
Landscape conservation: a new paradigm for the conservation of biodiversity

We are in the midst of one of the greatest ecological disasters ever to befall this planet. Species are vanishing worldwide at a rate rivaling the mass extinction events chronicled in the geological record, a rate which exceeds the “normal” or expected rate of extinction by several orders of magnitude (Wilson, 1988). Unlike previous mass extinctions, however, this one has been precipitated by a single species, *Homo sapiens*. It is no coincidence that the global biodiversity crisis occurs at a time when landscapes are being transformed at a rate unprecedented in human history. Humans have transformed up to 50% of the land surface on the planet, such that no landscape (or “aquascape”) remains untouched by the direct or indirect effects of human activities (Vitousek *et al.*, 1997). Habitat destruction, in the form of outright loss, degradation, and fragmentation of habitat, is the leading cause of the current extinction crisis (Wilcove *et al.*, 1998). Humans are the primary drivers of landscape change, and thus the current ecological crisis is really a cultural one (Naveh, 1995; Nassauer, this volume, Chapter 27). An understanding of the factors affecting land-use decisions, which involve cultural, political, and socioeconomic dimensions, must be integrated with the ecological consequences of landscape transformation if a full rendering of the biodiversity crisis is to be had and the crisis averted. This will require a holistic approach that transcends disciplines.

Conservation biology and landscape ecology are each touted as being newly emergent, holistic, problem-solving disciplines that transcend the traditional boundaries between science and policy, theory and practice, society and nature. While the historical and philosophical roots of both disciplines date back centuries, conservation biology and landscape ecology were formalized as scientific disciplines relatively recently, in the early 1980s. On the surface, conservation biology and landscape ecology appear to address both sides of the biodiversity crisis. Landscape ecology originated as the study of

the ways in which human systems affect land-use decisions and from a need to direct landscape planning at a regional scale (Turner *et al.*, 2001). Conservation biology is often defined as “the science of scarcity and diversity” and is concerned with halting and reversing the alarming loss of biodiversity (Soulé, 1986). Clearly, conservation strategies will have to be implemented within the context of human-dominated landscapes.

Landscape ecology and conservation biology should thus be able to tackle the major land-use and conservation issues that are at the core of the global biodiversity crisis. Why, then, has landscape ecology failed to fulfill its “obligation” (Hobbs, 1997) to provide the concepts and techniques to tackle these issues? If landscape transformation is acknowledged to be the primary driving force behind the recent mass extinctions, then why does the perception exist among conservation biologists that landscape ecology has little to offer in this regard (Hobbs, 1997)?

A mission for landscape ecology

Landscape ecology has long suffered from an “identity crisis” (Hobbs, 1994). While this is perhaps expected of any discipline in its adolescence, conservation biology was able to articulate a mission and statement of purpose from infancy. In part, this was due to the fact that it was conceived in response to a crisis, but also because conservation biologists were required to explain early on how their new discipline differed from existing fields such as wildlife biology. The response was that none of the resource management fields, which generally focused on the management of economically important species, was comprehensive enough to deal with the global biodiversity crisis (Edwards, 1989; Jensen and Krausman, 1993; Bunnell and Dupuis, 1995). Conservation biology also promised to provide a theoretical foundation required for developing the scientific framework and guiding principles necessary for the management of complex systems (Simberloff, 1988; With, 1997a).

In contrast, landscape ecology has not been expressly “crisis-driven” or “mission-oriented” in either its origin or subsequent development. Thus, it has lacked the focus and disciplinary cohesion that guided the development of conservation biology. There has never been a true synthesis of the disparate scientific and design professions that make up the nexus that is landscape ecology, and the discipline itself has evolved independently, in different directions, on different continents (Wiens, 1997). Little wonder, then, that landscape ecology has been viewed as lacking a comprehensive scientific framework for the analysis, planning, and management of landscapes. The development of this scientific framework was one of the goals of the 1998 mission statement of the International Association for Landscape Ecology

(IALE, 1998). It has been tackled in recent texts devoted to identifying the scientific basis and underlying landscape ecological principles for resource and land management (e.g., Dale and Haeuber, 2001; Liu and Taylor, 2002).

