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INTRODUCTION

Large-scale processes in ecology and hydrology

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Summary

1. Several papers published in the 1980s stressed the importance of scaling issues, the inter-relatedness of patterns and processes at different scales of time and space, to our understanding of ecological systems. Scaling issues are of major theoretical interest and increasingly are of considerable applied importance.

2. In recognition of this, the Natural Environment Research Council, in partnership with the Scottish Executive Rural Affairs Department, funded a Thematic Programme entitled 'Large-scale Processes in Ecology and Hydrology'. The principal aim of this Programme was to integrate recent major developments in information resources and technologies with current theory in order to improve understanding of large-scale patterns and processes and their relationship to patterns and processes at smaller scales.

3. The Thematic Programme, which ran from 1995 until 1999, funded six research projects that have generated a large body of published papers. This volume, dedicated to the findings of the Programme, brings together outputs from all six projects with the aim of ensuring a rapid and widespread dissemination of the Programme's findings. A brief résumé of each of the papers is presented.

4. The papers in this volume cover a wide variety of subjects ranging from ions to the flora and fauna of the United Kingdom. Nonetheless, each study has sought in various ways to quantify observed spatio-temporal patterns at a range of scales, to determine whether those patterns are consistent across scales and to identify the interactions between small-scale patterns and processes and those at larger scales. The importance of the spatial and temporal scales at which studies are conducted, the key role played by dispersal in spatial population dynamics, and the diversity of ways in which large-scale patterns and processes relate to those at smaller scales are highlighted in many of the papers.

4. All of the papers presented here have direct relevance to applied issues. These issues are diverse and include the control of invasive alien species, the conservation of declining, threatened or endangered species, the development of survey techniques, strategies for farmland, woodland and forestry management, and the assessment of pollution sensitivity. Thus, the Thematic Programme has addressed issues of considerable theoretical interest and has at the same time generated results and predictive models that are of considerable practical and policy relevance.

Key-words: population dynamics, scaling issues, spatial scale, temporal scale.

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Introduction

In the Robert H. MacArthur Award lecture presented in Canada in 1989, entitled 'The problem of pattern and scale in ecology' Simon Levin (Levin 1992) stated that 'The concepts of scale and pattern are ineluctably intertwined .... The description of pattern is the description of variation, and the quantification of variation requires the determination of scales'. At the same time, and in a similar vein, Powell (1989) noted that to discuss scale is to discuss variability, for one cannot assign a scale to a process or quantity that is uniform in space (or time). Wiens (1989) noted that '"scale" is rapidly becoming a new ecological buzzword'. Both Wiens (1989) and Levin (1992) concluded that scaling issues, the interaction among phenomena on different scales, should be considered as a primary focus of research efforts. Since then, there has indeed been an explosion of interest in scaling issues, individual-based models, metapopulation dynamics, landscape and spatial ecology (see recent compilations in Gilpin & Hanski 1991; DeAngelis & Gross 1992; Edwards, May & Webb 1994a; Tilman & Kareiva 1997; Bascompte & Solé 1998).

Due to a lack of insight, logistical limitations, reliance on an experimental approach, financial constraints or simply a desire to keep the mathematics simple, an astonishingly high proportion of ecological studies have focused on the ecology and behaviour of individuals or small groups at small spatial scales and over very short periods of time (May 1994). As the minutiae of ecological processes have been examined in progressively more detail there has been a strong tendency to ignore possible complicating factors operating over a larger scale (Edwards, May & Webb 1994b). On the other hand, general circulation models provide a good example of a situation in which large-scale processes are over-emphasized at the expense of the fine scale (Levin 1992). As stated by Levin (1992) 'the key to prediction and understanding lies in the elucidation of the mechanisms underlying observed patterns'. Because different processes are likely to be important on different scales, the key is to find ways to achieve their integration (Levin 1992).

The issue of scale in science is not just of theoretical interest but, because it is of critical importance to our understanding of how systems work, it is also of considerable applied interest (Omerod & Watkinson 2000). An understanding of scale influences our ability to predict the way in which systems are likely to respond to environmental change. The scale of environmental change has itself increased dramatically over the last few decades. Accordingly, the attention of conservationists and policy makers alike has broadened as shifts in agricultural practices have produced unprecedented countryside changes, and man-made pollution has resulted in continent-wide effects of acid precipitation and potentially, sea-level rise and global climate change. Increasingly, policy issues demand an understanding of ecological processes at the broadest spatial scales and over long-time periods.

