recognize and accept the importance of matrix.

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