

MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

The use and misuse of neutral landscape models in ecology

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Neutral landscape models (NLMs) were developed from percolation theory nearly a decade ago. Since then, the original random percolation maps have undergone adaptive radiation and NLMs now include a diverse array of spatially explicit models based on theoretical distributions derived from fractal geometry and spectral synthesis. The purpose of NLMs is to provide null models of landscape structure as a baseline for comparison with real landscape patterns, or for evaluating the effects of landscape structure on ecological processes. As the use of NLMs has expanded beyond the domain of theoretical landscape ecology to applications in other areas of ecology, there is an increased risk that NLMs will be used inappropriately, or that their function will be misunderstood or misinterpreted. NLMs are being subjected to the same general criticisms levied against null models in other areas of ecology. For this reason, we clarify the purpose of NLMs, review the contributions of NLMs to ecology, and evaluate the appropriate use of NLMs in ecological research. NLMs have already made several contributions to ecology: (1) development of spatial indices to describe landscape patterns; (2) prediction of critical thresholds in ecological phenomena; (3) definition of landscape connectivity; (4) development of “species’ perceptions” of landscape structure; (5) provision of a general model of spatial complexity; and (6) determination of the ecological consequences of spatial heterogeneity. In the future, emphasis on NLMs should shift from theoretical development to application and model testing.

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Neutral landscape models (Gardner et al. 1987) are neutral models of landscape pattern in the tradition of null or neutral models in ecology (Caswell 1976, Strong 1980, Connor and Simberloff 1986, Nitecki and Hoffman 1987, Gotelli and Graves 1996). Null models are valuable tools in the investigation of ecological systems. Recent statements by Schumaker (1996) that “the use

of artificial, computer generated landscapes” is inappropriate, or that “the use of computer generated landscapes could both inflate the value of poor predictors of ecological quality and diminish the power of useful indices” are misinformed and misleading. These views are characteristic of a more general misunderstanding of neutral landscape models (NLMs), one shared with

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null models in other areas of ecology (Gotelli and Graves 1996).

Neutral landscape models were introduced a decade ago and have played a major role in the development of theoretical landscape ecology (Turner et al. 1989, Gardner and O'Neill 1991). More recently, NLMs, and the tools and approaches developed alongside them, have found their way into applications outside the domain of theoretical landscape ecology (Lavorel et al. 1993, Andr en 1994, Lavorel et al. 1994, With and Crist 1995, Gustafson and Gardner 1996, Schumaker 1996, Wiens et al. 1997, With et al. 1997). The expanded use of NLMs increases the risk that they will suffer the same misunderstandings and misuse that have plagued the use of neutral models in other areas of ecology. In response, we provide a brief overview of NLMs, highlight their contributions to ecology, and emphasize what NLMs were designed to do and thus how they might be profitably employed in the investigation of the effects of spatial pattern on ecological processes.

The history of neutral landscape models

Neutral landscape models as null models

A neutral model is one used to generate an expected pattern in the absence of specific processes (Caswell 1976, Nitecki and Hoffman 1987, Wimsatt 1987), which is then tested against observation or against the predictions of alternative models that explicitly include the processes in question. The neutral model provides a "scale of reference" (Caswell 1976) or a baseline (Wimsatt 1987) for evaluating the effect of processes that are not in the model. The nearly synonymous null model (Harvey et al. 1983, Colwell and Winkler 1984, Gotelli and Graves 1996) emphasizes the corollary with null hypotheses; however, it also suggests randomness, and neutral models need not be random models (Caswell 1976). Accordingly, we prefer the term neutral model. The distinction between null and neutral model is subtle at best; in practice, the terms neutral model and null model are essentially interchangeable (Nitecki and Hoffman 1987). Examples of neutral or null models in ecology, especially community ecology and biogeography, can be found in Caswell (1976), Harvey et al. (1983), Strong et al. (1984), and Gotelli and Graves (1996).

Arguing that the relationship between pattern and process on real landscapes can be rigorously tested only if the response expected in the absence of the specific landscape pattern is known, Gardner et al. (1987) drew upon percolation theory (Stauffer and Aharony 1991) to develop neutral models of landscape pattern. The expected patterns are neutral to the physical and biotic processes that may shape real landscapes, such as topography, disturbance history, and ecological impacts

(Gardner et al. 1987, Gardner and O'Neill 1991). As such, they provide a basis for statistical tests of observed landscape patterns, or those generated by explicit models and hypotheses of how processes affect landscape pattern. Because experiments involving large landscapes are intractable, landscape ecologists must instead rely upon computer simulations based on NLMs to develop and test hypotheses. Replication at the landscape scale is difficult, if not impossible, and studies of landscape processes often focus on a single landscape. It is possible to generate many replicate NLMs that have the same statistical properties, however, and determine the expected relationship between a given ecological process and spatial complexity. By comparing actual landscapes to NLMs, one can determine statistically whether the observed pattern differs from theoretical expectations.

