

The Effect of Spatial and Temporal Heterogeneity on the Design and Analysis of Empirical Studies of Scale-Dependent Systems

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ABSTRACT: Processes interacting across scales of space and time influence emergent patterns in ecological systems, but to obtain strong inference and empirical generalities, ecologists need to balance reality with the practicalities of design and analyses. This article discusses heterogeneity, scaling, and design analysis problems and offers potential solutions to improve empirically based research. In particular, we recommend bridging the dichotomy between correlative and manipulative studies by nesting manipulative studies within a correlative framework. We suggest that building on variation, by designing studies to detect variability, rather than fighting it often leads to an increase in generality. We also emphasize the importance of natural history information for determining likely scales of spatial and temporal heterogeneity and the probable occurrence of feedback loops, indirect effects, and interacting processes. Finally, we integrate these concepts and suggest planned iterations between multiscale studies to build up natural history information and test the strength of relationships across space and time. This offers a way forward in terms of heuristically developing models and determining ecological generalities.

Keywords: scale, heterogeneity, empirical studies, interacting processes, study design, analyses.

Scale and heterogeneity in space and time have been acknowledged as important issues in ecology for many years

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(Pielou 1977; O'Neill et al. 1986; Levin 1992; Belovsky et al. 2004). The associated problems for scaling study results and assessing the validity of generalities across space and time have also been extensively discussed in the literature, for both empirical and modeling studies. Indeed, Lawton (1999) has concluded that the study of community ecology is dead because the complexity of ecological systems does not allow generalities to be developed.

Despite the recognition of the problems associated with scaling across heterogeneous systems, the designs and analyses of empirical ecological studies remain largely unchanged. Small-scale mechanistic experiments carried out in a few randomly selected locations and analyzed by categorical statistical methods still represent the majority of studies. There are a number of reasons, one of which is the reductionist approach, which seeks to reduce the variability encompassed by field studies at all levels. The strong emphasis on experimental manipulations in assigning causality and the practicalities of conducting manipulations across scales are also important. Moreover, statistical requirements (e.g., random collection of independent samples) can be at odds with the need to conduct studies within an understanding of natural history and environmental context (Futuyma 1998; Dayton 2003).

Although many advances have been made using small-scale manipulative experiments, many ecological systems are not easily reduced and manipulated. Emergent properties of such systems are context dependent and are produced by direct interactions and feedbacks that can operate across scales in spatially and temporally heterogeneous environments (DeAngelis and Waterhouse 1987). While this very complexity makes these systems exciting to study (Simberloff 2004), obtaining strong inference and generality requires new designs, analyses, and careful interpretation of empirical studies (Thrush et al. 2000; Simberloff 2004). This is not solely a problem for empirical studies because such studies provide the parameters, connections, rate estimates, and concepts for use in both the development and the validation of theoretical and statistical

models. If the data provided for models are scale or context dependent, then the model, although attempting to integrate over a number of scales, will be limited.

Working across scales can have a number of goals and encompass a variety of approaches: scaling through levels of biological organization (e.g., species to ecosystems), scaling between fine-scale measures and coarse-scale representations of the same variables, and extrapolating the effects of experiments conducted at a few locations or times to a more general set of conditions. Here we focus on generality and the effect of spatially and temporally heterogeneous processes acting at multiple scales on the bounds of extrapolation. While our examples are marine, the lessons apply equally to many fields of terrestrial and freshwater ecology.

Our purpose is to discuss means of empirically studying complex ecological processes. We review major problems posed for experimental design and analysis and, from the many studies available on design and analysis, derive practical guidelines for empirical ecologists. These guidelines rely on multiscale theory, which acknowledges that processes can operate over a continuum and interactions can occur across scales, for example, local relationships affecting broadscale processes (see Wu et al. 2000; O'Neill 2001; Denny et al. 2004). Another important element of our synthesis is an emphasis on incorporating natural history information and environmental context into design and interpretation.

Integrating Natural History and Environmental Context into Studies

Studies conducted in complex ecological systems frequently exhibit results that are difficult to interpret. However, the collection of natural history information or information on the surrounding environment often aids understanding. The type of information that will be useful is generally dependent on how spatial and temporal processes interact.