Against this theoretical and practical background, the Land Use Research Co-ordinating Committee of the Natural Environment Research Council (NERC) generated a proposal for an integrated research programme on large-scale processes in ecology. This was submitted to the Terrestrial and Freshwater Sciences Committee of NERC for consideration as an NERC-funded Special Topic. The proposal was submitted on the basis that a research programme on large-scale processes was technically feasible, and scientifically both challenging and desirable. The opportunity was provided by major developments in both information resources and technologies. The scientific challenge was to integrate these advances with appropriate ecological theories to understand processes at large scales. The desire to conduct such a programme of research was based on the expectation that it would provide strong theoretical insights as well as being both necessary and urgent for the future development of countryside management.

Final approval of funding for the proposal was given by NERC Council, which allocated £882 k to fund a Thematic Programme, entitled 'Large-scale Processes in Ecology and Hydrology'. Realizing the potential relevance of the proposed research programme to policy issues, the Scottish Executive Rural Affairs Department (SERAD) (formerly the Scottish Office Agriculture, Environment and Fisheries Department) and the Department of the Environment (DoE) agreed to co-fund the programme and to contribute £450 k and £600 k to the overall budget, respectively.

Announcements of opportunity were placed in *Nature* and *New Scientist* in mid-October 1994. Proposals were invited for innovative studies that included a strong element of theory and modelling to facilitate prediction, combined with observations, e.g. through remote sensing or field measurement, and the integration of existing data bases with modern information technologies. Proposed studies were also required to have clear practical and policy relevance. One hundred and thirty-six expressions of interest were submitted. Of these, 30 were selected by the Steering Committee for assessment as full proposals. In June 1995 the Steering Committee recommended that six projects be funded. This was fewer than originally hoped because, although SERAD increased its financial contribution to £600 k, the DoE was forced, for financial reasons, to withdraw from the funding consortium.

Over the course of the Programme, which ran from late-1995 until mid-1999, approximately 50 scientists at 14 research establishments were directly

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involved in work on the various projects. The cosponsors of the Programme, the Steering Committee and those involved in the research were keen to ensure a speedy and widespread dissemination of the Programme's findings. To this end, the final Programme workshop took the form of two sessions of the winter meeting of the BES held in January 1999 at the University of Leicester. Publication of the current volume, dedicated to the findings of the Thematic Programme, sees the fulfilment of the goal of widespread dissemination. However, the papers contained in this volume represent only a small proportion of the Programme's total output published to date. To date, the Programme has led to the publication of 47 refereed papers, in addition to those presented here, and the production of four PhD theses, four MSc. theses and five Honours theses. Many of the contributions to this volume refer to these existing publications and readers are strongly recommended to consult them in order to fully appreciate the diversity of findings generated by each of the projects of which only a sample is provided here.

The current volume contains 11 papers, two from each of five projects and one from the sixth. The first nine papers in this volume are primarily ecological and restrict their attention to terrestrial ecosystems, although the interests of Pettifor *et al.* (2000) extend to the edge of marine ecosystems. The last two papers in this volume arise from the one hydrochemically orientated project within the Programme, and differ from the others partly as a consequence of their subject matter, but also in the sense that they deal explicitly with the interaction between processes occurring within terrestrial, freshwater and indeed atmospheric systems. A brief résumé of each of the 11 papers is presented here.

A major theme of John Wiens' lecture (Wiens 1989) was that the spatial and temporal extent and resolution of ecological studies might have significant influences on the patterns that are observed and the conclusions that are drawn concerning the underlying processes. In the first paper in this volume Collingham *et al.* (2000) address these issues with a thorough analysis of the distribution of alien weeds recorded at a range of spatial resolutions and extents. They explore whether the environmental variables that appear to underlie the distribution of these plants varies depending on the resolution or extent of the sampling, and hence whether models derived from data at one resolution at one scale can successfully predict distributions at other resolutions and scales. There appears to be no hierarchy of environmental controls on the distribution of these species at different spatial scales, yet the ability to model species' distributions varied considerably as a function of both spatial resolution and extent. Predictive models based on studies of small spatial extent and coarse resolution are inadequate for making predictions of distributions either at finer resolutions or wider spatial extents. The possible influences of the scale-dependency of species' sparseness, the validity of the assumption of population equilibrium and spatial autocorrelation on these findings are discussed.

