Diversity and Distributions, (Diversity Distrib.) (2006) **12**, 229–235

SPECIAL FEATURE

Linking the concept of scale to studies of biological diversity: evolving approaches and tools

Erik A. Beever[1,2]*, Robert K. Swihart[3] and Brandon T. Bestelmeyer[4]

[1]*USGS Forest and Rangeland Ecosystem Science Center, Corvallis, Oregon 97331, USA,* [2]*NPS Great Lakes Network, 2800 Lake Shore Dr. E., Ashland, Wisconsin 54806, USA,* [3]*Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana 47907, USA,* [4]*USDA-Agriculture Research Service, Jornada Experimental Range, Box 30003, New Mexico State University, Las Cruces, New Mexico 88011, USA.*

*Corresponding author. Erik A. Beever, NPS Great Lakes Network, 2800 Lake Shore Dr. E., Ashland, Wisconsin 54806, USA.
E-mail: erik_beever@nps.gov

ABSTRACT

Although the concepts of scale and biological diversity independently have received rapidly increasing attention in the scientific literature since the 1980s, the rate at which the two concepts have been investigated jointly has grown much more slowly. We find that scale considerations have been incorporated explicitly into six broad areas of investigation related to biological diversity: (1) heterogeneity within and among ecosystems, (2) disturbance ecology, (3) conservation and restoration, (4) invasion biology, (5) importance of temporal scale for understanding processes, and (6) species responses to environmental heterogeneity. In addition to placing the papers of this Special Feature within the context of brief summaries of the expanding literature on these six topics, we provide an overview of tools useful for integrating scale considerations into studies of biological diversity. Such tools include hierarchical and structural-equation modelling, kriging, variable-width buffers, *k*-fold cross-validation, and cascading graph diagrams, among others. Finally, we address some of the major challenges and research frontiers that remain, and conclude with a look to the future.

Keywords

Biodiversity conservation, biological invasions, extent, future challenges, publication chronology, modelling, resolution.

INTRODUCTION

Understanding the processes affecting biological diversity is fundamental to the success of conservation efforts. Not surprisingly, research dealing with biological diversity has increased dramatically over the past 20 years. The number of publications mentioning biological diversity or biodiversity in titles, keywords, or abstracts has increased at an annual rate of 33% since 1985 (Fig. 1). Coincident with the explosion of research and management efforts pertaining to biological diversity has been an increased awareness among ecologists of the general importance of scale. The importance of explicitly considering scale when interpreting ecological patterns and their underlying processes can be traced to two seminal papers. Wiens (1989) first alerted ecologists to the dangers associated with ignoring scaling differences in patterns and the processes that produce them. Shortly thereafter, Levin (1992) reinforced the importance of scale mismatches in pattern and process as the central problem in ecology. Following these publications, scale received increasing attention in ecology and conservation biology, with publications mentioning scale increasing at an annual rate of 41% (Fig. 1). In addition to the increase in peer-reviewed articles, there has been a recent increase in the number of books dedicated wholly or substantially to the topic (e.g. Edwards *et al.*, 1994; Peterson & Parker, 1998; Brown & West, 2000; Gardner *et al.*, 2001; Scott *et al.*, 2002).

Despite the rapid rise in scientific interest regarding scale and biological diversity as independent areas of inquiry, integration of scale into studies of biological diversity has proceeded more slowly. The first publications that simultaneously mentioned scale and biological diversity in titles, keywords, or abstracts appeared in 1990 (Fig. 1). Since then, joint consideration of these two subject areas has increased at an annual rate of 10%, a rate three to four times below the level observed for either area separately (Fig. 1). One of our goals in assembling this special feature is to highlight the numerous ways in which issues of scale affect studies of biological diversity, and thereby encourage scientists and managers to explicitly incorporate consideration of scale into work targeting biological diversity.

Since the 1980s, biological diversity has attracted many definitions (e.g. see review by DeLong, 1996). These definitions have varied principally with respect to three characteristics. First, they differ in whether diversity is characterized by richness, evenness, composition, or some combination thereof. Second, definitions differ in the ecological components and processes encompassed, ranging from species alone to the inclusion of genes, species assemblages, ecological processes, ecosystems, and their interactions. Third, and perhaps less apparent, definitions have varied through time with respect to the spatial and temporal scales that they encompass.