Although the synthesis must come from within, it also needs to be developed externally by establishing stronger linkages with other disciplines that would benefit from the application of landscape ecological principles. Landscape ecologists have done a poor job in the past of effectively communicating to researchers and practitioners outside the discipline what landscape ecology is all about, what is unique about it, and what it has to offer above and beyond approaches developed in other resource-management disciplines. In the present context, this involves examining how landscape ecology can contribute to the resolution of the biodiversity crisis, by demonstrating how landscape ecology can be applied to problems in land use and conservation.

How can landscape ecology contribute to conservation biology?

Landscape ecology can contribute to the resolution or mitigation of the biodiversity crisis in a number of ways.

The adoption of a landscape perspective in conservation biology

There is a growing consensus that the landscape is the relevant scale at which to manage biodiversity (e.g., Noss, 1983; Salwasser, 1991; Petit *et al.*, 1995; Gutzwiller, 2002; Margules, this volume, Chapter 23). Conservation strategies need to be implemented at broad scales if they are to be effective. This follows from the recent shift in management focus away from individual species and toward entire ecosystems, which necessitates a broader-scale perspective (see below). In addition, nature reserves cannot be viewed in isolation of their landscape context. Human land-use activities in the surrounding matrix affect processes occurring within the reserve, and thus the ultimate success of the reserve in protecting biodiversity depends upon managing the entire landscape (Wiens, 1996; Jongman, this volume, Chapter 31).

Facilitating the shift from species to systems management in conservation

Conservation biology is undergoing a paradigm shift from single-species management to ecosystem management. Ecosystem management emphasizes the importance of maintaining the functional relationships among components of the system, and not just the components themselves

(Christensen *et al.*, 1996). This emphasis on functional relationships ultimately requires an understanding of how landscape structure affects the flows of energy, matter, or individuals across heterogeneous land mosaics. Landscape ecology focuses on how spatial patterns affect ecological flows (Turner, 1989). Although the description and analysis of landscape structure dominated much of the early research activity in landscape ecology (e.g., Turner and Gardner, 1991), there is now more emphasis being placed on the study of landscape function, particularly in regard to issues of flows among boundaries (e.g., Hansen and di Castri, 1992; Wiens *et al.*, 1993) and overall landscape connectivity.

Providing a landscape mosaic perspective in assessing connectivity

Connectivity is a dominant theme in both landscape ecology and conservation biology. In conservation biology, connectivity is an essential component of ecosystem integrity, reserve design, and metapopulation dynamics (Noss, 1991). While the importance of maintaining the functional connectivity of systems is often recognized, this is often interpreted literally to mean maintaining structural connectivity (e.g., actual physical linkages among system components). For example, habitat corridors have been suggested as an obvious means of connecting isolated reserves or habitat patches. Corridors have become a controversial issue in conservation biology, however (Hobbs, 1992; Simberloff *et al.*, 1992; Mann and Plummer, 1995). There is limited empirical evidence regarding the efficacy of corridors and the costs may outweigh the benefits if corridors also facilitate the spread of disease or predators (e.g., Simberloff and Cox, 1987; Hess, 1994). Structural connectivity is thus no guarantee of functional connectivity.

Because landscape ecology focuses on ecological flows across landscapes, it has provided a new paradigm for thinking about landscape connectivity. Landscapes are not viewed simply as patches embedded within an inhospitable matrix, but as integrated mosaics of different habitat types, land uses, and other structural features that may facilitate or impede movement to varying degrees across the landscape (Wiens, 1997; With, 1999). The landscape-mosaic approach emphasizes the importance of defining connectivity from the perspective of the species or process of interest (e.g., Taylor *et al.*, 1993; With *et al.*, 1997). In other words, connectivity is an emergent property of landscapes, resulting from an interaction between the scale at which the process or species operates and the scale of the landscape pattern. For example, species may possess different perceptions as to whether a given landscape is connected depending upon their ability or willingness to cross gaps of unsuitable habitat (Dale *et al.*, 1994; With, 1999). Dispersal or

gap-crossing abilities dictate the scales at which organisms interact with landscape pattern, and the gap or patch structure of a landscape is a function of the scales of disturbance or habitat destruction, whether natural or anthropogenic.