The general purpose of NLMs is twofold: (1) to determine the extent to which structural properties of landscapes (e.g., patch size and shape, amount of edge habitat, connectivity) deviate from some theoretical spatial distribution (e.g., random), and (2) to predict how ecological processes, such as animal movement, seed dispersal, gene flow, or fire spread, are affected by a known spatial structure. The first uses NLMs to investigate how processes affect landscape pattern (e.g., Gardner et al. 1987). The second uses NLMs to investigate the effects of landscape structure on ecological processes.

A phylogeny of neutral landscape models

The first generation of NLMs bore the legacy of percolation theory and were simple random distributions of habitat across a two-dimensional grid (Fig. 1). When habitat is abundant, the landscape is dominated by a single, continuous cluster – the "percolating cluster" – that spans the entire landscape (i.e., the landscape is "connected"). As habitat abundance (p) declines, a critical threshold (p_c) occurs in which the landscape is abruptly fragmented into small, isolated clusters. Exactly where this threshold occurs (the exact value of p_c) depends upon a number of factors such as lattice geometry, the underlying spatial distribution, and how the process of diffusion through the lattice is modeled (Plotnick and Gardner 1993). Random binary habitat maps generated by percolation models have been, and continue to be, important NLMs (Appendix). Strictly speaking, percolation theory deals only with binary lattices (i.e., habitat vs non-habitat), but percolation maps can be modified to include more than two states or cell types. The result is a NLM for heterogeneous landscapes with multiple randomly distributed habitat types (e.g., With and Crist 1995, With et al. 1997).

Not all NLMs are random maps. Spatial contagion was introduced early into percolation maps by adjust-

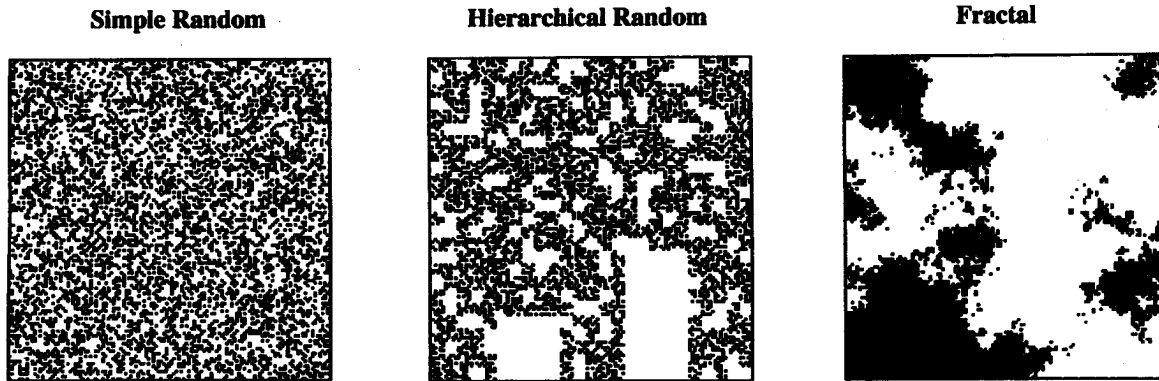


Fig. 1. Three generations of neutral landscape models. Each landscape map contains the same proportion of habitat ($p = 0.33$, shaded cells). The hierarchical random landscape was produced by adjusting the proportion of habitat available at three different levels ($p_1 = 0.85$, $p_2 = 0.75$, $p_3 = 0.50$; $p_1 \times p_2 \times p_3 = 0.33$).

ing the correlation among sites (e.g., O'Neill et al. 1988a, Gardner and O'Neill 1991, Gustafson and Parker 1992). The next speciation event in the evolution of NLMs, however, was the result of a hybridization of percolation maps and fractal algorithms. The second generation of NLMs were hierarchical random landscapes, generated by fractal curdling (Mandelbrot 1983), in which habitat is randomly distributed within nested map layers to reflect the hierarchical patch structure observed in real landscape patterns (O'Neill et al. 1992, Lavorel et al. 1993; Fig. 1). Although each level in the nested hierarchical maps has the same properties of any simple random map, the global properties of the entire landscape (e.g., connectivity) emerge as the aggregate result of interactions across all levels. Complex landscape patterns can be generated by varying the relative habitat abundance across levels, and by constraining habitat abundance at either fine or broad scales (Lavorel et al. 1995, Pearson et al. 1996).

