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EDITORIAL

Large-scale ecology and hydrology: an introductory perspective from the editors of the *Journal of Applied Ecology*

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Summary

1. Five key features characterize large-scale factors in ecology: (a) they incorporate some of the most major of all ecological phenomena – the ranges of organisms, patterns of diversity, variations in ecosystem character and environmental processes such as climate, biogeochemical cycles, dispersal and migration; (b) they involve interactions across scales through both top-down and bottom-up processes; (c) they are multifaceted, and hence require an interdisciplinary perspective; (d) they reflect the cumulative effects of anthropogenic change across all scales, and so have direct relevance to environmental management; (e) they invariably exceed the range of classical ecological experiments, and so require alternative approaches to hypothesis testing.

2. Against this background, a recent research initiative on large-scale ecology and hydrology was funded jointly by the Natural Environment Research Council (NERC) and the Scottish Executive Rural Affairs Department (SERAD). Outputs from this programme are reported in this special issue of the *Journal of Applied Ecology*, and they illustrate some of the ecological research that is currently in progress in the UK at large spatio-temporal scales.

3. The spatial scales investigated in the papers range from hectares to whole continents, and much of the work reported here involves modelling. Although the model outputs are intrinsically valuable, several authors express the need for improved validation and testing. We suggest that this is an area requiring much development, and will need considerable innovation due to the difficulties at the scales involved (see 1d). Possible methods include: model applications to new circumstances; large-scale environmental manipulations; large-scale surveys that mimic experimental protocols; support from process studies at smaller scales. These alternatives are not mutually exclusive, and all can allow robust hypothesis testing.

4. Much of the work reported here is interdisciplinary linking, for example, geographical, mathematical, hydrological, hydrochemical and ecological concepts (see 1c). We suggest that even stronger links between environmental disciplines will further aid large-scale ecological research.

5. Most important in the context of the *Journal of Applied Ecology*, the work reported in this issue reveals that large-scale ecology already has applied value. Sectors benefiting include the conservation of biodiversity, the control of invasive species, and the management of land and water resources.

6. Large-scale issues continue to affect many applied ecologists, with roughly 30–40% of papers published in the *Journal of Applied Ecology* typically confronting such problems. This special issue adds to the growing body of seminal contribu-

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tions that will add impetus to further large-scale work. Moreover, occurring in a period when other areas of biology are increasingly reductionist, this collection illustrates that, at least with respect to large-scale environmental problems, ecology still holds centre ground.

Key-words: models, management, conservation, biodiversity, invasive species.

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Background: large-scale issues in ecology

There can be few ecologists who do not recognize the importance of large-scale pattern and process in ecology (Levin 1992; Ricklefs & Schluter 1993; Edwards, May & Webb 1994; Caldow & Racey 2000). Among the many key elements, five are central.

First, large-scale factors simultaneously reflect and affect some of the most important aspects of ecological systems: the ranges of organisms, patterns of diversity, variations in ecosystem character, and environmental processes such as climate, biogeochemical cycles, dispersal or migration. All of these factors embrace the largest possible geographical scales on earth.

Secondly, the effects of processes at large scales interact with those at small scales in complex ways. On the one hand, large-scale variation can subsume small-scale pattern. On the other, large-scale patterns are often the aggregate effect of smaller-scale phenomena. Large spatial scales and temporal scales thus present clear difficulties for interpreting cause, even where pattern is apparently clear (e.g. see Collingham *et al*. 2000).

Thirdly, the processes involved at large spatio-temporal scales embrace all possible types of environmental variation: physical, chemical and biological. Large-scale issues require an equally multifaceted and strongly interdisciplinary perspective from researchers and environmental managers.

Fourthly, many large-scale phenomena are affected directly by global-scale change, or by the cumulative effects across regions of factors generated more locally: species extinctions; pollution from point or diffuse sources; piecemeal change in habitat quality. In other words, large-scale ecological issues interface directly with the scales at which many applied ecological problems are generated, and at which environmental management must be aimed. A large-scale perspective and sustainable environmental management are flip-sides of the same ecological coin.