In addition to the plurality in definitions of biological diversity, the term 'scale' can have several meanings in ecology.

DOI: 10.1111/j.1366-9516.2006.00260.x
www.blackwellpublishing.com/ddi

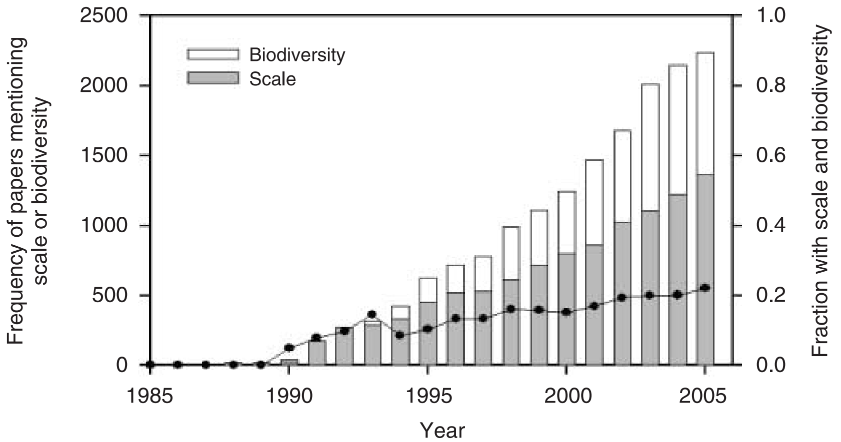

Figure 1 A chronology of the growth in use of the terms biodiversity, biological diversity, and scale. Vertical white bars represent the number of articles, in publications recognized by Web of Science®, containing either 'biodiversity' or 'biological diversity' in the title, abstract, or key words, 1985–2005. The portion of vertical bars in grey represents the number of articles dealing with ecology or conservation biology and mentioning scale or a variant (i.e., scaling, multiscale, or multiple scales). Solid circles represent the fraction of articles on biological diversity that also mentioned scale in the title, abstract, or key words.

Scale can refer to either grain (also known as 'resolution'), extent (i.e., the total domain under consideration), or when used loosely, both concepts simultaneously (Turner *et al*., 2001). Scope, which has been defined as the extent : resolution ratio, is a more definitive and useful combination of the two concepts (Schneider, 1994). For brevity, we will continue the loose, non-specific usage of scale in this article to reflect extent and/or grain. Similarly, although scale, extent, and resolution apply to both spatial and temporal domains, in this article, scale refers to spatial aspects, unless stated otherwise.

The papers comprising this special feature reflect the diversity of scales and concepts about biological diversity found in a vast literature. Here, we briefly review the contributions in this special feature within a broader context of short reviews of key topics from literature on scale and species diversity.

CONSIDERATION OF SCALE IN STUDIES OF BIOLOGICAL DIVERSITY

Recently, the relationship of scale to biological diversity has figured most prominently in six subject areas: (1) the creation of heterogeneity within and among ecosystems or their components, including patterns in richness; (2) incorporation of multiple scales in assessing the effects of disturbances such as herbivory and fire; (3) incorporation of scale considerations into conservation and restoration efforts; (4) investigation of the role of scale in invasion biology; (5) the importance of temporal scale for understanding processes; and (6) species responses to environmental heterogeneity.

Heterogeneity within and among ecosystems has been recognized through the paradigms of self-organization (e.g. Rietkerk *et al*., 2002), patchiness (e.g. Forman & Godron, 1981; Kotliar & Wiens, 1990), metapopulations (Hanski, 1998), gradient analysis (McGarigal & Cushman, 2005), diversity components (Crist *et al*., 2003), spatial autocorrelation (Legêndre, 1993), and richness–productivity relationships (Chase & Leibhold, 2002), among others. Many of the studies that investigate heterogeneity at multiple spatial or temporal scales conclude that patterns or dynamics of the component of interest would be incompletely understood if only one or few scales were examined. Although the causes of heterogeneity differ among ecosystem components, common determinants include variation in the biophysical environment, competitive interactions, consumer–resource feedbacks, demographic processes, and dispersal and vicariance events. Variation in patterns of richness and diversity across scales due to combinations of factors is a topic of considerable interest (Rahbek & Graves, 2000, 2001; Whittaker *et al*., 2001; Leponce *et al*., 2004; Turner & Tjørve, 2005). In this Special Feature, Fleishman & MacNally (2006) illustrate how patterns of spatial autocorrelation can be used to investigate the scale-dependent relationships between species diversity and environmental properties. Within a set of mountain ranges of the Great Basin, USA, they show that the spatial structure of bird species composition is most similar to that of vegetation composition rather than vegetation structure or productivity.