Another fractal algorithm, referred to as "midpoint displacement" (Saupe 1988), has been used to generate the third generation of neutral landscapes whose surfaces exhibit continuous environmental variability (Palmer 1992). These continuous surfaces can be sectioned to produce patchy landscapes that bear a striking resemblance to real landscape patterns (Keitt and Johnson 1995, Moloney and Levin 1996, With et al. 1997; Fig. 1). The advantage of fractal landscapes is that both the abundance and spatial contagion (clumping) of habitat can be easily and systematically varied across a range of parameter states. This makes it possible to tease apart the ecological consequences of habitat loss (change in p) from those resulting from habitat fragmentation (the contagion factor).

The speciation of NLMs is really only limited by imagination. Other spatial distributions that have been employed as NLMs include regular point patterns (Adler and Nuernberger 1994), checkerboard and sinusoidal distributions (Milne 1992), and gradient percola-

tion maps (Keitt and Johnson 1995, Milne et al. 1996). The latter have been used to model environmental gradients or "ecotones". An exciting new synthesis applies spectral methods (e.g., Fourier transforms, sine and cosine functions, wavelet transforms) to generate neutral landscapes (T. H. Keitt unpubl.). Spectral representation of landscapes provides an underlying mathematical framework for understanding the relationships among various neutral models (e.g., percolation maps, hierarchical random, fractal landscapes), and may thus contribute to the development of a generalized model of neutral landscapes.

The contribution of neutral landscape models to ecology

Beyond their general contribution to the development of theoretical landscape ecology, NLMs have made a number of specific contributions to ecology.

1) Development of spatial indices to describe landscape patterns

Quantitative methods that link spatial patterns and ecological processes at broad spatial scales are needed in basic ecological research and in applied management problems (Turner and Gardner 1991). A plethora of spatial indices and statistics has been developed to describe landscape patterns (e.g., O'Neill et al. 1988b, Turner and Gardner 1991, Gustafson and Parker 1992, Plotnick et al. 1993). The performance of spatial indices on neutral landscapes has been used to help interpret the significance of these indices when calculated on real landscapes, by separating the effects of topography, natural disturbances and human activities from the expected behavior of the indices in the absence of such effects (Gardner and O'Neill 1991, Gustafson and Parker 1992, Gardner et al. 1993, Schumaker 1996). In

this sense, neutral landscapes provide a statistical benchmark for comparisons with real landscapes, a comparison facilitated by the grid-based structure common to both NLMs and raster-based GIS data sets.

2) Prediction of critical thresholds

Many ecological processes may exhibit critical behavior (e.g., Green 1994). By definition, a critical threshold is "the point at which there is an abrupt change in a quality, property, or phenomenon" (Turner and Gardner 1991: 7). At the critical threshold there is a fundamental change in the pattern or process being measured. System behavior is predictable above or below the threshold, but cannot be predicted at or near the threshold. For example, a critical threshold may be encountered in extrapolation across spatial scale (Gardner et al. 1989); the threshold delineates the spatial domains across which information can be extrapolated. NLMs have been used to identify critical thresholds in landscape pattern and the spread of disturbance or organisms across a landscape (e.g., Gardner et al. 1989). Furthermore, critical thresholds in landscape structure may have important ecological consequences for the structure and dynamics of populations (With and Crist 1995). Habitat loss may contribute to "extinction thresholds" (sensu Lande 1987) in which a population abruptly (and unpredictably) crashes. It is therefore advantageous to identify where threshold events are likely to occur. The oft-reported percolation threshold value of $p_c = 0.59$ is restricted to particular assumptions regarding the underlying spatial distribution (random), the type of lattice (square grids with "site" percolation), and the movement rule (4 nearest neighbors). For example, if movement involves leapfrogging over cells of unsuitable habitat, the landscape is functionally connected (by dispersal) across a greater range of available habitat and $p_c = 0.25$ (Pearson et al. 1996). Fractal landscapes are inherently more connected than random maps and exhibit critical thresholds at lower p ; for example, p_c varies from 0.5 for highly clumped fractal landscapes ($D = 2.01$) to 0.44 to highly fragmented fractal landscapes ($D = 2.99$) if movements are constrained to neighboring cells (compare with $p_c = 0.59$ for random landscapes). The exact threshold value is thus sensitive to the underlying assumptions of the neutral model. Just as predictions from other models in ecology are sensitive to their assumptions, so too does the prediction of critical thresholds depend on lattice geometry, the process being modeled, and the way in which the process is modeled (Plotnick and Gardner 1993).