How can we quantify connectivity or predict when landscapes become disconnected? A number of approaches for quantifying landscape connectivity have been developed (Tischendorf and Fahrig, 2000a, 2000b; Urban and Keitt, 2001). For example, applications of percolation theory, in the form of neutral landscape models, were developed within the discipline of landscape ecology and have provided a means of modeling ecological flows across structured landscapes (Gardner *et al.*, 1987; Gardner and O'Neill, 1991). Neutral landscape models have been used to quantify when landscapes become disconnected, and thus when the functional integrity of systems may become compromised (With, 1997b; With and King, 1997; With, 2002). Landscape connectivity is predicted to be disrupted abruptly, as a threshold phenomenon, which may have dire consequences for biodiversity. Critical thresholds in landscape connectivity may not coincide with ecological thresholds, such as in dispersal success or population persistence, however (e.g., With and Crist, 1995; With and King, 1999a, 1999b). Nevertheless, landscape thresholds may precipitate other ecological thresholds, setting off a "threshold cascade." Evidence for this has been found in the relationship between landscape thresholds and thresholds in the search efficiency of biocontrol agents (biocontrol thresholds; With *et al.*, 2002). This has implications for the field of conservation biological control, which seeks to manage landscapes so as to enhance the efficacy of natural enemies in controlling pest outbreaks (Barbosa, 1998). Predicting thresholds in the ecological consequences of habitat loss and fragmentation has thus been identified as a major unsolved problem facing conservation biologists (Pulliam and Dunning, 1997).

Developing a general landscape ecological theory

Although conservation biology is viewed as having a strong theoretical framework, there has been very little theory developed specifically for conservation (With, 1997a). Conservation biology has borrowed heavily from the theoretical foundations of its parent disciplines (population genetics, population and community ecology; Simberloff, 1988). Because this theory was not developed with conservation applications in mind, however, it may contain restrictive assumptions that ultimately limit its utility for management or result in its misuse if such constraints are ignored. Some conservation biologists therefore discredit the use of theory in conservation, failing to recognize

that the problem lies not so much with the theory itself as with the misapplication of theory (Doak and Mills, 1994). Furthermore, much of the ecological theory that is used in conservation biology is patch-based (e.g., metapopulation theory, theory of island biogeography), which ignores the spatial complexity of real landscapes and thus offers little insight into how scenarios of land-use change might affect population persistence in managed landscapes. Geographical Information Systems (GIS) have become powerful tools in both landscape ecology and conservation biology. For example, population simulation models linked with landscape maps in a GIS can be used to evaluate extinction risk for species under different land-management plans or scenarios of land-use change (e.g., Dunning *et al.*, 1995). Such “spatially realistic models” tend to be site- or species-specific, however, and thus are not able to provide a general landscape theory.

Although landscape ecology has been criticized for lacking a theoretical foundation (Wiens, 1992), landscape ecologists have at least been able to build upon general systems theory which has given rise to hierarchy theory (Allen and Starr, 1982; O'Neill *et al.*, 1986; O'Neill, this volume, Chapter 3). This could be a useful framework for the management of complex integrated systems now targeted in conservation, particularly in contributing to an understanding of the extent to which phenomena at a given scale are simultaneously the product of processes operating at finer scales and system constraints at broader scales. In addition, there is an urgent need for a theoretical framework for assessing the impacts of landscape transformation on biodiversity. Neutral landscape models, coupled with computer simulation models of dispersal, gene flow, population dynamics, or species interactions, provide one example of how a general landscape theory might be developed (With and Crist, 1995; With, 1997b; With and King, 1999b, 2001; With *et al.*, 2002).

Using landscape design principles to guide conservation efforts

Reserve design is still primarily governed by principles derived (supposedly) from the theory of island biogeography – e.g., the debate over the advantages of “single large or several small” (SLOSS) reserves. As discussed previously, reserve systems must be developed within the context of human land-use activities. This is illustrated, for example, by UNESCO’s Man and the Biosphere reserve model, in which strictly protected core areas are surrounded by buffer zones and transitional zones that allow varying degrees of research, restoration, resource extraction, recreation, and human settlement. Regional reserve networks take this concept a step further by adopting a landscape perspective that emphasizes the importance of maintaining functional connectivity (or at least structural connectivity) by the creation of

broad corridors to facilitate animal movement among reserves (Noss, 1983).