For example, feedback loops between large-scale variability in environmental conditions (e.g., variation in resources) and ecological processes (e.g., predation) can result in indirect effects on spatial patterns in community composition and trophic dynamics. Dayton et al. (1974) demonstrated such linkages in the coastal community of McMurdo Sound, Antarctica, between the sea stars *Acodontaster conspicuosus* (a sponge predator) and *Odontaster validus* (an omnivore, consuming both benthic primary production and *Acodontaster*). In areas with high benthic primary production, *Odontaster* reached densities sufficient to limit *Acodontaster* abundance. In both shallow-water areas with low benthic primary production and

deeper areas, *Odontaster* were rare and *Acodontaster* predation was sufficient to control sponge distributions.

Counterintuitive and variable results often result from spatially and temporally variable processes interacting with each other. Thrush et al. (1994) observed seasonally variable and counterintuitive decreases in abundance of prey species from a predator exclusion experiment. A series of studies on the natural history of both predators and prey explained the results as follows: (a) predation rates, spatial scales of feeding, and predator species varied over the year (shore birds [winter-spring] and eagle rays [summer; Cummings et al. 1997; Hines et al. 1997]) and (b) the major prey item of both was adult *Macomona liliana*, conspecific juveniles of which are highly mobile and avoid adults (Cummings et al. 1993; Thrush et al. 1996a).

Implications of Scale and Heterogeneity for Common Empirical Study Designs

Manipulative Experiments

The overwhelming advantage of manipulative experiments is their strict application of the hypothetico-deductive method. A specific hypothesis is stated and tested in such a way that the hypothesized mechanism is isolated from other potential mechanisms. However, scale and heterogeneity can cause a number of problems. First, variance in ecological systems tends to increase with spatial and temporal extent (Schneider 1994). Thus, experiments designed to encompass larger scales need to increase replication to control variability. Second, many aquatic species move actively or passively, and high lateral flux rates may swamp small-scale demographic or biotic processes and potentially confound small-scale field experiments (Schneider et al. 1997; Englund and Cooper 2003). However, passive movement generated by environmental forces is often not strong or persistent enough to override biological processes (Barry and Dayton 1991; Schneider 1991; Hewitt et al. 1997a). Thus, a key to successful experimentation is to account for both the degree of mobility of organisms and their ability to make an active habitat choice. Third, there are problems with generalizing results from studies conducted at one or a few locations or times, as broadscale processes can affect the outcome of small-scale processes, even to the point of changing the direction of responses (Smith and Brumsickle 1989; Greenlee and Callaway 1996; Thrush et al. 1996b). The importance of constraints to experimental outcomes becomes more apparent as a greater range of locations in space and time are studied (Bertness and Callaway 1994; Dayton et al. 1998; Thrush et al. 2000).

Correlative Studies

Properly designed correlative studies solve most of the problems noted for manipulative experiments, as they are more easily conducted over larger scales and are generally designed to incorporate spatial or temporal heterogeneity. Their major problem is not related to scale or heterogeneity but is the potential for spurious correlations to affect inferential strength (Eberhardt and Thomas 1991; Peters 1991). However, assigning causality is not the exclusive domain of manipulative experiments (Hill 1965; Rigler 1982; Peters 1991), even though, as Fabricius and De'ath (2004) note, that is the perception of many empirical ecologists. Gradients in the strength of effect and consistency among studies are often used to infer causality in medicine (e.g., epidemiology; Susser 1986; Fox 1991). Plausibility, that is, a general theory or accepted mechanism to account for effects, is used in physics and oceanography. Analogy (i.e., similar causes leading to similar effects) can also be used as a line of evidence.

A Way Forward

The need for rigorous design of ecological studies has frequently been highlighted (e.g., Eberhardt and Thomas 1991; Underwood et al. 2000; Legendre et al. 2004). Unfortunately, rigor is often defined as a design philosophy rather than a desire to increase generality by improving the understanding of the processes that underpin relationships. Statistically, random samples ensure generality but only within the population sampled. Ecologically, if random sampling is not conducted over large scales with high replication, then generality of results is unlikely. Thus, the careful selection of site locations along gradients (or among strata) and study scales (extent, lag, grain, and resolution) is needed. Measurement of variables that represent possible confounding or explanatory factors is also important. This enables spatial and temporal variability to be converted from noise into useful information so that we can understand why responses vary from location to location (rather than simply documenting that nature is variable). By doing so, it allows the study results to be extended from a specific location (Cottenie and De Meester 2003) to more general situations (Thrush et al. 2000; Belovsky et al. 2004).