Authors increasingly acknowledge the multiscale nature of disturbances in a generic sense (Perry & Amaranthus, 1997; Wickham *et al*., 1997) as well as that of many specific disturbances. This is true not only because disturbances such as wildfire and herbivory are spatially and temporally heterogeneous, but also because landscapes possess differential vulnerability to disturbances (Perry & Amaranthus, 1997; Kepner *et al*., 2000; Bestelmeyer *et al*., 2004). Furthermore, some landscapes tend to absorb and dampen the spread of disturbances, whereas other landscape patterns magnify the spread (Perry & Amaranthus, 1997, Peters *et al*., 2004).

Specific disturbances such as herbivory and wildfire have recently attracted research attention across several scales. Various aspects of biological diversity, such as species richness, may be affected by factors at scales from size of bare patches (Desoyza *et al*., 2000) to structure of the landscape (Wickham *et al*., 1997). Both herbivory and wildfire can produce gradients of disturbance effects at several different scales, and the direction and magnitude of their impacts on ecosystems vary widely within different extents. Many temporal and spatial scales are required to address adequately the impacts of herbivory (Brown & Allen, 1989; Bisigato *et al*., 2005). Herbivore movements are affected by the heterogeneous nature of vegetation and geology (Skarpe *et al*., 2002; Milchunas & Noy-Meir, 2002), and herbivore activity can modify the pattern of vegetation and soils at multiple spatial scales (Augustine & Frank, 2001; Bisigato *et al*., 2005). Herbivore impacts on ecosystem components at different scales may vary due to topographical position (Fowler, 2002), species of herbivore, (Warner & Cushman, 2002), timing and duration of herbivory, presence of other interacting disturbances (Fuhlendor & Smeins, 1997; Hobbs, 2001; Harrison *et al*., 2003), levels of resources such as light, water, and soil nutrients (Milchunas *et al*., 1993; Hawkes & Sullivan, 2001), and the taxon being disturbed by herbivory (Milchunas *et al*., 1998). Bowyer & Kie (2006) review the effects of large herbivores at multiple scales as agents of ecosystem change that affect biological diversity. They note that the scale at which foraging sites, birth sites, traditional birthing areas, wintering areas, or migratory routes are chosen can have substantial effects on other taxa. In a specific example, Beever *et al*. (2006) similarly demonstrate the existence of patterns in soil-aggregate stability and invasive species that were related to grazing intensity at several spatial resolutions.

Third, effective conservation and restoration actions occurring in landscapes and individual ecosystem components must consider the appropriate scale for those actions. The importance of scale is seen in topics as diverse as conservation-reserve selection (Warman *et al*., 2004), management and conservation of native fishes occupying heterogeneous riparian habitat that are affected by processes interacting within and among many scales (Fausch *et al*., 2002), restoration of wildlife habitat (Block *et al*., 2001), and re-establishment of native plant communities to disturbed ecosystems (Palik *et al*., 2000). Beever *et al*., (2006) describe local- and landscape-scale gradients in plant and soil response variables both during grazing by burros and cattle and after their removal. Using information-theoretical analyses, they find that within a given year, the slope of the disturbance-response gradient often differs with time since removal of grazing. In this Special Feature, explicit consideration of scale in conservation and restoration efforts also is deemed important by Swihart *et al*. (2006) and Meyer & Thuiller (2006).

Invasive species constitute one of the largest challenges for conservation and restoration of biological diversity, and there is increasing attention to the role of scale in the processes governing invasion. For example, regression-tree analysis of GIS-based data on plant distributions in South Africa at four spatial scales identified very different suites of factors governing invasion patterns at the various scales (Rouget & Richardson, 2003). Whereas factors relating to propagule pressure (e.g. distance to sources) were most important at finest scales, environmental and climatic factors such as length of growing season better predicted distributions at broader scales. Attempts to scale-up or scale-down, by extrapolating predictions from one model to another spatial scale, led to low classification accuracy and poor predictive ability (Rouget & Richardson, 2003). In related work that addressed the planting of alien trees as 'natural experiments', Richardson *et al*., (2004) further suggest that spatial scale strongly influences the type of models that can be used to predict species distributions. Whereas correlative models are well suited for use at scales of landscapes, regions, or countries, mechanistic models appear to have greatest predictive ability at smaller spatial scales (Richardson *et al*., 2004). Natural experiments are one of several tools that permit space-for-time substitution, which not only provides insights into the role of temporal scales, but does so across a range of spatial resolutions.