Building on the analyses of Collingham *et al.* (2000), Wadsworth *et al.* (2000) present a spatially explicit GIS-based model of the spread of riparian alien weeds at two spatial scales. As is apparent in several other papers in this volume, this paper provides a clear example of the dependence of spatial models of population dynamics on a detailed understanding of species' dispersal functions and in particular the incidence and distance of long-range dispersal events. The implications of this insight are illustrated by using the model to identify the most effective means of controlling the invasive spread of alien weeds. It is clear that, given the capacity of such species for infrequent, long-range dispersal, within-catchment, locally based strategies are less likely than larger-scale, regional approaches to be successful in controlling populations of these invasive aliens.

One of the most general and robust patterns in ecology is the positive relationship between species' abundance and their range (Lawton *et al.* 1994). This relationship has considerable implications for various aspects of applied ecology including the control of invasive species such as those discussed in the first two papers. In the third paper in this volume Gaston *et al.* (2000) present a synthesis of an extensive and thorough analyses of this relationship, drawing on many recently published papers that are derived from this Programme. The existence of the relationship, and the analyses discussed in the paper, emphasize the importance of ensuring that data analyses, ecological surveys and conservation targeting are all structured appropriately in space and time given the spatial and temporal variability in the abundance and distribution of the study species. Although the abundance–occupancy relationships are remarkably robust, occurring intraspecifically, interspecifically, in a range of taxa, and across multiple spatial scales, the general conclusion is that, although some proposed mechanisms can be discounted, no single mechanism can explain all the relationships. Different processes are likely to be acting within and between species, and depending on the spatial scale of the assemblage.

A second component of this project exploring the abundance–occupancy relationship is presented in Cowley *et al.* (2000). This paper is concerned with the patterns of occupancy of Lepidoptera at a range of spatial scales and exploration of whether these can be explained on the basis of the densities of the butterflies in differing habitats and the distribution of those habitats at local and regional scales. Cowley *et al.* (2000) found that there were highly signifi-

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cant relationships between habitat-based predictions of the probability of occurrence of butterflies at both local and regional scales and their observed occupancy at those scales. Variability in the distribution of many species of butterflies in a heterogeneous, fragmented landscape would seem to be predictable simply from the distributions of their habitats within the landscape, at least up to regional scales. It is interesting that, as was found in the case of the three riparian alien weeds (Collingham *et al.* 2000), there would appear not to be any hierarchy of environmental controls of butterfly distribution at least up to regional scales.

Classic metapopulation models divide a landscape into patches of suitable habitat embedded within an unusable matrix. Debatably, this model structure may be a reasonable approximation for many invertebrates such as butterflies, but it is not a particularly realistic description of landscapes as perceived by most vertebrates. Models that can deal with continuously distributed organisms, such as source–sink and balanced dispersal models, are more appropriate in these cases. These models rely upon different assumptions about spatial variation in breeding performance and these can lead to different predictions regarding population dynamics. In an analysis that parallels that presented by Collingham *et al.* (2000), Paradis *et al.* (2000) investigate the spatial correlates of reproductive output of two species of common bird and the scale-dependence of these correlates. They develop a predictive modelling approach that can be used to evaluate the implications of current and proposed countryside management for variation in breeding performance of these and, with appropriate data, other species. Paradis *et al.* (2000) found that in both species there was considerable spatial variation in each of the components of reproductive output. Importantly, whereas some components varied primarily on a large spatial scale, others did so in relation to environmental factors that varied on a small spatial scale. Thus, although large-scale patterns in overall reproductive output are observed (and predicted), a fine-scale patchy variation in reproductive output is superimposed on this larger-scale pattern by the response of key components of reproductive output to local environmental conditions. Understanding the variation in breeding performance of these, and probably many other species, clearly requires a multiscale approach.