Statistical methodology alone should not drive ecological studies; a relevant question addressed at an appropriate scale is of more use than a superbly designed but small experiment answering an irrelevant question (Dayton and Sala 2001; Oksanen 2001; Cottenie and De Meester 2003; Belovsky et al. 2004). An important first decision for any ecological study, therefore, is whether to use a manipulative experiment or a correlative study, a decision that

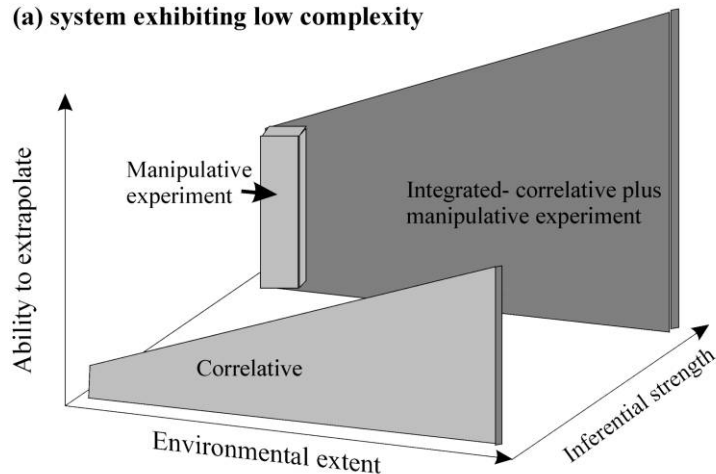
has to balance any lack of ability to extrapolate from the former against the lack of causality/inferential power associated with the latter (fig. 1). While the faults of both can be strengthened by integration of an underlying mechanism and knowledge of the natural history of the organisms (Dayton and Sala 2001; Belovsky et al. 2004), we suggest that nesting small-scale experiments into a broad-scale correlative framework is frequently best. In many systems, this will improve predictive power and result in stronger generalities (fig. 1).

There are a number of ways that manipulative and correlative studies can be combined. First, experiments can be nested within measured larger-scale patterns (Schneider 1978; Wiens 1989; Menge et al. 1994), broadscale environmental gradients (Keddy 1991), or temporal cycles. For example, large-scale kelp forest experiments replicated in space (Dayton et al. 1999) found consistent patterns. However, replication in time resulted in very different experimental outcomes. Correlation with El Niño–Southern oscillation oceanographic conditions revealed a strong linkage between temperature/nutrients and long-term patch structure of macroalgae.

Second, companion experimental manipulations and surveys may be carried out over the same extent, to determine whether experimental responses (or lack of them) are related to the experimental scale. For example, Bell et al. (1995) conducted a multisite experiment on drift algae accumulation in sea grass beds at two different scales and matched the results with a survey of macroalgal abundance in natural sea grass beds. Thrush et al. (2001) integrated a multisite time-manipulative experiment on the density of *Atrina zelandica* (an epifaunal bivalve) with a multisite survey of *Atrina* and infaunal densities in the same location. Similar environmental variables affecting the results of both experiments and surveys justify expansion of the scale over which results of the experiment are valid.

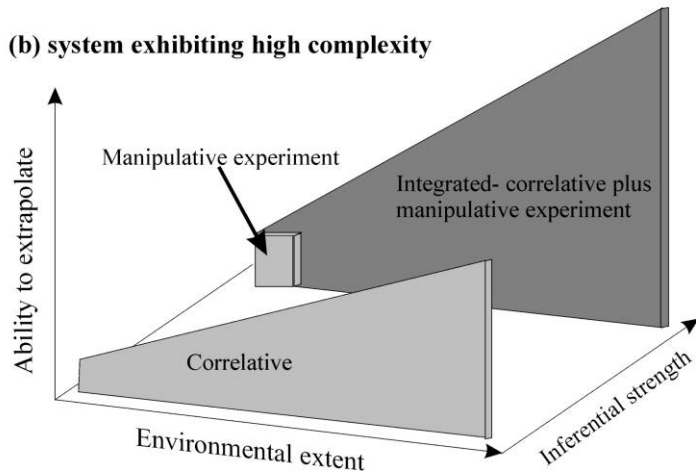
Third, a series of studies may be conducted within an integrated framework (Eberhardt and Thomas 1991). This is often the most practical method, allowing the buildup of information from small studies. However, care has to be taken to build an overarching framework; otherwise, individual studies never connect. It is also important to recognize the limitations of early studies, which frequently have to be conducted with little ecological/environmental context. Indirect effects generated by feedbacks and spatial or temporal variability in direction and strength of ecological responses generally emerge later in the research processes. For example, Bonsdorff and coworkers (Bonsdorff 1992; Bonsdorff et al. 1995a, 1995b; Norkko and Bonsdorff 1996a, 1996b, 1996c) conducted a series of studies in the Archipelago Sea in southwest Finland ranging from surveys and field experiments to laboratory experiments. This work included interactions between predators,