In addition to variable responses across **spatial** scales, many studies have found that the magnitude and direction of results depended critically on either the **temporal** resolution or the extent of the investigation (e.g. Rosenzweig, 1995, Hadley & Maurer, 1999). Boyce (2006) addresses the importance of temporal scale when interpreting results of habitat-selection studies, and suggests that variation in seasonal and annual processes can generate distinctive patterns that are overlooked or misunderstood when viewed from an inappropriate temporal resolution or extent. Temporal scale also affects interpretation of population dynamics. For example, abundances of syntopic rodents in Kansas old fields varied in their periodicities and only some species pairs covaried positively. However, other species exhibited time-lagged cross-correlations, suggesting that regular cycles of species were out of phase (Brady & Slade, 2004). Similarly, disturbances may have very different effects on the same plots or the same organisms during different years (Holm *et al*., 2002; Teague *et al*., 2004, Beever *et al*., 2006), often as a result of different weather conditions. Often, temporal heterogeneity in response to conservation or restoration efforts can only be well documented after long series of data have been amassed (Fuhlendorf & Smeins, 1997).

Sixth and finally, consideration of the influence of environmental heterogeneity on species increasingly has been addressed at multiple scales. Studies of the distribution or movement of species across the landscape have shown that beetles, lizards, small mammals (Jorgensen, 2004), and ungulates (Johnson *et al*., 2001; Kie *et al*., 2002) exhibit scale-dependent responses. Swihart *et al*. (2006) compare the distribution of 33 vertebrate species among multiple patches across 35 landscapes in an intensively agricultural river basin of east-central USA. Using the fraction of patches of a species' primary habitat within landscapes within the basin in Indiana, they show that proportion of patches occupied within the basin explained 47% of the variation in occupancy among species and related positively to niche breadth, yet negatively to the proximity of the nearest geographical range boundary. Additionally, occupancy rates varied significantly among landscapes within the basin for 16 of the species studied. They conclude that even among species surviving disturbances such as habitat loss and fragmentation for over a century, differences operating at multiple spatial scales (geographical range to landscape) can have substantial influences on patch occupancy.

Bowyer & Kie (2006) review the effects of spatial and temporal scales on ecological patterns observed for large terrestrial ungulates and carnivores, with a focus on habitat selection related to specific life-history traits. They provide evidence that (1) numerous life-history traits for large mammals are extremely scale-sensitive, (2) for a given life-history trait, one scale can provide superior explanatory power over others, and (3) multiple scales often are needed to understand patterns of habitat selection in ungulates and carnivores. Boyce (2006) provides a review of methods used to incorporate scale in studies of habitat selection. Resource selection functions (RSFs, Manly *et al*., 2002) can be used to characterize the distribution and abundance of organisms. Boyce concludes that selection is most likely to vary among scales when there exists substantial topographical relief or when trade-offs exist between selections of different resources. Both Boyce (2006) and Bowyer & Kie (2006) suggest that foraging considerations are more likely to involve selection at finer scales, whereas predation, dispersal, and other population processes that operate across larger scales will exert effects on resource selection functions when measured at correspondingly larger scales.

Despite the many studies of individual taxa, ecologists generally have lacked an integrative and quantitative understanding of resource use across numerous taxa. Meyer & Thuiller (2006) amalgamate information on resource-selection functions for 886 species. They standardize the definitions of different scales, use Cohen's kappa (κ) and Somers' D_{xy} (D_{xy}) to quantify classification accuracy, and show that models incorporating predictors from multiple spatial scales usually predict distributions of species better than do models with factors from only one scale. They advocate, as we do (see below), that the correct scale for investigation should be based on the life-history and dispersal/movement patterns of the species under investigation. For example, effects of fragmentation on mobile animals were explained better by incorporating landscape-level covariates for vagile compared to sedentary butterflies. Furthermore, the scales examined should include not only the focal one, but also one immediately below and one above the pattern under investigation (O'Neill & King, 1998).