3) Definition of landscape connectivity

Landscape connectivity is the key to understanding system behavior (e.g., Taylor et al. 1993, Green 1994). Connectivity figures prominently in a diverse array of ecological processes including metapopulation dynam-

ics and reserve design (Wiens 1996), fire spread and disturbance propagation (Turner et al. 1989), dispersal success and colonizing ability (Lavorel et al. 1995, Gustafson and Gardner 1996, Schumaker 1996), and gene flow (Green 1994). NLMs provide quantitative predictions as to when landscapes become fragmented (i.e., disconnected). Critical thresholds identify the domain where spatial pattern is important (e.g., below the critical threshold; Andr en 1994).

The definition of landscape connectivity is a process-oriented one; it ultimately depends upon how the process (e.g., animal movement, spread of disturbance) links cells. If animal movement, for example, occurs not only among contiguous cells but can also skip across cells (e.g., across gaps of unsuitable habitat), then the landscape will be connected across a much greater range of habitat availability (i.e., p_c occurs at lower levels of p). There is thus a difference between structural connectivity – the physical adjacency of habitat sites – and functional connectivity – the linkage of habitat sites by a process.

4) Development of "species' perceptions" of landscape structure

This is a necessary vista if we are to adopt meaningful and effective conservation strategies (Hansen and Urban 1992). Simulating the movement of species with different dispersal abilities, habitat affinities and life-history traits on neutral landscapes help predict what types of species are likely to be affected by habitat loss or land-use change and when, which is an important tool in management applications (Dale et al. 1994, With and Crist 1995, Pearson et al. 1996, With et al. 1997). For example, habitat specialists are more constrained by absolute habitat abundance than the spatial patterning of habitat (With and Crist 1995). Species with large area requirements and limited gap-crossing abilities (an inability or unwillingness to cross forest clearings) were most sensitive to deforestation in a tropical forest; availability of habitat for such species was reduced at a rate disproportionately greater than the actual rate of habitat loss (Dale et al. 1994).

5) Provision of a general model of spatial complexity

Representation of the spatial dimension in ecological theory is often limited to implicit or explicit assumptions about the arrangement and geometry of patches. For example, patch-based metapopulation models (e.g., Levins 1969) are spatially implicit because all patches are assumed to be the same size and equidistant and the spatial location of populations is ignored (Hanski and Simberloff 1997). Although spatially explicit or "spatially realistic" metapopulation models have been developed (Hanski and Simberloff 1997), metapopulation theory generally ignores the complexity of the landscape matrix in which patches are embedded; this is considered to be the unique domain of landscape ecol-

ogy (Wiens 1997). The cell-based NLMs provide a more general model of landscape structure, and do not dissect the landscape a priori into elements such as patches, matrix and corridors (Pearson et al. 1996). The size of the cells in the landscape grid can be changed to alter the resolution of landscape pattern and heterogeneity. Cells can be aggregated into patches. Different rules of aggregation will generate different patch structure. The resulting patch structure is defined by the scale at which the process (e.g., animal movement) interacts with the spatial patterning of the landscape. This has important implications for designing conservation reserves, for example. A reserve network of patches may not function as intended since different species may perceive the same landscape differently and their perceptions of what constitutes a patch may differ (Pearson et al. 1996). Similarly, it may not be possible to identify a priori corridors that enhance linkage among patches. Areas that facilitate dispersal may not appear as discrete features on landscape maps (Gustafson and Gardner 1996). The generality of cell-based NLMs makes it possible to explore alternative characterizations of landscape pattern and spatial structure on ecological processes.

