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Ecological Scaling in Space and Time

A New Tool in Plain Sight?

Elizabeth T. Borer

Rapid changes in climate and nutrient deposition in regions around Earth are inducing equally rapid changes in the biosphere (Schimel et al. 1997, Ellis et al. 2010, Running 2012). These abiotic factors are not changing at the same rate or in the same direction in all locations, so organisms are increasingly experiencing novel combinations of precipitation, temperature, and nutrient deposition (Williams et al. 2007, Rockström et al. 2009). The reliance of humans on processes provided by organisms and their interactions within the local biotic and abiotic environment, such as carbon fixation, nutrient cycling, disease transmission, and the quantity, quality, and persistence of freshwater, provides a pressing reason for ecologists to develop a mechanistic understanding of the links between organisms, ecosystem processes, and regional and global cycles (Worm et al. 2006, Kareiva 2011, Cardinale et al. 2012). Yet, the combination of climate and nutrient supply experienced by organisms also results from feedbacks between the physiology of individual organisms and global biogeochemical cycles (Ehleringer and Field 1993, Vitousek et al. 1997, Arrigo 2005, Hooper et al. 2005), making clear our need to better understand processes that span temporal scales from minutes to millennia and spatial scales from suborganismal to Earth's atmosphere to predict future effects of the changing environments on Earth.

The problem of scaling in ecology is not new. Three decades ago, scaling occupied the minds of many ecologists. For example, three decades ago John Wiens wrote an essay calling for a shift to multiscale thinking, development of new theory, and greater focus on collecting data to resolve discontinuities in processes across spatial scales (Wiens 1989). A few years later, Simon Levin published another excellent synthesis of the state of ecological knowledge of scaling (Levin 1992), arguing that knowledge of both large-scale constraints and the aggregate behavior of organisms will be necessary for achieving a predictive, mechanistic understanding of the feedbacks between organisms and ecosystem

fluxes. A key topic raised by both Wiens and Levin also was addressed in a book published at nearly the same time (Ehleringer and Field 1993) in which many authors tackled the issue of scaling and cross-scale feedbacks from organismal physiology to global climate and back again.

In the decades since these papers were written, ecologists have continued to develop an understanding of long-term feedbacks, heterogeneity, and links across spatial scales. For example, the effects of forest warming over the short term have been demonstrated to stimulate soil respiration, whereas turnover in microbial composition can increase the carbon use efficiency of the community, leading to attenuation of soil respiration under continuous long-term warming (Melillo et al. 2002, Frey et al. 2013). The effects of diversity on productivity also function via long-term feedbacks. For example, long-term, chronic nutrient addition causes productivity to increase initially, but these effects attenuate over multiple decades because of ongoing loss of species diversity (Isbell et al. 2013). In a different subfield of ecology, research using metagenomic tools is highlighting the links and feedbacks among spatial scales that determine the resident microbial composition, or microbiome, of a host. For example, the identity and relative abundance of microbial species inhabiting an individual is determined at the regional scale by the composition and relative transmission ability of microbial species and at the local scale by the relative abundance of hosts and microbial competitive ability and fitness within individual host species (reviewed in Borer et al. 2013). Many factors, including the abiotic environment (Fenchel and Finlay 2004), host quality (Smith et al. 2005), and host behavior (Lombardo 2008), can play a role in these interactions and feedbacks across spatial scales.

In spite of the forward progress of this field, the fundamental issue of effectively using information about processes at one scale in predictions about outcomes at another scale remains unsolved. In 2011, the Macrosystems Biology program at the National Science Foundation (NSF) was launched to stimulate research and advance greater mechanistic understanding of processes spanning spatial scales (Dybas 2011). Although the availability of funding is certainly a key constraint on intellectual progress, identifying and collecting the types of data that will be useful for making predictions that span scales also represents a major challenge (Levin 1992, Ehleringer and Field 1993, Leibold et al. 2004, Elser et al. 2010, Nash et al. 2014). Perhaps most importantly, ecologists studying feedbacks and linkages across spatial scales are faced with tradeoffs in our capacity to gather data about the biosphere at any scale: the spatial extent versus the temporal extent of a study, the local replication versus the spatial extent of a study, or site-based experimental work versus large-scale observation (Soranno and Schimel 2014).

