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## Large-scale questions and small-scale data: empirical and theoretical methods for scaling up in ecology

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Most experimental work is done at small spatial scales due to scientific, logistical, and financial constraints. Unfortunately, ecologists (and society) require answers to problems about dynamics that arise at larger scales than often can be studied experimentally. Thus, it is imperative to develop empirical and theoretical methods for scaling up the results of small-scale studies to predictions at larger scales. These methods should also identify the limits to scaling up: i.e., clarify when results from small-scale experiments cannot be extrapolated to larger scales. In this special topic, we identify three important hurdles associated with scaling up in population biology and methods of addressing these problems: (1) increased spatial heterogeneity with increasing spatial scale, (2) changes to species pools and species identities with changes in spatial scale, and (3) behaviors and trait-mediated indirect effects that emerge at larger scales, but are absent in small, relatively homogeneous experimental settings.

Larger spatial scales will usually incorporate greater abiotic and biotic heterogeneity than small scales, including greater genetic or phenotypic variation among individuals. Simple extrapolations that assume linear scaling relationships will not provide good predictions when there are both spatial heterogeneities and nonlinear interactions among species or between species and abiotic resources. Thus it may be troubling that spatial heterogeneity is ubiquitous and many ecological interactions are known to be non-linear. Fortunately, if both the degree of nonlinearity and the amount of spatial heterogeneity at different scales were quantified, available methods may allow integrating large-scale obser-

vatational studies with small-scale experiments to account for the influence of heterogeneities on the outcome of nonlinear interactions. Alternatively, models or experiments can be used to directly examine the effects of changing levels of variance and to determine the importance of different sources of heterogeneity in different systems.

Three of the contributions illustrate ways to account for effects of increasing heterogeneity and non-linearities. Melbourne and Chesson use scale-transition theory to develop an expression for regional population dynamics that accounts for non-linear local density dependence and spatial heterogeneity in resources. Incorporating spatial variances and covariances, they predict the regional responses of caddisfly populations to riffle disturbance regimes. Inouye describes data collected at two nested spatial scales on the variances and covariances of distributions of competitors in a patchy and ephemeral habitat. These data are used to parameterize a model for the regional population dynamics of these competitors that includes spatial heterogeneity at both spatial scales. Helms and Hunter show that using observed spatial variation in local population growth parameters can produce regional population dynamics that are different from those obtained using average parameter values.

A second hurdle in scaling up is that at larger scales, one is likely to encounter additional species or habitats within the domain of the study. In moving from studying a single species or pair of species interacting within a microcosm to studying the same species and interaction embedded in a landscape, the indirect effects of additional species may swamp whatever direct effects were measured in the microcosm. To address these problems, we need to include information on how species pools change as the spatial scales of studies increases. Srivastava addresses the relative roles of local biotic interactions and regional abiotic influences in aquatic treehole communities across a range of spatial scales and levels of diversity. Although local treehole communities are similarly structured around the world, communities

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that draw from different species pools do not respond similarly to drought stresses. This study illustrates the challenge, perhaps insurmountable, to scaling up ecological predictions that is presented by changing species pools across scales.

Finally, few ecologists have addressed population and community level effects of individual behaviors whose expression changes with spatial scale. In particular, habitat or microhabitat preferences may emerge that affect how individuals experience heterogeneities in their environment. Better knowledge of a species' natural history and use of dimensional analyses may allow minimizing artifacts due to smaller-scale experimental arenas, or anticipating behavioral shifts and incorporating them into predictions of dynamics at larger scales. Petersen and Englund illustrate guidelines for designing experimental arenas that minimize experimental artifacts in behaviors and physical processes affecting species interactions. Use

of these dimensional approaches may help to remove some barriers to scaling up by increasing the realism of smaller-scale experiments. Schmitz uses data from two plant–herbivore systems with different characteristic spatial scales to show that the trade-off between foraging and predation risk avoidance can be a relatively scale-independent principle, useful for scaling up from small scale experiments to landscape management.

Our hope is that this collection of papers will illustrate a variety of approaches to making predictions about large-scale phenomena from data collected at smaller, more experimentally tractable scales. These studies include work on competition, predation, community properties and single-species dynamics in both terrestrial and aquatic species from a variety of taxonomic groups, underscoring the fact that the goal of scaling up inferences in ecology spans all subdisciplines in our field.