6) Determination of the ecological consequences of spatial heterogeneity

Because much of existing ecological theory ignores the spatial dimension, or deals with it in a simplistic way, recent advances in the application of NLMs have been directed at incorporating explicit spatial structure into classical ecological theory, such as predator-prey interactions (Keitt and Johnson 1995) and metapopulation dynamics (K. A. With and A. W. King unpubl.). These efforts attempt to relax implicit and explicit assumptions of spatial homogeneity or randomness and examine how model predictions change with alternative spatial distributions (e.g., fractal distributions of habitat or gradients in resource distribution). In a more general way, simulations of species interactions on neutral landscapes have identified complex relationships between species life-history characteristics, dispersal abilities, and spatial patterning and have contributed to a spatially explicit understanding of population and community processes (Palmer 1992, Lavorel et al. 1994, 1995, Moloney and Levin 1996, With et al. 1997). For example, species coexistence is affected by the fractal scaling of resource variability, which produces scale-dependent patterns in species diversity at the microsite and broader scales of the landscape (Palmer 1992).

On the use and misuse of neutral landscape models

The earliest NLMs were random maps. Does that mean that the landscape ecologists who developed these mod-

els actually believed that landscape patterns were random? No, of course not. Robert Gardner and others purposefully set out to develop null or neutral models of landscape pattern (Gardner et al. 1987). An assumption of no pattern – randomness – is an appropriate null hypothesis from which to test for spatial pattern. If there is no statistical difference between observed pattern and that of a random NLM, then there is no need to invoke a more complex model of spatially explicit process. Conversely, it is because we have null models of landscape pattern that we can conclude real landscapes are not random (Gardner et al. 1987, Schumaker 1996).

If we know that real landscapes are not random assemblages of habitat, then of what practical value is a neutral model that postulates a random distribution, a null hypothesis that will invariably be falsified whenever it is tested? As Caswell said about neutral models in general, “if it can be claimed that the model’s predictions are absurd, then its use even as a scale of reference could be questioned” (Caswell 1976: 350). The predictions of random NLMs are not absurd. There are circumstances, for example when the fraction of habitat cells is above p_c , where random maps and observed landscapes are statistically similar (e.g., in terms of connectivity; Gardner et al. 1987). The surprise has been not that landscapes are *not* random (e.g., Schumaker 1996), but the extent to which they behave as if they are. In this domain (above p_c), it does not matter whether the model is false (i.e., landscape is not random). Spatial pattern is not always important in understanding ecological processes, and NLMs have been useful in identifying the domain where landscape structure matters. For example, if habitat covers 75% of the landscape, it may not matter to a dispersing organism whether the habitat is random or clumped; the landscape is connected in either case and the specific spatial arrangement of habitat is not important.

There are circumstances, such as below p_c , where it does matter that the NLM is false. For example, when a landscape is only 30% habitat, the explicit patch structure may affect dispersal success (e.g., Schumaker 1996). If the null hypothesis of a random habitat distribution is inconsistent with observation, do we then conclude that NLMs are useless? No. It is precisely in these circumstances that NLMs, and neutral models in general, are most useful. How useful has the Lotka-Volterra equation been in population and community ecology? How useful has the Hardy-Weinberg equation been in population genetics? We know that the environment is not perfectly homogeneous, just as we know it is not random. We know systems are not in a balanced equilibrium. Yet in all cases, these models have provided a baseline for comparison, for making predictions about system behavior. When the model predictions are not consistent with observation, the model assumptions can be revisited, revised, and additional complexity

added, if needed. If we can explain seemingly complex phenomena with simple models, so much the better. Neutral models and NLMs can help constrain the addition of complexity to just that which is necessary to explain observations. Wimsatt (1987) has argued that models we know or believe to be false can be, and are, used as baselines for gaining new or better understanding about processes that are not in the false neutral models.

NLMs, even those with assumptions shown to be false, will continue to function as baselines for evaluating and interpreting observations and for developing new models of landscape structure. For example, fractal landscapes have an inherent "clumping" (Fig. 1), which may provide a better estimate of spatial correlation in real landscapes than a random distribution. The inclusion of fractal processes and fractal geometry may thus be appropriate to explain landscape structure, at least in situations where explicit spatial pattern matters, such as below p_c .

Alternatively, it is a misuse of NLMs, and neutral models more generally, to interpret agreement between model predictions and observations as proof that the NLM is true (Caswell 1976). Rather, the observations provide no compelling evidence for introducing more complex processes to explain the observed pattern. This does not mean that the excluded processes do not operate at all (Wimsatt 1987). Additional observation will be required to demonstrate their role, if any, in explaining the observed pattern.