A New Tool Hiding in Plain Sight

Over the past several decades, a fairly continuous stream of publications has identified conceptual areas of spatial scaling where our ignorance remains vast (e.g., Wiens 1989, Levin 1992, Ehleringer and Field 1993, Peters et al. 2007, Borer et al. 2013). However, ecological science has changed a great deal during this time, giving us a range of new tools and more highly resolved data to study ecological scaling relationships. Meta-analysis has become an accepted tool for quantitative synthesis of the ecological literature and has been used, for example, to examine support for a range of hypotheses about the key determinants of species diversity across spatial scales (Field et al. 2009). Sequencing technology and metagenomics is rapidly extending the conceptual realm and spatial scales being actively considered by ecologists (Borer et al. 2013). Electronic technology also has changed our ability to tackle questions about scaling in myriad ways, including computerization of data acquisition and access, satellite imagery, remote sensing, drone technology, and interpolation of a wide array of environmental data (Campbell et al. 2013). One example of the exciting cutting-edge of technology to examine scaling in ecology is research that is advancing our ability to use remotely sensed spectral variation as a tool for estimating local and regional biodiversity, and concurrently documenting leaf-level traits and functional differences among taxa (Cavender-Bares et al. 2016).

However, the change in the past 30 years that is perhaps most underappreciated for its potential to advance this field is neither statistical nor technological; it is the shift in the culture of ecological science from a field dominated by single investigator projects to one of collaboration (Hampton and Parker 2011, Goring et al. 2014).

Distributed Experimental Networks

Most ecological research is conducted by one or a few scientists over relatively short time scales and small spatial scales (Heidorn 2008), and whereas large-scale, multi-investigator collaborations have become increasingly common in ecology over the past several decades (Nabout et al. 2015), the vast majority of these collaborations generate, share, and analyze observational data (e.g. Baldocchi et al. 2001, Weathers et al. 2013). Although observations of ecological systems represent an exceptionally important tool for characterizing and comparing among systems, manipulative experiments are a far more powerful tool for forecasting a system's behavior under novel environmental conditions. Given the pressing need to effectively forecast ecological responses in a changing global environment,

multifactorial experiments measuring responses and feedbacks spanning spatial and temporal scales will be a key tool to complement meta-analyses, large-scale observations, and models.

Although most experiments in ecology are conceived of and performed by single investigators, large-scale, grassroots distributed experimental collaborations are rethinking ecological experimentation and are overcoming the historical tradeoffs in our capacity to gather long-term experimental data across multiple spatial scales (Borer et al. 2014a). By replicating the same experimental treatments and sampling protocols and openly sharing data with each other, ecologists collaborating in distributed experimental networks are able to replicate experiments and directly compare biological and abiotic responses across spatial scales ranging from centimeters to continents. Depending on the question, sampling can occur at multiple scales within sites (e.g., within individual, within plot, plot, block, site) to quantify a plethora of responses to experimental treatments that map onto future scenarios (e.g., multiple nutrients, herbivory, high-latitude warming, drought, and loss of biodiversity; see Arft et al. 1999, Borer et al. 2014b, Duffy et al. 2015, Fay et al. 2015).

This emerging approach to network science is requiring a rethinking of collaboration and a change in scientific culture (Guimerà et al. 2005, Hampton and Parker 2011, Borer et al. 2014a). By using common experimental treatment and sampling protocols and sharing data openly among collaborators, every site improves the dataset through contribution and each investigator benefits from the opportunity to contribute data and ideas as a result of their efforts (Borer et al. 2014a). As with any effective collaboration, careful fostering of a culture of trust and sharing means that contributors have confidence that their efforts will be included and rewarded (Hampton and Parker 2011). In this model, participation is voluntary, and for most distributed experiments organized as grassroots efforts, investigators at each site shoulder the cost of implementing the treatments and collecting the data rather than funding such efforts through a single centralized grant. This pay-to-play funding model means that participation, particularly by international collaborators in understudied regions of the world, is increased when costs are low. And, for a field that seems to perpetually struggle with physics envy, this model of egalitarian collaboration was once called “the dream” by the Director General of the European Center for Particle Research (CERN), Dr. Robert Aymar (Ford 2008).

To forecast future scenarios for ecological responses and feedbacks in nonanalog environmental conditions (Williams and Jackson 2007, Rockström et al. 2009), we need experiments that manipulate multiple global

change factors over long periods of time, and we need to understand how novel conditions influence the resulting spatial patterns and processes across multiple scales. Without multifactorial experiments replicated across many sites, it remains difficult to effectively estimate interactions among factors and contingencies in responses associated with, for instance, climate, evolutionary, or geological history. Distributed experimental networks provide such an opportunity.

The benefits of a distributed experiment for tackling questions about processes spanning and feeding back across spatial scales are enormous. This widespread collaboration among scientists dramatically expands the spatial extent of observation while retaining resolution (grain) at the scale of individuals, but also generating data that can be aggregated to capture patterns at larger grain such as block or site. The spatial replication generated by a network with many collaborators allows clear quantification of responses that are shared among sites as well as responses that are contingent on site characteristics (e.g., climate, soils, or evolutionary history). The replication of experimental treatments across many sites and conditions also allows investigation into the patterns and feedbacks resulting from multiple interacting factors by breaking up the colinear and confounded variables that plague single-site studies. By working as a widespread collaborative team to establish multiple treatments and sample at locations spanning regions and continents, distributed experiments overcome the tradeoff between the spatial and temporal scales of sampling that has caused ecologists to rely so heavily on models and meta-analysis for which interactions among treatments and site variables are difficult (and usually impossible) to disentangle.