The tendency of ecological studies to focus on small areas necessarily means that they are often subject to regular immigration and emigration as a result of dispersal. Baillie *et al.* (2000) present a modelling approach to explore whether a large-scale approach, in which patches of habitat are viewed in the context of the wider landscape is, due to dispersal, likely to give different results from more traditional, focused studies. Using empirically derived dispersal functions and demographic parameters, Baillie *et al.* (2000) present a spatially explicit model of the dynamics of passerines in artificial and more realistic landscapes comprising patches of high-quality habitat within a matrix of less-suitable habitat. Simulations reveal that dispersal can have a markedly negative effect on the density achieved in high-quality patches and that this effect is exacerbated as blocks of such habitat shrink and become increasingly fragmented. Interestingly, the model demonstrates that deterioration in a lower-quality habitat can lead to population declines in better quality habitat where conditions remain unchanged. Indeed, Baillie *et al.* (2000) demonstrate that the density of birds in one location can be significantly positively correlated to the density of birds in surrounding areas, up to a distance of at least 20 km. This is analogous to the analyses of domains of spatial synchrony presented by Sherratt *et al.* (2000). Studies carried out at a local scale may lead to completely false conclusions concerning the processes determining abundance, even within a local study site, let alone at the level of the wider population.

Baillie *et al.* (2000) point out that in spite of the obvious importance of the density dependence of key demographic parameters to population models, there are considerable problems in quantifying such functions. They also point out that caution must be exercised when models based on such empirically derived functions are used to generate predictions of population dynamics under scenarios that differ widely from those under which the key parameter values and functions are derived. There is no guarantee that such functions will remain the same under the new conditions for which predictions may be required. Pettifor *et al.* (2000) present a behaviour-based modelling approach which avoids these problems.

The models of Pettifor *et al.* (2000) concern the year-round dynamics and movement of two populations of long-distance migrant geese. These models, by adoption of a spatially explicit and year-round approach, represent an advance on current single-site and single-season, behaviour-based models. They are not only successful in mimicking observed density-dependent functions, but also a number of 'lower-level' phenomena such as the seasonal variation in the energy reserves carried by geese. Because this is the key to their survival, this suggests that the models' predictions of mortality are unlikely to be 'right' for the 'wrong' reasons. Simulations illustrate the way in which single-site and more realistic multi-site models can differ in their predictions of density dependence and how spatially explicit models can reveal the consequences of differing patterns of environmental change. It is clear that, as alluded to by Baillie *et al.* (2000), the effect of habitat change on populations depends not only on the quality of the habitat that is affected but also on the precise location of the habitat change. Simulations confirm theoretical expectations that the response of a population to habitat change depends upon the strength and interaction of density dependence in both the breeding and non-breeding seasons. This is almost certainly a general rather than a goose-specific conclusion.

An area of particular interest in theoretical spatial ecology has been the determination of the causes of pattern in homogenous systems. Related to this, the questions of how and why local populations separated by varying distances fluctuate in synchrony have also been of great interest. In line with the theoretical background provided by reaction–diffusion models, it has been hypothesized that nomadic avian predators may be responsible for generating synchrony in microtine rodent populations over large geographical areas. Petty *et al.* (2000) take advantage of a natural experiment in one of the largest man-made forest in Europe to test this hypothesis. In this instance, there is, however, no evidence in support of the hypothesis. There is also no evidence that sedentary, territorial predators act to synchronize vole populations over smaller spatial scales. It is suggested that the synchrony in the abundance of field voles in this system may be driven by vole dispersal rather than by predators. This idea is explored in the companion paper by Sherratt *et al.* (2000).

Sherratt *et al.* (2000) develop a variety of spatially explicit models with which they explore whether small-scale local dispersal between otherwise independently oscillating local populations can generate large-scale patterns in vole abundance, i.e. synchrony. Consistent with existing studies of the role of small amounts of movement between cities in synchronizing disease infections, Sherratt *et al.* (2000) demonstrate that small-scale dispersal alone can readily generate large-scale synchrony. Indeed, once scaled to mimic the sizes and distribution of clear-cut patches in the study system, models with low rates of local dispersal generate domains of synchrony consistent with the observed speed of travelling waves of vole abundance. Indeed, it would seem that it may be the very patchiness of this man-made system, and the restrictions this imposes on voles' dispersal abilities, that may generate the relatively small-scale waves of abundance in comparison with the much larger domains of synchrony observed in more natural landscapes. Sherratt *et al.* (2000) also demonstrate that extremely low rates of local dispersal can generate extensive synchrony domains if there is infrequent long-distance dispersal. Nonetheless, they conclude that the scale of the factors generating oscillatory dynamics is more likely to be local rather than regional or global.