Similarly, it would be a misuse of NLMs to interpret lack of agreement between the model prediction and observations as proof that the excluded processes are in fact responsible for the observed pattern (Caswell 1976). Divergence between model prediction and observation is evidence that other processes may be at work. Additional tests with models that explicitly include those processes are required to gain confidence that the hypothesized processes are responsible (Gardner and O'Neill 1991).

It is a misuse of NLMs to assume that the results from simulations on neutral landscapes can be applied directly to real landscapes. The predictions from NLMs are part of a larger theory of landscape pattern and process from which hypotheses are generated. These hypotheses are meant to be tested, and provide the basis from which to test for statistical significance. For example, it would be naive to assume that real landscapes percolate when at least 59.28% of the landscape is habitat. As noted earlier, this particular quantitative result is specific to a particular set of model assumptions. It would therefore be a misuse of NLMs to design a conservation reserve with at least 59.28% habitat based on the results from random NLMs. On the other hand, approaching the design of the reserve with an appreciation of the importance of connectivity reinforced by the results from NLMs and exploring the

design of the reserve with alternative NLMs would be an appropriate application.

Finally, it is a misunderstanding of NLMs to reject them in toto as "artificial" or misleading when tools associated with NLMs fail to be good predictors of ecological processes on landscapes (Schumaker 1996). Schumaker's results are evidence that many common indices of landscape pattern are not particularly good predictors of simulated dispersal success for the landscapes of old-growth forest in the Pacific Northwest. Schumaker's argument is, or should be, with the failure to apply or test indices of landscape pattern to ascertain their relationship with ecological process and not with the tools, the NLMs, used in developing those indices. One should not confuse failure to use a hammer in a useful way with failings of the hammer itself or, worse yet, with shortcomings in the tools used to build the hammer. An appropriate use of NLMs is to show that patch cohesion of old-growth forest landscapes differs from that of random landscapes (Schumaker 1996: Fig. 9); that is, the old-growth landscapes are not random (Schumaker 1996: 1222–1223). From this point, a new NLM with assumptions other than random habitat distribution could be developed and tested. How, for example, does Schumaker's patch cohesion index behave on the fractal neutral landscapes generated by mid-point displacement? These neutral landscape are equally "artificial," but they show a greater clumping of habitat than random landscapes, a patch structure that appears to be more characteristic of real landscapes.

The future of neutral landscape models

Much of the use of NLMs has been theoretical to date (Appendix). The next phase in the development of NLMs should focus on application and model testing. Many of the landscape indices developed on NLMs have been calculated for real landscapes, but, as noted by Schumaker (1996), there has been little attempt to link these with some ecological process. We share Schumaker's desire for more balance between the development of indices and their utilization. We do not share his interpretation of the failure to do so as an indictment of NLMs or their potential utility in ecological applications, however.

A few studies have attempted to test empirically results from simulation models using neutral landscapes. Plant species diversity in Mediterranean old-fields was consistent with simulated species interactions on hierarchical random landscapes (Lavelle et al. 1994). The distribution of two grasshopper species in a grassland mosaic matched predictions of a simulation experiment which modeled species- and habitat-specific rates of movement on heterogeneous random landscapes (With and Crist 1995).

The most compelling test of a NLM, however, is a carefully designed and executed field experiment that controls for the assumptions of the NLM. It is desirable, for example, to test the hypothetical threshold effects of landscape connectivity on some ecological process. Manipulative experiments at the spatial scales normally associated with landscapes are difficult, if not impossible. However, smaller-scale "microlandscape" experiments have been devised in which neutral landscape patterns are created in the field (with sand and sod, in this case) to assess how connectivity affects dispersal. Wiens et al. (1997) ran tenebrionid beetles through random mazes with different habitat abundances and discovered that beetles exhibited a fundamental shift in movement behavior between 0–20% grass cover. In a similar field experiment, With et al. (unpubl.) subjected crickets to fractal microlandscapes that differed in contagion (fractal dimension of pattern) and amount of habitat. It is intriguing that ecological processes may not exhibit threshold behavior at the point predicted by percolation theory; that is, the threshold at which movement behavior is affected, or dispersal success declines, or populations become fragmented or go extinct, may occur at p less than the p_c predicted by NLMs. This was the case in the beetle maze experiment, and a threshold of 10–30% emerged from a literature survey comparing the abundance and diversity of birds and mammals in landscapes with different proportions of habitat (Andrén 1994).