(a) system exhibiting low complexity



(a) In a low complexity system, the small extent that manipulative experiments are conducted over is not a drawback. The high degree of inferential strength of such studies results in a better ability to extrapolate from them than from correlative studies conducted over small - medium extents.

(b) system exhibiting high complexity



(b) In systems of high complexity, however, processes interacting over a variety of scales reduce the ability to extrapolate from small-scale (grain or extent) manipulative experiments. The ability to extrapolate from correlative studies, is unaffected by complexity.

Figure 1: Illustration of the relationship between study designs, system complexity, environmental extent, inferential strength, and the ability to extrapolate to larger scales and enhance generality across environments/systems. The figure demonstrates that manipulative experiments, when they are possible to use and control, are the cornerstone of strong inference (Platt 1964), but in some systems, inferential and extrapolative strengths can be gained through integrated correlative studies.

drifting algae, and infaunal communities associated with eutrophication. Early evidence pointed at purely negative effects of drifting algae on the benthic community, whereas later studies pointed at potential benefits for certain organisms, through the provision of secondary habitats (above the sediment surface) or substrate for rafting, enhancing the potential for dispersal of sediment-dwelling organisms (Norkko et al. 2000; Salovius et al. 2005).

Making Decisions about Study Design and Integration

But how can we decide when integrated studies are essential? Haury (1978) effectively modified the original concept of Stommel (1963) to demonstrate that planktonic studies should concentrate more on collecting longer-term

coarse-scale information to determine how hydrodynamics and biotic processes interact to form and maintain the patterns that define the ecosystem. The Stommel diagram plots variability in processes against increases in space and timescales. Employing this concept, we can be guided by a series of questions (box 1), together with natural history information, in the choice of study designs (fig. 2). It is important to note that while ecologists often do not have in-depth information on spatial and temporal variability, informed guesses can help guide the decision-making process. When in doubt, we advocate for an awareness of the value of multiple strands of evidence derived from different approaches encompassing different scales of heterogeneity rather than a reliance on a single manipulative experiment.

Box 1: Questions relevant to selecting study design

1. *What is the range of scales over which the studied process causes variability?* The processes under study should not cause high variability at spatial scales larger than the experimental scale for periods shorter than that of the study duration (Haury 1978). The temporal equivalent is that processes under study should not cause high variability over time periods longer than the study duration at spatial scales smaller than that of the study.

2. *Do other processes interact with the process of interest?* These can be important in a number of ways: (a) high mobility or strong temporal variation in abundance of organisms interacts with the response to process under study; (b) emergent patterns depend on broader-scale processes to be enacted (e.g., postsettlement transport controlled by hydrodynamic processes can influence adult-juvenile interactions; Thrush et al. 2000); (c) broadscale gradients in other factors affect the outcome (e.g., stress-induced switches between facilitation and inhibition; Bruno et al. 2003); (d) other processes cause high variability at scales similar to those of the process of interest, leading to difficulty in correctly isolating mechanisms; (e) feedback loops at a scale similar to or smaller than that at which the process of interest has high variability (e.g., density of epibenthic organisms affecting broadscale hydrodynamics through surface roughness or feeding currents).

Many ecologists have been concerned with the role of change in variability in affecting ecological processes (e.g., variance-mean relationships [Taylor 1961] and density-vague relationships [Strong 1986]). Recently, the explicit incorporation of variance at the treatment level in manipulative experiments has been employed (Benedetti-Cecchi et al. 2005). While insightful, this approach still suffers from the scale limitations generated by most manipulative experiments (see debate between Inouye [2005] and Benedetti-Cecchi [2005]). Integrating experimental manipulations into larger-scale landscapes of density variation in the species of interest (e.g., Thrush et al. 1997) is a practical solution to the problems identified by Inouye (2005).