THE ECOLOGIST'S EVOLVING TOOLKIT FOR INTEGRATING SCALE CONSIDERATIONS INTO STUDIES OF BIOLOGICAL DIVERSITY

In addition to the greater analytical capacities obtained by ever-more-efficient computers, a number of recently developed tools have expanded the ability of ecologists to explicitly incorporate the concept of scale into their research. For example, hierarchical models (Bryk & Raudenbusch, 1992; see Beever *et al*., 2006 for application) form a special class of statistical models that address multilevel structures of data. Through these models, researchers investigate how large-scale characteristics influence finer-scale relationships within their contexts. Structural equation modelling represents another statistical tool that has been used to incorporate information from multiple spatial resolutions, through explicit specification of relationships among the multiple predictor and response variables.

In addition to these modelling approaches, numerous exciting tools have been developed to analyse various aspects of biological diversity in spatially explicit contexts, such as kriging to move from one resolution to another, buffers of variable width, ArcGIS's SpatialAnalyst, *k*-fold cross-validation to examine phenomena in different extents (Swihart *et al*., 2006; Boyce, 2006), and statistical approaches that account for both broad-scale trend and fine-scale autocorrelation (Lichstein *et al*., 2002). Furthermore, the frameworks of metapopulations, patch dynamics, and landscape ecology address how patch-specific, local dynamics may be largely independent, yet be connected by infrequent, larger-scale events of emigration and recolonization. Finally, cascading graph diagrams (*sensu* Aarsen, 2004) are a new conceptual modelling approach. This tool can be used to 'search for maximum parsimony by distilling and clarifying synthetic linkages between several potential causes of variation and covariation in … (response variables) at … distinctly different spatial scales …' (Aarssen, 2004).

CHALLENGES AND TRADE-OFFS INVOLVED IN ADDRESSING THE ISSUE OF SCALE

Trade-offs between sampling intensity and extent caused by budget limitations are often the main reasons why research is performed within limited spatial and temporal domains, and why past research often has been restricted to one or occasionally two spatial scales. A common conundrum is to decide whether one is interested in sampling more intensively with a finer grain or more extensively with a coarser grain. Allocation of a limited number of sampling units is of critical importance, because it determines statistical power and inference space and, thus, the utility of the results. The allocation decision should reflect project objectives and specific hypotheses. With respect to spatially explicit analyses, a further challenge is that some digital layers may currently be unavailable at fine grains. This is unfortunate, because the coarsest-grain data often determine the resolution of the analysis. In addition to lack of high-resolution data, in some cases the technology may not yet exist to sample organisms or other aspects of biological diversity in a cost-effective manner at very small or very broad scales.

CONCLUSIONS

The consequences of selecting suboptimal resolutions and extents for the study organism and question may include an unnecessarily restricted spatial domain of inference, incomplete or faulty understanding of dynamics governing the response variable(s), and inefficient use of study resources. A focus on a single spatial scale in a study or management action reduces our ability to understand the roles of spatial (or temporal) heterogeneity and context that repeatedly have been proven to be important in determining the outcomes of disturbance, restoration, and many other phenomena (e.g. MacMahon *et al*., 1987; Palmer *et al*., 2003, Bestelmeyer *et al*., 2003).

Although many advances have been made in linking scale with the study of biological diversity, several frontiers remain. There are increasing uses of multiple-resolution models and analyses to investigate phenomena (e.g. Meyer & Thuiller, 2006; Beever *et al*., 2006). However, there are few investigations or conservation actions that consider dynamics interacting across spatial and temporal scales (see Peters *et al*., 2004; DeWoody *et al*., 2005; Hooten & Wikle, 2006), even though the dynamic nature of landscapes often is embedded within naturally occurring spatio-temporal scales that reflect species interactions with their environment. Furthermore, for many ecological phenomena, few comprehensive investigations exist that summarize the importance of alternative spatial and temporal resolutions for large numbers of species (but see Meyer & Thuiller (2006) for a spatial example). Finally, there is currently a poor integration of social and ecological systems across multiple spatial scales, though it is a focus of current syntheses (Walker & Meyers, 1994; Holling, 2004, Peters *et al.*, in preparation).