These findings suggest that ecological systems are more resilient to habitat destruction than predicted by percolation theory, but they may also suggest lagged effects in ecological responses to habitat loss. Given the latter possibility, determination of threshold effects and the ecological consequences of disrupting landscape connectivity becomes even more urgent. The development of NLMs that include the appropriate assumptions about landscape pattern and ecological processes are ideally suited to address these concerns.

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Appendix. Summary of selected papers utilizing neutral landscape models in ecology.

Type of neutral model	Description	Use/application	Contribution/significant findings	Citation
Random	Percolation map	Theoretical: Generation of neutral landscape models Application: Comparison with structure of real landscapes	Seminal paper. Showed domain where processes may be important in structuring landscapes (e.g., below critical threshold)	Gardner et al. 1987
		Theoretical: Modeling of disturbance frequency and intensity to predict rate of spread as a function of landscape structure	Propagation of disturbance is constrained by landscape connectivity (e.g., whether landscape is above or below the critical threshold)	Turner et al. 1989
		Theoretical: Simulation modeling of various processes (dispersal, spread of disturbance, gene flow)	Emphasized that landscape connectivity is the key to predicting system behavior; many ecological processes may exhibit critical behavior	Green 1994
		Comparison of pattern indices applied to random maps and landscapes to predict effects on simulated dispersal success (i.e., habitat connectivity)	Many commonly employed landscape indices were not good predictors of dispersal success on real landscapes. Presented a new "patch cohesion" index that performed better	Schumaker 1996
		Literature review: Comparison of data on abundance and distribution of birds and mammals in landscapes with different proportions of habitat to predictions of percolation theory	A threshold in species richness and abundance occurred between 10–30%, below the expectations of percolation theory. Habitat loss is the most important determinant above the critical threshold, whereas fragmentation effects come into play below the threshold	Andrén 1994
		Experimental: Study of beetle movement through random "microlandscapes" ($5 \times 5\text{-m}^2$ plots) comprised of sand and sod	First experimental test of an ecological application of percolation theory. The percolation threshold for beetle movement occurred much lower (between 0–20% grass cover) than predicted by percolation theory	Wiens et al. 1997
Random	Heterogeneous percolation maps (3 habitat types)	Theoretical: Simulation modeling of how dispersal range and species' habitat affinities interact with landscape structure to predict shifts in population distributional patterns Application: Prediction of population distributions of 2 grasshopper species	Extension of percolation theory to heterogeneous (> 1 habitat type) landscape mosaics. Empirical distribution of 2 grasshopper species matched predictions of simulation exercise on neutral landscapes	With and Crist 1995
Random/ Clumped Random	Percolation map/percolation map generated with contagion (adjacency matrix, Q_{ij})	Theoretical: Determination of resource utilization scales on landscapes with different resource abundances	Spatial patterning alters the resource utilization scale of organisms (e.g., sparse resources below critical threshold require organism to operate at larger scales). Multiple critical resources also increase resource utilization scales, whereas substitutable resources ease scale requirements	O'Neill et al. 1988a

Appendix. (Contd.)

Type of neutral model	Description	Use/application	Contribution/significant findings	Citation
Random/ Clumped Random	Percolation map/percolation map generated with contagion (adjacency matrix, Q_{ij})	Theoretical: Comparison of properties between these two types of neutral models	Contagion (habitat clumping) altered structural properties of maps, landscape indices and prediction of threshold effects thus dependent upon type of neutral model	Gardner and O'Neill 1991
Random/ Clumped Random	Percolation map/percolation map generated as a random distribution of rectangular patches of random length and width	Comparison of landscape indices applied to neutral models and real landscapes	Most indices behaved similarly in the two neutral models, although usually at different magnitudes. Real landscapes differed significantly from neutral landscapes for almost all indices	Gustafson and Parker 1992
Random/ Patterned Maps	Percolation map/deterministic placement of habitat cells	Theoretical: Relate animal movement to landscape pattern, explore effects of changing spatial scale on movement, and estimate problems in extrapolating information across scales	Knowledge of critical thresholds defines where extrapolations between scales can occur	Gardner et al. 1989
Hierarchical	Curdling algorithm from fractal geometry	Theoretical: Generation of neutral landscape models in which habitat abundance can be controlled at different scales. A variety of landscape patterns can be produced while controlling the amount of overall habitat abundance	The second generation of neutral landscape models. Natural landscape patterns may have hierarchical patterns	O'Neill et al. 1992
Hierarchical	Curdled maps (3 levels)	Theoretical/Analytical: Analysis of hierarchical random landscapes generated with different proportions of habitat at three scales	Overall landscape connectivity is a function of connectivity at all levels (e.g., maps percolate if habitat abundance exceeds critical threshold at all levels). It is not possible to predict connectivity based on overall habitat abundance (combined probabilities of habitat at each level), unlike simple random maps	Lavorel et al. 1993
		Theoretical: Simulation of species coexistence as a function of seed dispersal and dormancy strategies for plants on different hierarchically structured random landscapes Application: Simulation results compared to a study of plants in Mediterranean old-fields	Coexistence of species with different life-history characteristics depends on complex interaction between landscapes structure and disturbance frequency. Results of modeling exercise were consistent with patterns of coexistence for plant communities in southern France	Lavorel et al. 1994
		Theoretical: Simulation model of seed dispersal to predict effective colonization strategies in different patterned landscapes	Colonizing ability and extinction probability are sensitive to the mean dispersal distance of the species, although these effects were ameliorated at highly connected landscapes (e.g., above percolation threshold)	Lavorel et al. 1995
Random/ Hierarchical	Percolation map/Curdled maps (3 levels)	Theoretical: Simulation of different consumer populations on theoretical landscapes	The size of different consumer populations was best predicted by the scale at which	Gardner et al. 1993