Implications of Scale and Heterogeneity for Common Analyses

Spatial and Temporal Heterogeneity

An increasing number of analytical techniques have been developed, both to deal with the effects of spatial and temporal heterogeneity and to enhance our ability to analyze new study designs. Important developments include increased ability to use continuous rather than categorical variables, to partition variance between a number of measured explanatory variables, and to use different null models (e.g., nonindependence of samples due to temporal or spatial autocorrelation).

While improvements have been made to ANOVA (e.g., allowing the incorporation of spatial correlation), the technique is still limited in its utility to, for example, simple experimental designs that are not confounded by other scales of variability. When the categories actually form a gradient (e.g., depth, concentration), categorical analyses such as ANOVA can be particularly insensitive (Ellis and Schneider 1997; Somerfield et al. 2002; Cottingham et al. 2005).

Continuous analyses (e.g., ANCOVA, regression) can be used for most study designs, including manipulative experiments (Thrush et al. 1997). A major advantage of analyses based on continuous variables is that measures of other potentially important variables can be easily incorporated and variability can then be separated into that associated with the main variable of interest, other measured variables, and noise, allowing clearer identification of effects. This is particularly important because a number of articles have demonstrated that treating all variance, except the factor(s) of interest, as noise is not efficient because this variation can contain useful information (e.g., Legendre 1993; Osenberg and Schmitt 1996; Hewitt et al. 2001). For example, spatial and temporal variability in populations and communities can be decomposed into that associated with environmental variables of interest and that which is purely spatial or temporal or both (Borcard et al. 1992; Legendre et al. 1997; Anderson and Gribble 1998).

Initially, techniques for exploring relationships between continuous data were limited to linear relationships (or those that could be transformed to linearity) with normal error structures. But procedures allowing other types of error structures and a variety of ways for exploring nonlinear relationships have increased (for a review, see Miller et al. 2004). Fitting complex curves (e.g., techniques such as splines, general additive models) or multiple breaks (e.g., regression trees) to data frequently results in a high degree of explanatory power, although there is a high potential for overfitting (Venables and Ripley 2002). Importantly, ecologists must decide whether the complex curve or resultant tree makes any ecological sense, a decision that will be based on understanding natural history, environmental heterogeneity, and ecological processes.

Another area of concern in analysis is the form of the null model. First, although concern over the nonindependence of samples due to spatial patterns has been raised in ecology for many years, many ecological studies still use analyses based on a null model of randomness, relying on techniques to remove effects of spatial or temporal correlation. However, inclusion of spatial or temporal information into null models (e.g., autoregressive moving average models) makes intuitive sense in many situations and increases the sensitivity of analysis (Hewitt et al. 2001;