Finally, and most germane to this special issue, our ability to respond with appropriate methods to the challenges of large-scale ecological problems is far from mature. Ecology has shifted progressively in the last 30 years to become one of the most experimentally orientated of all environmental disciplines. With increasing interest in large-scale pattern and processes, however, the realization has grown that scale limits the possibilities for ecological research: manipulation, control and replication all become increasingly difficult as the geographical size of our interests increase. The scales attainable in conventional ecological experiments are invariably far smaller than the scales required to capture large-scale phenomena (Kareiva & Anderson 1989). In other words, large-scale issues have been accompanied by the need to develop and test large-scale hypotheses in ways that move beyond classical experiments without compromising scientific rigour. The problems and possibilities in each potential approach are still widely debated so that there is clear need for applied case studies, like those in this volume.

Large-scale Ecology and Hydrology: the NERC/SERAD Special Topic

In many respects, the contributions to this special issue of the *Journal of Applied Ecology* are a response to all five key points above. They touch on all of them, but in particular they offer positive and innovative responses to the methodological challenge posed by the scale problem. Stemming from a special topic funded jointly by the UK Natural Environment Research Council (NERC) and the Scottish Executive Rural Affairs Department (SERAD), the papers offer largely informatic or model-based paradigms to a range of applied issues. For example, Gaston *et al.* (2000) provide one of the most explicitly macroecological perspectives in the whole volume. They explore large-scale relationships between the abundance and occupancy of organisms, both within and between species. They illustrate how range size and abundance are linked such that range reductions are often accompanied by reductions in the average density of organisms. In their own right, these ideas are not new, but Gaston and his co-workers explore both biological explanations of the resulting pattern and, importantly in the context of this Journal, they highlight some of the practical applications of the resulting knowledge. They tell us, for example, about the difficulties of appraising biodiversity, particularly for rare species; they reveal the difficulties of conserving species that are both low in abundance and apparent over narrow geographical ranges; conversely, they show us that invasive species will occur not only in large numbers, but also at many locations. In so doing, this work gives a key example not only of the importance of macroecology, but of macroecology in application.

At the regional scale, Cowley *et al.* (2000) conclude that basic habitat features can be used to predict the presence and absence of butterflies using statistical methods of the types that are already in wide use in studies published in the *Journal of Applied Ecology* (Ferreras & Macdonald 1999; Rodriguez & Andren 1999; Sanchez-Zapata & Calvo 1999). In keeping with material that we publish often (see Ormerod, Pienkowski & Watkinson 1999), this work illustrates the utility of presence–absence modelling with respect to one of the most conservationally important insect groups (Hill 1999). Perhaps more importantly, in a special issue in which modelling approaches appear to dominate large-scale ecology, Cowley *et al.* (2000) conclude that their models and methods require testing over wider areas than hitherto.

Turning from conservation to invasive species, Collingham *et al.* (2000) use similar logistic techniques to assess potential influences on the distribution of three non-indigenous weeds. Interestingly, the dynamic distributional nature of these invasive organisms reveals how the goodness of fit in logistic models can sometimes be compromised; apparently suitable sites for a given species might not yet be occupied. This lesson will have wide value to anyone attempting to model dynamic populations, of which there will be many examples. Several scale-dependent problems result – for example, in assessing whether species have expanded to fill their whole range, or appraising distributions by scaling-up from fine scales or scaling-down from coarse scales. Wadsworth *et al.* (2000) also modelled the spread and dispersal of riparian weeds from parameters describing dispersal and demography, exploring control strategies through a GIS environment. Their conclusions – once again with real utility and value in the spirit of this Journal – reveal the need to understand species distribution, spatial population structure and available habitat in the control of invasive organisms.