Given the expense that is involved with obtaining multiscale data across very broad spatial extents, such data sets tend to be relatively uncommon. Progress in relating scale and various aspects of species diversity will be accelerated greatly by groups of ecologists and scientists in related disciplines that coordinate their work to address scale dependence and cross-scale interactions in particular regions and with respect to particular processes or phenomena. We are hopeful that the papers contained in this Special Feature will provide a roadmap for progress in integrating considerations of scale into studies of biological diversity.

REFERENCES

Aarsen, L.W. (2004) Interpreting co-variation in species richness and productivity in terrestrial vegetation: making sense of causations and correlations at multiple scales. *Folia Geobotanica*, **39**, 385–403.

Augustine, D.J. & Frank, D.A. (2001) Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. *Ecology*, **82**, 3149–3162.

Beever, E.A., Huso, M. & Pyke, D.A. (2006) Multi-scale responses of soil stability and invasive plants to removal of non-native grazers from an arid conservation reserve. *Diversity and Distributions*, **12**, 258–268.

Bestelmeyer, B.T., Herrick, J.E., Brown, J.R., Trujillo, D.A. & Havstad, K.M. (2004) Land management in the American Southwest: a state-and-transition approach to ecosystem complexity. *Environmental Management*, **34**, 38–51.

Bestelmeyer, B.T., Miller, J.R. & Wiens, J.A. (2003) Applying species diversity theory to land management. *Ecological Applications*, **13**, 1750–1761.

Bisigato, A.J., Bertiller, M.B., Ares, J.O. & Pazos, G.E. (2005) Effect of grazing on plant patterns in arid ecosystems of Patagonian Monte. *Ecography*, **28**, 561–572.

Block, W.M., Franklin, A.B., Ward, J.P. Jr, Ganey, J.L. & White, G. (2001) Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. *Restoration Ecology*, **9**, 293–303.

Bowyer, R.T. & Kie, J.G. (2006) Effects of scale on interpreting life-history characteristics of ungulates and carnivores. *Diversity and Distributions*, **12**, 244–257.

Boyce, M.S. (2006) Scale for resource selection functions. *Diversity and Distributions*, **12**, 269–276.

Brady, M.J. & Slade, N.A. (2004) Long-term dynamics of a grassland rodent community. *Journal of Mammalogy*, **85**, 552–561.

Brown, B.J. & Allen, T.F.H. (1989) The importance of scale in evaluating herbivory impacts. *Oikos*, **54**, 189–194.

Brown, J.H. & West, G.B. (2000) Scaling in biology. Oxford University Press, Oxford.

Bryk, A.S. & Raudenbush, S.W. (1992) *Hierarchical linear models: applications and data analysis methods*. Sage Publications, Newbury Park.

Chase, J.M. & Leibhold, M.A. (2002) Spatial scale dictates the productivity–biodiversity relationship. *Nature*, **416**, 427–430.

Desoyza, A.G., Whitford, W.G., Turner, S.J., van Zee, J.W. & Johnson, A.R. (2000) Assessing and monitoring the health of western rangeland watersheds. *Environmental Monitoring and Assessment*, **64**, 153–166.

DeWoody, Y., Feng, Z. & Swihart, R.K. (2005) Merging spatial and temporal structure within a metapopulation model. *American Naturalist*, **166**, 142–155.

Edwards, P.J., May, R.M. & Webb, N.R., eds. (1994) *Large-scale ecology and conservation biology*. British Ecological Society, Oxford.

Fausch, K.D., Torgersen, C.E., Baxter, C.V. & Li, H.W. (2002) Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *Bioscience*, **52**, 483–498.

Fleishman, E. & MacNally, R. (2006) Patterns of spatial autocorrelation of assemblages of birds, floristics, physiognomy and primary productivity in the central Great Basin, USA. *Diversity and Distributions*, **12**, 236–243.

Forman, R.T.T. & Godron, M. (1981) Patches and structural components for a landscape ecology. *BioScience*, **31**, 733–740.

Fowler, N.L. (2002) The joint effects of grazing, competition, and topographic position on six savanna grasses. *Ecology*, **83**, 2477–2488.

Fuhlendor, S.D. & Smeins, F.E. (1997) Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus–Quercus* savanna. *Journal of Vegetation Science*, **8**, 819–828.

Gardner, R.H., Kemp, W.M., Kennedy, V.S. & Peterson, J.E. (2001) *Scaling relations in experimental biology*. Columbia University Press, New York.