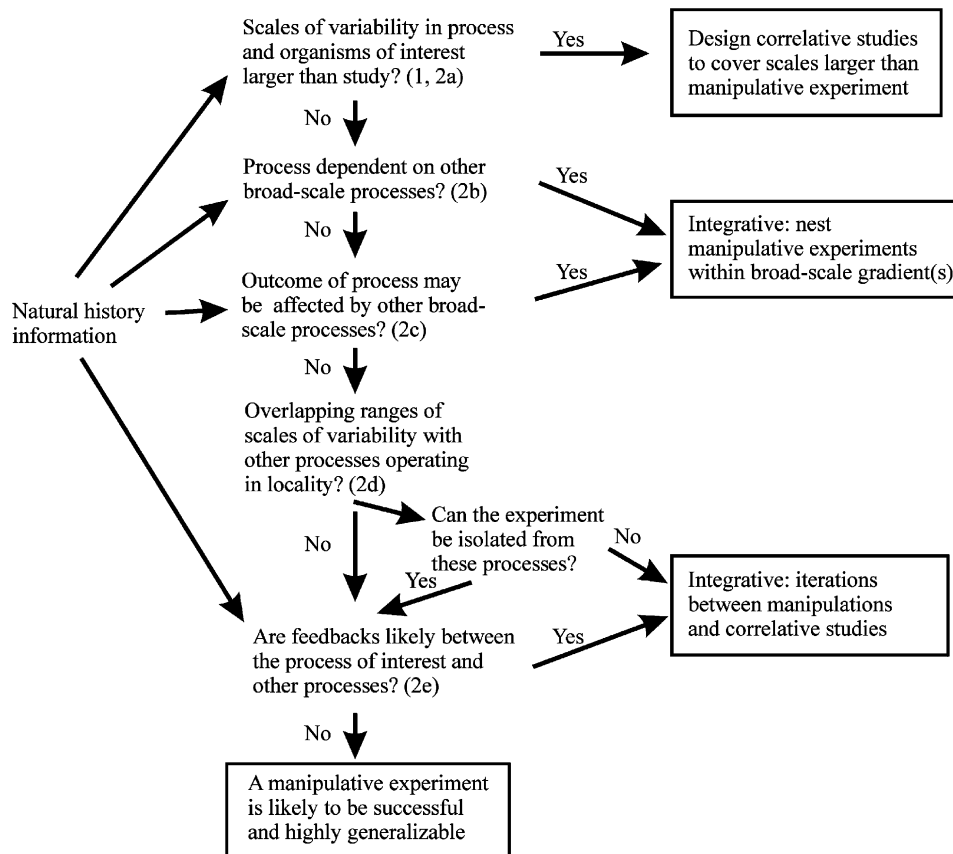


Figure 2: Flowchart demonstrating method for deciding study design, based on answers to questions in box 1 (designated in boxes).

Stewart-Oaten and Bence 2001; Legendre et al. 2002). Second, regressions based on mean responses may not detect a relationship when a clear pattern can be observed in the scatterplot (Blackburn et al. 1992; Thomsen et al. 1996). Recently, quantile regression has allowed us to progress from investigating mean responses to investigating constraining factors and defining envelopes in which certain sets of interactions occur (Scharf et al. 1998; Cade et al. 1999). Quantile regression also offers a new way to investigate variance in population responses and interactions between processes (Cade et al. 2005).

Effects of Scale

The effect of scale on the development of analyses has been equally important and will be discussed here in three categories: direct analysis of scale effects, development of techniques to move between scales, and statistical model validation. Scale effects can be analyzed by studies that directly or indirectly incorporate scale into their design. Scale can be incorporated directly into both experimental

manipulations (e.g., Smith and Brumsickle 1989; Thrush et al. 1996b; Whitlatch et al. 1997) and correlative studies (e.g., Hatcher 1989; Hodda 1990; Hewitt et al. 1997b). Further gains in understanding have also been made by comparing results from manipulative and correlative studies. For example, the interaction between experimental plot size used by Cummings et al. (2001) and the effect of a habitat-forming species on macrofauna were illustrated by including analyses on the effect of plot size (Hewitt et al. 2002). The effect of scale can also be analyzed indirectly by incorporating variables measured at different scales as additional explanatory factors (e.g., Keddy 1991; Thomsen et al. 1996).

There is a large amount of literature focusing on formal mathematical techniques for scaling functional relationships and for translating results from one resolution to another (see, e.g., Schneider 1994; Jones and Lawton 1995; Englund and Cooper 2003; Seuront and Strutton 2003 and references therein). Techniques vary from the use of fractals to extrapolation by expected value, explicit integration, and scale transition theory (King 1991; Rastetter et al.

1992; Borda-de-Agua et al. 2002; Melbourne and Chesson 2005). While these techniques are far too varied to adequately summarize here, our focus provides insight into a major problem. Such techniques rely largely on the assumption that a full range of interactions between processes and responses at different resolutions has been observed. This clearly is a problem for data derived from location- and time-specific empirical experiments. Even sophisticated scaling techniques will be scale dependent if only a limited range of the actual heterogeneity has been captured. For example, Melbourne and Chesson (2005) emphasized the need to identify key interactions between nonlinear responses and spatial variation when scaling up from local interactions to large-scale outcomes in population dynamics.

Statistical models represent emergent relationships determined by the grain, lag, and extent of the data modeled, and such models can often be developed even when the underlying mechanisms are complex and difficult to unravel. There are a variety of ways of validating regression models (Olden and Jackson 2000); often paired samples are collected, and one sample from each pair is used to build the model, or half the data are selected using a stratified random protocol to derive the model, and the other half are used to test the model. Such tests are useful but do not assess general applicability or spatial and temporal space dependence of processes (Ysebaert and Herman 2002). Rather than model performance merely being checked at the scale used to build the model, performance should be assessed with independent data collected at scales different from those from which the model was derived (Thrush et al. 2005).