Applied ecology not only involves demonstrating instances where ecology has management value, but it also involves exploring instances where applied issues aid in testing ecological theory (Ormerod, Pienkowski & Watkinson 1999). Petty *et al.* (2000) and Sherratt *et al.* (2000) provide particularly clear examples of the latter. They examine how basic ecological hypotheses about synchronous patterns of small mammal abundance involve avian predation and forest management. Even this near-fundamental study turns up recommendations for forest managers.

Some of the most well established instances of large-scale ecology apply to river catchment ecosystems, one of the most traditional areas both of whole-ecosystem manipulation and large-scale analysis of pattern (Johnson & Gage 1997; Manel *et al.* 1999; Manel, Buckton & Ormerod 2000). This is an area also where ecological and physical sciences – hence ecology and hydrology – blend most appropriately. Both the contributions on this theme take catchment attributes and illustrate how they can be used to model empirically large-scale aspects of hydrochemistry (Cresser *et al.* 2000; Edwards *et al.* 2000). Both also point to areas where our understanding of interactions between land use, chemical flux and aquatic biology need development. In so doing, these contributions reveal the potential importance of large-scale models to integrate land and water management.

Finally in this issue are three contributions that explore the ecology of a group of organisms whose individual range, movements and life cycles are among the most pertinent of all to large-scale ecology: the birds (Baillie *et al.* 2000; Paradis *et al.* 2000; Pettifor *et al.* 2000). In instances of population change, for example, birds respond to features across a whole graded patchwork of scales from the local (e.g. nest failure due to corvids; Paradis *et al.* 2000) to the intercontinental (e.g. habitat change over migratory ranges; Pettifor *et al.* 2000). Also with increasingly recognized importance in conservation, dispersal movements between habitat patches might markedly affect population processes (Baillie *et al.* 2000). These ornithological contributions not only provide potential models for other organisms, but also emphasize the value of an integrated, whole-landscape perspective to nature conservation. Conservation involving purely 'protected areas' might not be sufficient. This view will find much favour among those with interest in organisms whose numbers in the wider environment are in the midst of dramatic change (Duncan *et al.* 1999; Henderson *et al.* 2000; Siriwardena *et al.* 2000).

Large-scale ecology and hydrology in the *Journal of Applied Ecology*

The *Journal of Applied Ecology* has traditionally been in the vanguard of pursuing large-scale approaches to ecology like those in this issue. Roughly 30–40% of our published studies typically confront large spatial scales (> hectares) and long time scales (> 5–10 years) (Ormerod, Peinkowski & Watkinson 1999; Ormerod & Watkinson 2000). Equally, the Natural Environment Research Council (NERC) – the UK government's independent leading body for research, survey, monitoring and training in the environmental sciences – has positively embraced large-scale and interdisciplinary science, most recently forming the Centre for Ecology and

Hydrology from some of its previous component NERC Institutes. We suggest that initiatives like this – which foster cross-disciplinary interaction – can serve to further augment the capability of large-scale ecology.

The *Journal*'s editors are therefore enthusiastic in commending this important series of papers to our readers: they demonstrate not only that large-scale approaches are developing strongly, but also that large-scale and multidisciplinary perspectives are making real contributions to the application and institutionalisation of ecology. Furthermore, we believe that this collected body will now act as a further spur for applied work involving some of the major large-scale approaches available to us: macroecology (Gaston *et al.* 2000); multivariate analysis to assess large spatio-temporal pattern (Chamberlain *et al.* 1999); testable models (Manel *et al.* 1999); large-scale intervention studies (Peet *et al.* 1999); surveys or *a priori* contrasts between locations selected to allow blocking and matching in ways that mimic experimental protocols (Henderson *et al.* 2000); large-scale observations supported by careful process studies (Peach, Siriwardena & Gregory 1999). All of these approaches will not only advance our understanding of large-scale ecological phenomena, but they can also provide for much-needed testing of models of the type described in this issue. That this collection of explicitly large-scale papers should arise at a time when other areas of biology are increasingly reductionist illustrates that, at least with respect to large-scale environmental problems, ecology still holds centre ground.

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