Hadley, E.A. & Maurer, B.A. (2001) Spatial and temporal patterns of species diversity in montane mammal communities of western North America. *Evolutionary Ecology Research*, **3**, 477–486.

Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.

Harrison, S., Inouye, B.D. & Safford, H.D. (2003) Ecological heterogeneity in the effects of grazing and fire on grassland diversity. *Conservation Biology*, **17**, 837–845.

Hawkes, C.V. & Sullivan, J.J. (2001) The impact of herbivory on plants in different resource conditions: a meta-analysis. *Ecology*, **82**, 2045–2058.

Hobbs, R.J. (2001) Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in southwestern Australia. *Conservation Biology*, **15**, 1522–1528.

Holling, C.S. (2004) From complex regions to complex worlds. *Ecology and Society*, **9** (1), 11. [online at: http://www.ecologyandsociety.org/vol9/iss1/art11/main.html].

Holm, A.M., Loneragan, W.A. & Adams, M.A. (2002) Do variations on a model of landscape function assist in interpreting the growth response of vegetation to rainfall in arid environments? *Journal of Arid Environments*, **50**, 23–52.

Hooten, M.B. & Wikle, C.K. (2006) A hierarchical Bayesian non-linear spatio-temporal model for the spread of invasive species with application to the Eurasian collared-dove. *Environmental and Ecological Statistics*, in press.

Johnson, C.J., Parker, K.L. & Heard, D.C. (2001) Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. *Oecologia*, **127**, 590–602.

Jorgensen, E.E. (2004) Small mammal use of microhabitat revisited. *Journal of Mammalogy*, **85**, 531–539.

Kepner, W.G., Watts, C.J., Edmonds, C.M., Maingi, J.K., Marsh, S.E. & Luna, G. (2000) A landscape approach for detecting and evaluating change in a semi-arid environment. *Environmental Monitoring and Assessment*, **64**, 179–195.

Kie, J.G., Bowyer, R.T., Nicholson, M.C., Boroski, B.B. & Loft, E.R. (2002) Landscape heterogeneity at different scales: effects on spatial distribution of mule deer. *Ecology*, **83**, 530–544.

Kotliar, N. & Wiens, J.A. (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, **59**, 253–260.

Legêndre, P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology*, **74**, 1659–1673.

Leponce, M., Theunis, L., Delabie, J.H.C. & Roisin, Y. (2004) Scale dependence of diversity measures in a leaf-litter ant assemblage. *Ecography*, **27**, 253–267.

Levin, S.A. (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur Award Lecture. *Ecology*, **73**, 1943–1967.

Lichstein, J., Simons, T., Shriner, S. & Franzreb, K. (2002) Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs*, **72**, 445–463.

MacMahon, J.A. (1987) Disturbed lands and ecological theory: an essay about a mutualistic association. *Restoration ecology: a synthetic approach to ecological research* (ed. by W.R. Jordan III, M.E. Gilpin, and J.D. Aber), pp. 221–237. Cambridge University Press, Cambridge.

Manly, B.F.J., McDonald, L.L. & Thomas, D.L. (2002) *Resource selection by animals: statistical design and analysis for field studies*, 2nd edition. Chapman and Hall, London.

McGarigal, K. & Cushman, S.A. (2005) The gradient concept of landscape structure. *Issues and perspectives in landscape ecology* (ed. by J. Wiens and M. Moss), pp. 112–119. Cambridge University Press, Cambridge.

Meyer, C.B. & Thuiller, W. (2006) Accuracy of resource selection functions across spatial scales. *Diversity and Distributions*, **12**, 288–297.

Milchunas, D.G. & Lauenroth, W.K. (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, **63**, 327–366.

Milchunas, D.G., Lauenroth, W.K. & Burke, I.C. (1998) Livestock grazing: animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. *Oikos*, **83**, 65–74.

Milchunas, D.G. & Noy-Meir, I. (2002) Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos*, **99**, 113–130.

O'Neill, R.V. & King, A.W. (1998) Homage to St. Michael; or, why are there so many books on scale? *Ecological scale: theory and applications* (ed. by D.L. Peterson and V.T. Parker), pp. 3–15. Columbia University Press, New York.

Palik, B.J., Goebel, P.C., Kirkman, L.K. & West, L. (2000) Using landscape hierarchies to guide restoration of disturbed ecosystems. *Ecological Applications*, **10**, 189–2002.