Deciding where to establish reserves is another problem in landscape reserve design, which has been addressed using gap analysis to identify current gaps in the protection of biodiversity at a regional level (Scott *et al.*, 1993). Overlays of existing reserves with the distribution of species across the landscape may reveal "hotspots" of species diversity that are currently unprotected and thus vulnerable to future landscape development and human depredations. Gap analysis also provides a means of prioritizing conservation efforts and directing land acquisition and future land-use activities. What it fails to take into account is whether such areas are actually capable of supporting viable populations of these species. Species richness may be high on a landscape because the landscape is productive and therefore capable of sustaining viable populations of many species. Alternatively, high species richness may arise from the juxtaposition of various habitat types or land uses (i.e., high habitat diversity). Populations may not be viable (self-sustaining) within some or even most of these different habitats, yet persist there owing to immigration from elsewhere. Gap analysis does not discriminate between these two alternatives (Maurer, 1999).

Finally, the mitigation of land-use activities for the conservation or restoration of biodiversity can only be achieved through careful landscape planning and management (Hobbs, this volume, Chapter 22; Margules, this volume, Chapter 23). Landscape ecologists need to become more involved as active partners in the development of conservation strategies to ensure that these will be based on sound land-management and design principles.

Landscape conservation: the new paradigm?

The landscape approach to conservation involves much more than the adoption of a broader-scale, regional perspective in species or ecosystem management. One of the hallmarks or distinguishing characteristics of landscape ecology is its emphasis on how spatial pattern affects ecological processes. Subsequently, landscape ecology can be profitably applied at any scale. For example, connectivity must be assessed and managed across a range of scales, from the spatial patterning of resources or habitat required to fulfill an individual's minimum area requirements, to populations within a metapopulation, to reserves in a regional network. Landscape ecology also explicitly addresses the importance of landscape context and recognizes the mosaic nature of landscape structure. It thus affords a new perspective on connectivity and for understanding how landscape structure affects ecological processes, as well as the consequences of human land-use activities on the structural and

functional integrity of terrestrial and aquatic ecosystems. Although theory development has not been a particularly vigorous activity in landscape ecology, the synthesis of neutral landscape models, based on percolation theory with ecological theory, may help contribute to a general landscape theory. This is required if a predictive science of the ecological consequences of landscape transformation is to emerge. Landscape ecology possesses the design principles necessary for effective land management and planning, and thus could play an active role in directing land-use activities and reserve design so as to benefit conservation and restoration efforts. The goal for the future should be to establish “landscape conservation” as the new paradigm for the conservation of biodiversity – not for the conservation of landscapes per se, but for conservation that is founded on landscape ecological principles (Gutzwiller, 2002).

Acknowledgments

I thank John Wiens for inviting me to contribute to this volume, thereby giving me the opportunity to explore how landscape ecological principles can contribute to the conservation of biodiversity. My research on applications of landscape ecology for the conservation of biodiversity has been supported by past grants from the National Science Foundation, and most recently by a STAR grant from the Environmental Protection Agency (R82-9001).

References

- Allen, T. F. H. and Starr, T. B. (1982). *Hierarchy: Perspectives for Ecological Complexity*. Chicago, IL: University of Chicago Press.
- Barbosa, P. (1998). *Conservation Biological Control*. San Diego, CA: Academic Press.
- Bunnell, F. L. and Dupuis L. A. (1995). Conservation biology’s literature revisited: wine or vinaigrette? *Wildlife Society Bulletin*, 23, 56–62.
- Christensen, N. L., Bartuska, A., Brown, J. H., et al. (1996). The report of the Ecological Society of America committee on the scientific basis for ecosystem management. *Ecological Applications*, 6, 665–691.
- Dale, V. H. and Haeuber R. A. (2001). *Applying Ecological Principles to Land Management*. New York, NY: Springer.
- Dale, V. H., Pearson, S. M., Oferman, H. L., and O’Neill, R. V. (1994). Relating patterns of land-use change to faunal biodiversity in the central Amazon. *Conservation Biology*, 8, 1027–1036.
- Doak, D. F. and Mills, L. S. (1994). A useful role for theory in conservation. *Ecology*, 75, 615–626.
- Dunning, J. B., Stewart, D. J., Danielson, B. J., et al. (1995). Spatially explicit population models: current forms and future uses. *Ecological Applications*, 5, 3–11.
- Edwards, T. C. Jr. 1989. The Wildlife Society and the Society for Conservation Biology: strange but unwilling bedfellows. *Wildlife Society Bulletin*, 17, 340–343.
- Gardner, R. H. and O’Neill, R. V. (1991). Pattern, process, and predictability: the use of neutral models for landscape analysis. In *Quantitative Methods in Landscape Ecology*, ed. M. G. Turner and R. H. Gardner. New York, NY: Springer, pp. 289–307.