Random/ Hierarchical	Percolation map/Curdled maps (3 levels)	Application: Comparison of real landscapes to hierarchical random landscapes	fragmentation occurs (e.g., fragmentation at the finest scale in hierarchical maps produced the lowest level of abundance). While real landscape patterns were quite different from random landscapes, they were quite similar to the hierarchical maps	Pearson et al. 1996
Random/ Hierarchical	Percolation map/Curdled maps with "wheys" (3 levels)	Theoretical: Interaction of species' dispersal abilities (different movement rules) with landscape pattern	Different species are predicted to have different "perceptions" of landscape structure (i.e., connectivity) depending on dispersal ability	
Random/ Hierarchical	Percolation map/Curdled map (2 levels)/deterministic placement of habitat patches	Theoretical: Dispersal and patch colonization in theoretical landscapes Application: Simulated patch colonization in real landscapes comprised of a complex, heterogeneous matrix	Almost 90% of dispersal success is based on the relative size and isolation of patches. Changes in the matrix heterogeneity affected colonization success, however. Transfer rates between patches were not symmetrical and "corridors" were often diffuse structures that are difficult to identify from structural features of the landscape	Gustafson and Gardner 1996
Fractal	Fractal brownian surface (midpoint displacement algorithm)	Theoretical: Influence of correlated spatial pattern on species coexistence	Increasing the fractal dimension of the landscape (decreasing correlation among sites) enhanced species richness at both the microsite and landscape scale. Fewer species coexist at the landscape scale in extremely variable environments (very high fractal dimensions), however	Palmer 1992
		Theoretical: Simulated rate and spatial/temporal autocorrelation of disturbance on population dynamics Empirical: Simulations tied to the population dynamics of three plant species in the serpentine grasslands of California	Spatial and temporal "architecture" of disturbance regime interacts in complex ways with species' life-history traits to affect diversity and the population dynamics of individual species. Disturbance rate and the temporal autocorrelation of the disturbance regime were the most important factors affecting population dynamics. Spatial factors (size of local disturbances, spatial autocorrelation among disturbances) played a minor role in species' responses to disturbance	Moloney and Levin 1996
Fractal/ Random	Segmented fractional brownian surface (midpoint displacement algorithm); heterogeneous (3 habitat types)	Theoretical: Simulated dispersal on random and fractal landscapes to determine the relative effects of habitat abundance, distribution and quality in structuring population distributional patterns	Scale-dependent effects emerged on fractal landscapes. At fine scales, habitat abundance was the biggest determinant of population distribution, whereas species' habitat affinities were most important at broad scales. Habitat abundance influenced population distributions on random maps at all scales	With et al. 1997
Fractal/ Random/ Gradient	Percolation maps/Segmented fractional brownian surface (midpoint displacement algorithm)/probability gradient	Theoretical: Spatially explicit simulation model of predator-prey interactions (i.e., neutral landscape models coupled with a reaction-diffusion model corresponding to the Lotka-Volterra equations)	Relaxes assumption of spatial homogeneity inherent in predator-prey models (Lotka-Volterra dynamics) and incorporated diffusion-limited dispersal	Keitt and Johnson 1995