Palmer, S.C.F., Hester, A.J., Elston, D.A., Gordon, I.J. & Hartley, S.E. (2003) The perils of having tasty neighbors: grazing impacts of large herbivores at vegetation boundaries. *Ecology*, **84**, 2877–2890.

Perry, D.A. & Amaranthus, M.P. (1997) Disturbance, recovery, and stability. *Creating a forestry for the 21st century: the science of ecosystem management* (ed. by K.A. Hohm and J.F. Franklin), pp. 31–56. Island Press, Washington, D.C., USA.

Peters, D.P., Pielke, R.A. Sr, Bestelmeyer, B.T., Allen, C.D., Munson-McGee, S. & Havstad, K.M. (2004) Cross–scale interactions, nonlinearities, and forecasting catastrophic events. *Proceedings of the National Academy of Sciences USA*, **101**, 15130–15135.

Peterson, D.L. & Parker, V.T., eds. (1998) *Ecological scale: theory and applications*. Columbia University Press, New York.

Rahbek, C. & Graves, G.R. (2000) Detection of macro-ecological patterns in South American hummingbirds is affected by spatial scale. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **267**, 2259–2265.

Rahbek, C. & Graves, G.R. (2001) Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences USA*, **98**, 4534–4539.

Richardson, D.M., Rouget, M. & Rejmánek, M. (2004) Using natural experiments in the study of alien tree invasions: opportunities and limitations. *Experimental approaches to conservation biology* (ed. by M.S. Gordon and S.M. Bartol), pp. 180–201. University of California Press, Berkeley, USA.

Rietkerk, M., Boerlijst, M.C., van Langevelde, F., HilleRisLambers, R., van de Koppel, J., Kumar, L., Prins, H.H.T. & de Roos, A.M. (2002) Self-organization of vegetation in arid ecosystems. *American Naturalist*, **160**, 524–530.

Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.

Rouget, M. & Richardson, D.M. (2003) Understanding patterns of plant invasion at different spatial scales: quantifying the roles of environment and propagule pressure. *Plant invasions: ecological threats and management solutions* (ed. by L.E. Child, J.H. Brock, G. Brundu, K. Prach, P. Pyšek, P.M. Wade and M. Williamson), pp. 3–15. Backhuys Publishers, Leiden, the Netherlands.

Schneider, D.C. (1994) *Quantitative ecology: spatial and temporal scaling*. Academic Press, San Diego, California, USA.

Scott, J.M., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.A. & Samson, F.B., editors (2002) *Predicting species occurrences: issues of accuracy and scale*. Island Press, Washington, D.C.

Skarpe, C., Bergström, R., Bråten, A.L. & Danell, K. (2000) Browsing in a heterogeneous savanna. *Ecography*, **23**, 632–640.

Swihart, R.K., Lusk, J.J., Duchamp, J.E., Rizkalla, C.E. & Moore, J.E. (2006) The roles of landscape context, niche breadth, and range boundaries in predicting species responses to habitat alteration. *Diversity and Distributions*, **12**, 277–287.

Teague, W.R., Dowhower, S.L. & Waggoner, J.A. (2004) Drought and grazing patch dynamics under different grazing management. *Journal of Arid Environments*, **58**, 97–117.

Turner, W.R. & Tjørve, E. (2005) Scale-dependence in species–area relationships. *Ecography*, **28**, 721–730.

Walker, B. & Meyers, J.A. (2004) Thresholds in ecological and social–ecological systems: a developing database. *Ecology and Society*, **9** (2), 3. [online at: http://www.ecologyandsociety.org/vol9/iss2/art3].

Warman, L.D., Sinclair, A.R.E., Scudder, G.G.E., Klinkenberg, B. & Pressey, R.L. (2004) Sensitivity of systematic reserve selection to decisions about scale, biological data, ad targets: case study for southern British Columbia. *Conservation Biology*, **18**, 655–666.

Warner, P.J. & Cushman, J.H. (2002) Influence of herbivores on a perennial plant: variation with life history stage and herbivore species. *Oecologia*, **132**, 77–85.

Whittaker, R.J. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453–470.

Wickham, J.D., Wu, J. & Bradford, D.F. (1997) A conceptual framework for selecting and analyzing stressor data to study species richness at large spatial scales. *Environmental Management*, **21**, 247–257.

Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.