- Gardner, R. H., Milne, B. T., Turner M. G., and O'Neill, R. V. (1987). Neutral models for the analysis of broad-scale landscape pattern. *Landscape Ecology*, 1, 19–28.
- Gatzwiller, K. J. (ed.) (2002). *Applying Landscape Ecology in Biological Conservation*. New York, NY: Springer.
- Hansen, A. J. and di Castri, F. (eds.) (1992). *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows*. New York: Springer.
- Hess, G. R. (1994). Conservation corridors and contagious disease: a cautionary note. *Conservation Biology*, 8, 256–262.
- Hobbs, R. J. (1992). The role of corridors in conservation: solution or bandwagon? *Trends in Ecology and Evolution*, 7, 389–392.
- Hobbs, R. (1994). Landscape ecology and conservation: moving from description to application. *Pacific Conservation Biology*, 1, 170–176.
- Hobbs, R. (1997). Future landscapes and the future of landscape ecology. *Landscape and Urban Planning*, 37, 1–9.
- IALE (1998). IALE mission statement. *IALE Bulletin*, 16, 1.
- Jensen, M. N. and Krausman, P. R. (1993). Conservation biology's literature: new wine or just a new bottle? *Wildlife Society Bulletin*, 21, 199–203.
- Liu, J. and Taylor, W. W. (2002). *Integrating Landscape Ecology into Natural Resource Management*. Cambridge: Cambridge University Press.
- Mann, C. C. and Plummer, M. L. (1995). Are wildlife corridors the right path? *Science*, 270, 1428–1430.
- Maurer, B. A. (1999). *Untangling Ecological Complexity: The Macroscopic Perspective*. Chicago, IL: University of Chicago Press.
- Naveh, Z. (1995). Interactions of landscapes and cultures. *Landscape and Urban Planning*, 32, 43–54.
- Noss, R. (1983). A regional landscape approach to maintain diversity. *BioScience*, 33, 700–706.
- Noss, R. F. (1991). Landscape connectivity: different functions at different scales. In *Landscape Linkages and Biodiversity*, ed. W. Hudson. Washington, DC: Island Press, pp. 27–39.
- O'Neill, R. V., DeAngelis, D. L., Waide, J. B., and Allen, T. F. H. (1986). *A Hierarchical Concept of Ecosystems*. Princeton, NJ: Princeton University Press.
- Petit, L. J., Petit, D. R., and Martin, T. E. (1995). Landscape-level management of migratory birds: looking past the trees to see the forest. *Wildlife Society Bulletin*, 23, 420–429.
- Pulliam, H. R. and Dunning, J. B. (1997). Demographic processes: population dynamics on heterogeneous landscapes. In *Principles of Conservation Biology*, 2nd edn, ed. G. K. Meffe and C. R. Carroll. Sunderland, MA: Sinauer, pp. 203–232.
- Salwasser, H. (1991). New perspectives for sustaining diversity in US national forest ecosystems. *Conservation Biology*, 5, 567–569.
- Scott, J. M., Davis, F., Csutin, B. et al. (1993). Gap analysis: a geographic approach to protection of biological diversity. *Wildlife Monographs*, 123.
- Simberloff, D. (1988). The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics*, 19, 473–511.
- Simberloff, D. and Cox, J. (1987). Consequences and costs of conservation corridors. *Conservation Biology*, 1, 63–71.
- Simberloff, D., Farr, J. A., Cox, J., and Mehlman, D. W. (1992). Movement corridors: conservation bargains or poor investments? *Conservation Biology*, 6, 493–504.
- Soulé, M. E. (ed.) (1986). *Conservation Biology: the Science of Scarcity and Diversity*. Sunderland, MA: Sinauer.
- Taylor, P. D., Fahrig, L., Henein, K. and Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos*, 68, 571–573.
- Tischendorf, L. and Fahrig, L. (2000a). On the usage and measurement of landscape connectivity. *Oikos*, 90, 7–19.
- Tischendorf, L. and Fahrig, L. (2000b). How should we measure landscape connectivity? *Landscape Ecology*, 15, 633–641.
- Turner, M. G. (1989). Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics*, 20, 171–197.
- Turner, M. G. and Gardner, R. H. (eds.) (1991). *Quantitative Methods in Landscape Ecology*. New York, NY: Springer.