We provide a few case studies to develop how we envision that this type of approach, harnessing the intellectual and data collection power of scientists spanning regions and continents, could interlink with existing approaches (e.g., modeling, streaming data) to generate a predictive understanding of how biological processes will change and feed back across scales in response to changing environments on Earth.

Case Study 1: Plant Productivity

As we move across spatial and temporal scales of observation, the key controls on the processes and resulting patterns in primary productivity shift (Wiens 1989, Ehleringer and Field 1993, Polis 1999, Peters et al. 2007). For example, roots foraging for soil resources may occur at the scale of millimeters, inducing organismal constraints on productivity (Tian and Doerner 2013). At the scale of meters, intraspecific and interspecific interactions among organisms seeking the same resources may generate

webs of direct and indirect interactions that may determine the net carbon fixation and annual productivity of a plant community. For example, concurrent changes and feedbacks in plant quality and composition in response to grazing (Zheng et al. 2012) or chronic nutrient addition (Isbell et al. 2013) can lead to long-term declines in productivity within fields. At regional scales, solar radiation, precipitation, nutrients, or other physical factors may impose the most important constraints on productivity (Polis 1999, Del Grosso et al. 2008). Although local, long-term patterns of evapotranspiration can predict the dominant flora, and thus biome, of a region, direct measurements of leaf-scale transpiration or small-scale measurements of local plant communities may fail to predict the larger-scale pattern (Wang and Dickinson 2012). Thus, we remain limited in our ability to use observed responses at the scale of roots and stomata to interpret satellite information or predict regional climate, although we believe that these changes are important pieces of the puzzle.

The use of meta-analysis has advanced our understanding of the role and interactions among climate, plant chemistry, and vegetation type on regional-scale patterns of plant productivity (Del Grosso et al. 2008). However, in spite of the important insights arising from synthesis across studies, such studies have relied on interpolation and derived metrics of production that may underestimate the role of local-scale processes and overestimate the role of regional climatic drivers (Shoo and Ramirez 2010). They also fail to provide a strong estimation of trajectories of productivity under future scenarios of climate and nutrient deposition. Thus, our ability to predict productivity responses to multiple interacting factors (e.g., concurrent changes in the supply rates of multiple nutrients or climate factors) and feedbacks from plant productivity to climate and nutrient cycles remains limited by the lack of simultaneous, direct manipulations of the environment and measurements of the rates of primary productivity within and among sites.

A coordinated, long-term experiment spanning a wide range of climate and nutrient supply could produce data to test the multiscale hypotheses generated with meta-analysis. By concurrently manipulating factors most likely to determine productivity within sites, regions, and across continents (e.g., climate, local nutrient supply, herbivory; Milchunas and Lauenroth 1993, Del Grosso et al. 2008, Fay et al. 2015), such a study could generate data to clarify the likely trajectories of change in productivity in future, nonanalog environments. These direct estimates of primary productivity, under a wide variety of natural and manipulated environments, produced through large-scale collaboration among scientists, would generate data to clarify the interactions among factors, spatial and temporal feedbacks, and spatial scales at which each factor most strongly constrains

primary productivity. Far from supplanting other approaches to studying ecological systems (e.g. observations, meta-analysis, models), this is a complementary approach that takes advantage of the collective power of the research community to generate directly comparable data spanning unprecedented spatial scales.

Case Study 2: The Microbiome

Developments in metagenomics over the past decade have shown that most of the genes and approximately half of the carbon in a human is of microbial origin (Shively et al. 2001, Nelson et al. 2010, Bruls and Weissenbach 2011), leading to a fundamental reassessment, among other things, of what it means to be an individual. Metagenomic studies have demonstrated that an individual's microbiome, the identity and relative abundance of microbial species inhabiting an individual, plays many important functional roles for animal and plant hosts, including digestion and nutrient acquisition, production of anti-inflammatory compounds, and resistance to pathogens (van der Heijden et al. 1998, Gill et al. 2006, DiBaise et al. 2008, Rodriguez et al. 2009, Fraune and Bosch 2010). Thus, the accumulation of microbes and turnover of species within the microbial community of a host are fundamentally important processes that define the composition and function of each host's microbiome. Although what we do know suggests that these processes span and feed back across spatial scales from biotic interactions at microscopic scales within hosts to regional drivers of the abiotic environment, our understanding of the spatial scaling and feedbacks across scales that control host–microbe interactions remains poorly developed (Medina and Sachs 2010).