Analyzing Integrated Studies

Analysis of integrated studies can be undertaken statistically or more informally. Meta-analyses can be particularly useful for statistically analyzing integrative studies and for summarizing results of similar experiments conducted at different places and times (Rosenthal 1991; Gurevitch and Hedges 1993; Oksanen 2001). Meta-analysis, at its simplest, can statistically combine the statistical significance of individual studies. However, depending on the similarity between studies and the information available, the analysis can be used to determine whether variability in results of the individual studies can be explained by other measured factors (Downing et al. 1999). The ideal analysis is one based on identical experiments conducted along gradients, for example, when slopes of the relationship between adult and juvenile densities found in a number of identical manipulative experiments were regressed against broadscale measurements of wave energy (Thrush et al. 2000).

Studies to be used in meta-analysis do not have to be

identical. Osenberg et al. (1999) discusses a number of applications of meta-analysis with respect to five sources of variation among studies. Their conclusions are that selecting the series of studies used in the analysis and developing the metric that is to serve as the measure of ecological response are important issues affecting results. We suggest that problems of bias resulting from the process of selecting studies for inclusion in meta-analysis, noted by Englund et al. (1999), can be minimized when working with studies that were carefully developed within an integrated framework and intended to be analyzed by meta-analysis (Thrush et al. 2003).

Informal integration of studies can be as simple as using the results of one study in the design of another or conducting another study to answer a question raised specifically by a previous one. However, results from a number of studies can also be analyzed to determine the frequency of similar responses (Mittelbach et al. 2000) or to construct multiple lines of evidence. For example, Fabricius and De'ath (2004) use information from a series of laboratory and field studies to assess the effect of agricultural pollution on the Australian Great Barrier Reef.

We have emphasized empirical studies that assess the strength of local interactions, feedbacks, and nonlinearities and estimate rate and functional responses. While this information is useful in developing models, leading to improved predictions (e.g., Mooij and DeAngelis 2003), use of an iterative framework of empirical studies and model building will lead to substantive gains for ecologists. Models can be used to indicate the potential for endpoints to be particularly sensitive to the scale dependence of processes (Levin 1993; Perry 1995; Clark et al. 2001) and how the relative importance of processes changes with scale. Complex system models, in particular, allow exploration of the effect of past history and conditions on present ecological processes and responses (Grimm et al. 2005; van de Koppel et al. 2005). Empirical studies can then test the predictions and develop new information for incorporation into the models.

Conclusions

Ecologists generally acknowledge the importance of scale, but few empirical studies explicitly measure and discuss the effects of scale on their results. There is a perception that detailed understanding requires manipulative experiments, even though practicalities, ethics, and funding usually limit them to assessing effects at small scales over a limited range of spatial and temporal heterogeneity. If the issue of scale has not appreciably changed study designs, acknowledgment of its importance is superficial, and it would appear that there are major stumbling blocks to

studying the complexities that scale and heterogeneity bring to ecology.

We suggest that there are a number of techniques that currently offer a way forward to strengthen ecological generalities. First, natural history information should be used to suggest the likelihood and scale of spatial and temporal heterogeneity, feedbacks, indirect effects, and interacting processes. Second, correlative studies should be integrated with manipulative experiments and designed cognizant of environmental heterogeneity. Third, while long-term research projects are frequently difficult to fund, planned iterations between integrated studies can be used to increase natural history information and slowly build both conceptual models and quantitative information of system linkages. Fourth, analytical techniques, wherever possible, should use continuous explanatory variables, and analyses across studies should be used to determine reasons for variable results. Finally, iteratively integrating models with empirical studies offers a way to develop and test ecological generalities.

We believe that advances in the way that ecologists design experiments and analyze complexity and variability across scales will invigorate community ecology. Importantly, these advances will also help ecologists address pressing large-scale questions associated with habitat destruction and fragmentation, climate change, and eutrophication and the implications of these threats for biodiversity loss and changes in the delivery of ecosystem services. We are confident that our suggested guidelines for design and analysis will enable ecologists to answer such questions.

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