- Turner, M. G., Gardner, R. H., and O'Neill, R. V. (2001). *Landscape Ecology in Theory and Practice: Pattern and Process*. New York, NY: Springer.
- Urban, D. and Keitt, T. (2001). Landscape connectivity: a graph-theoretic perspective. *Ecology*, 82, 1205–1218.
- Vitousek, P. M., Mooney, H. A., Lubchenco, J., and Melillo, J. M. (1997). Human domination of Earth's ecosystems. *Science*, 277, 494–499.
- Wiens, J. A. (1992). What is landscape ecology, really? *Landscape Ecology*, 7, 149–150.
- Wiens, J. A. (1996). Wildlife in patchy environments: metapopulations, mosaics, and management. In *Metapopulations and Conservation*, ed. D. R. McCullough. Washington, DC: Island Press, pp. 53–84.
- Wiens, J. A. (1997). Metapopulation dynamics and landscape ecology. In *Metapopulation Biology: Ecology, Genetics, and Evolution*, ed. I. A. Hanski and M. E. Gilpin. San Diego, CA: Academic Press, pp. 43–62.
- Wiens, J. A., Stenseth, N. C., Van Horne, B., and Ims, R. A. (1993). Ecological mechanisms and landscape ecology. *Oikos*, 66, 369–380.
- Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A., and Lossos, E. (1998). Assessing the relative importance of habitat destruction, alien species, pollution, over-exploitation, and disease. *BioScience*, 48, 607–616.
- Wilson, E. O. (1988). *Biodiversity*. Washington, DC: National Academy Press.
- With, K. A. (1997a). The theory of conservation biology. *Conservation Biology*, 11, 1436–1440.
- With, K. A. (1997b). The application of neutral landscape models in conservation biology. *Conservation Biology*, 11, 1069–1080.
- With, K. A. (1999). Is landscape connectivity necessary and sufficient for wildlife management? In *Forest Fragmentation: Wildlife and Management Implications*, ed. J. A. Rochelle, L. A. Lehmann, and J. Wisniewski. Leiden: Brill, pp. 97–115.
- With, K. A. (2002). Using percolation theory to assess landscape connectivity and effects of habitat fragmentation. In *Applying Landscape Ecology in Biological Conservation*, ed. K. J. Gutzwiller. New York, NY: Springer, pp. 105–130.
- With, K. A. and Crist, T. O. (1995). Critical thresholds in species' responses to landscape structure. *Ecology*, 76, 2446–2459.
- With, K. A. and King, A. W. (1997). The use and misuse of neutral landscape models in ecology. *Oikos*, 79, 219–229.
- With, K. A. and King, A. W. (1999a). Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. *Landscape Ecology*, 14, 73–82.
- With, K. A. and King, A. W. (1999b). Extinction thresholds for species in fractal landscapes. *Conservation Biology*, 13, 314–326.
- With, K. A. and King, A. W. (2001). Analysis of landscape sources and sinks: the effect of spatial pattern on avian demography. *Biological Conservation*, 100, 75–88.
- With, K. A., Gardner, R. H., and Turner, M. G. (1997). Landscape connectivity and population distributions in heterogeneous environments. *Oikos*, 78, 151–169.
- With, K. A., Pavuk, D. M., Worchuck, J. L., Oates, R. K., and Fisher, J. L. (2002). Threshold effects of landscape structure on biological control in agroecosystems. *Ecological Applications*, 12, 52–65.