Apart from acidification, one of the main interests in river-water quality assessment, is the anthropogenic influence on nutrient budgets and in particular the spatio-temporal variation in concentrations of nitrogen (N) and phosphorus (P). In the penultimate paper, Edwards *et al.* (2000) present a detailed analysis of spatio-temporal variation in the concentration of various forms of N and P and, in particular, of N:P ratios in river-water along an upstream–downstream gradient. Edwards *et al.* (2000) describe substantial upstream–downstream variation in the concentration and load of a variety of chemical species and seasonal effects that differ between locations. This highlights the complexity of river-water nutrient dynamics and the need for large-scale, long-term studies to understand such cycles within heterogeneous river systems. Interestingly, Edwards *et al.* (2000) note that although concentrations of both N and P increased downstream within the main river, concentrations there were always substantially lower than those within individual lowland tributaries. This provides a clear example, paralleled in several of the other studies, of the way in which local environmental effects on spatio-temporal patterns in abundance, in this case of nutrients, can be heavily influenced or even confounded by larger scale processes, in this case the process of catchment-wide drainage.

The necessity of adopting an approach that encompasses both a large spatial scale and long-term processes to predicting spatio-temporal variation in natural systems is further exemplified in the final, hydrochemically orientated paper. Cresser *et al.* (2000) present a rigorous analysis and validation of a modelling approach that, being based on readily available catchment characteristics, should enable reliable predictions to be made of several key water-quality parameters in a range of catchments. The key finding of this study is that through the long-term process of weathering, the chemical composition of parent rock material, when weighted to take account of the water flow distribution within a catchment, provides a very powerful basis for predicting short-term spatio-temporal variation in several key water-quality parameters in upland catchments. More importantly, these underlying geological processes were also key components of models that, together with a few simple parameters describing catchment land-use, were extremely successful in predicting water-quality parameters in a range of upland and lowland catchments of a range of sizes and complexities. Particularly interesting is the insight that certain key water-quality parameters within freshwater systems can be strongly influenced by atmospheric inputs from maritime sources. This is an unexpected and salutary example of the interaction between processes that occur at a range of spatial scales.

The six research projects funded by the Thematic Programme, and the resultant papers presented here, have dealt with a diverse array of systems and have tackled a variety of spatial issues. Reference to the publications listed at the beginning of this introduction will show these issues to be of considerable theoretical interest. All of the studies have sought, in their various ways, to quantify spatio-temporal patterns at a range of scales. They have then sought to determine whether those patterns are consistent across scales and to identify the interactions between small-scale patterns and processes and those at larger scales, i.e. they have sought to relate phenomena across scales. Levin (1992) considered this to be 'the central problem in biology and in all of science'. The importance of the spatial and temporal scales at which studies are conducted, the key role played by dispersal in spatial population dynamics, and the diversity of ways in which large-scale patterns and processes relate to those at smaller scales are highlighted in many of the papers.

Each of the six projects has also addressed issues of considerable applied interest. They have provided insights into issues as diverse as the management strategies to control the spread of alien weeds, the potential of habitat-based models to facilitate survey and conservation targeting, the role that species' dispersal may play in the effectiveness of conservation 'islands', the importance of the spatial configuration of habitat loss to migratory populations, the influence of forestry felling regimens on the dynamics of voles and their predators, and novel methods to predict the susceptibility of river systems to acid flushes.

To conclude, the Large-scale Processes in Ecology and Hydrology Thematic Programme has provided many insights of relevance to the theoretical issue of scaling in both hydrological and ecological processes, as can be judged from the papers in this volume, and those already published elsewhere. Having generated a substantial number of predictive models, the Programme has also been of value to the future development of countryside management, planning and policy.

In accord with the Natural Environment Research Council, the Scottish Executive Rural Affairs Department and all those involved in the research projects funded by the Thematic Programme, we would like to express our thanks to each of the members of the Steering Committee for their work in ensuring the success of the Thematic Programme. Those who served on the Steering Committee are as follows: Professor Ian Calder, Dr Kevin Flynn, Dr Glen George, Professor Charles Godfray, Professor John Grace, Dr Terry Hegarty, Dr Richard Law, Dr Mike Pienkowski, Professor Keith Richards, Professor Bryan Shorrocks, Dr Andrew Skinner, Dr Mutsunori Tokeshi, Mrs Lindsay Turl, Dr Sarah Webster and Dr Toby Willison. We would also like to thank Mike Pienkowski, Steve Ormerod, Andrew Watkinson, Gillian Kerby and Penny Baker for their contributions to ensuring the publication of this special issue and John Baker, Cathy Garretty and Anne McFarlane of NERC for their involvement in the Programme.

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