Recent syntheses of this body of empirical work demonstrate that there are many links and feedbacks from local microbial interactions within a host to larger-scale distributions of microbes (Borer et al. 2013, Borer et al. 2016). Studies of microbes have demonstrated that some taxa are capable of extremely long-distance dispersal, leading to the increasingly debated hypothesis that microbes lack dispersal limitation, and local microbial communities are determined solely through environmental tolerance and selection (Baas-Becking 1934, Cho and Tiedje 2000, Fenchel and Finlay 2004, Antony-Babu et al. 2008, Peay et al. 2010). In addition to regional-scale selection, the abiotic environment also can determine the outcome of competition among microbes within a host (Yatsunenکو et al. 2012, Lacroix et al. 2014) and alter the composition of a host's microbiome through feedbacks that alter the nutritional quality of host tissues, from a microbe's perspective, as well as the relative abundance of conspecific hosts (Smith et al. 2005, Keesing et al. 2006, Clasen and Elser 2007, Borer et al. 2010). Another key finding is that hosts are not vessels, but rather play a role in

sanctioning and turnover of microbes to favor more beneficial species or strains (Kiers and Denison 2008), thereby feeding back to alter the local and regional composition of microbial taxa. Related to this, recent work has revealed that the composition and relative abundance of the microbes that make up a host's microbiome is constantly changing, likely determined by processes such as host sanctioning, competition, and succession of microbial taxa that feed back across spatial scales (Yatsunenکو et al. 2012, Copeland et al. 2015).

However, most studies of the microbiome within hosts are observational, not experimental, and are performed at single sites, focused on single microbial species, examine only a single host species, and do not characterize the regional microbial pool (but see U'Ren et al. 2010, U'Ren et al. 2012). Thus, our knowledge of the relative importance of processes operating at different scales is lacking. Because of this, our ability to predict the response of within-host microbial community diversity and function in a changing biotic and abiotic world is limited by the lack of simultaneous, direct manipulations of the environment and measurements of within-host microbial communities across sites.

Sampling the microbiome of hosts within a distributed experimental network could lay the foundation for predicting how global changes will alter the function of microbial communities inhabiting hosts and feed back to determine the relative abundance of hosts, themselves. For example, by quantifying the effects of experimentally manipulated global change factors on the identity, diversity, and relative abundance of microbes among host plant tissues (scale of millimeters), individual host plants (centimeters to meters), among plots (meters), among species and treatments within a site, among sites (kilometers or greater), and as a function of regional and experimentally imposed environmental gradients, we could better characterize dispersal distances and the role of environmental filtering and, importantly, understand the conditions and scales at which this community filtering is a dominant process controlling the microbiome of individual hosts.

The microbiome is a community of species and interacting individuals; ecological metacommunity paradigms (Leibold et al. 2004, Borer et al. 2016) can help us sort through patterns and responses by the microbiome to experimental treatments spanning spatial scales. For example, a distributed experiment would allow us to determine whether within-host microbial richness increases as a saturating function with increasing microbial taxon pool size (Fukami 2004) and whether this consistently differs by experimental treatment among sites. If niche-based processes (e.g., host chemistry, environmental nutrients) primarily determine microbial composition at the local scale, we expect a strong correlation between host microbial composition and the local environment (Cottenie et al. 2003, Leibold et al. 2004, Chase 2007). Thus, by directly measuring the response

of host-associated microbes to multiple concurrent global change factors across a globally relevant range of conditions, a distributed experimental network could generate critical empirical data about the interactions and feedbacks among factors controlling the microbiome. By harnessing the capacity of the research community deeply invested in these questions, these data could effectively complement insights from metagenomic observations, single-site (or lab) studies, and models, providing insights about generality and contingencies determining a host's microbiome at an unprecedented range of spatial scales.

Conclusions

Perhaps this will simply be another essay pointing out our need for progress in understanding the mechanisms underlying ecological relationships spanning spatial and temporal scales. If so, it will be an essay in venerable company. However, as a discipline, we have an ever richer and more diverse set of young scientists spanning the globe. This growth and diversity of ecologists can become a direct asset that can position our field to rethink how we work as a society of scientists. We can harness the collective skills and knowledge of our amazing colleagues to create the newest tool in our own toolbox for generating previously unattainable experimental data documenting processes and feedbacks across scales. More generally, innovation and progress can come in many forms, including rethinking our approach to science. By rethinking how we study the world, redefining how we collect data, and pursuing avenues outside the range of conventional approaches, ecologists may be able to push this field further in the coming decades than we have in the preceding ones.

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