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Taking the Mumbo Out of the Jumbo: Progress Towards a Robust Basis for Ecological Scaling

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Abstract

The challenges of the Anthropocene have forced ecologists into the public space, to contend with issues manifest at scales of tens of kilometers and more, unfolding over decades to centuries. Our long fascination with issues of scale is no longer academic. We need to be able to aggregate observations and process understanding derived at the scale of a homogeneous patch to the landscape, region, and the world, and disaggregate changes and limits at the planetary scale to their local outcomes and responses. Several robust approaches to scale-appropriate research and translation in ecology are becoming widely used, but the observation technologies have in some respects outrun both the theory and the general practice for scaling up and scaling down. The project for the next decade is to work simultaneously at multiple scales, using mechanistic, reduced-form, and empirical models to link the scales. The issues related to scale transitions are a manifestation in the spatial and temporal domain of the general problem of 'emergence,' which remains suspect in ecology, because it seems to invoke an element of magic. A key challenge for all complex system science, including ecology, is to make the prediction of patterns at one scale from mechanisms operating at different scales into a respectable and reliable practice.

Key words: scale; spatial; temporal; emergence; complexity; downscaling; upscaling.

Introduction

Ecologists need to understand the behavior of systems at or near the scales in space and time at which the phenomena of interest operate. Typically, this is not a single scale, but a range of scales, because the outcomes usually have several drivers which respond in different ways to scale. Scale-related issues are fundamental to ecosystem ecology because ecosystems exist at scales that bridge about 10 orders of magnitude in both time and space (Figure 1), usually nested one within the other. Many of the phenomena of interest are manifest at scales substantially different from the scale of scientific experimentation. Problems arising from mismatches between the scales of ecological processes, human observation, and management intervention have long been recognized in ecology (Schneider 2001). A flurry of influential publications about 25 years ago (Weins 1989; Holling 1992; Levin 1992) gave hope that the issue might soon be resolved, but it is still with us.

On the positive side, scale-related issues are now widely acknowledged in ecology and greater

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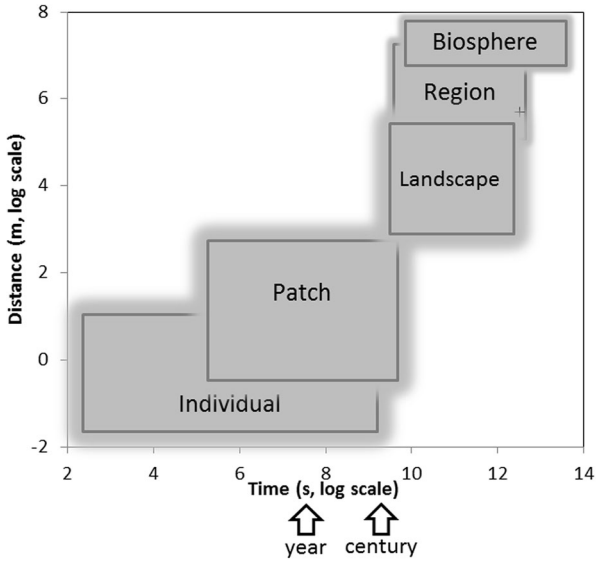


Figure 1. The domains in time and space of the suggested natural scales in ecology, corresponding to the descriptions in Table 1. They are deliberately shown as fuzzy-edged. If the 'three-step' postulate is correct, the maximum scale stretch on both the time and space axes is 2 to 3 orders of magnitude.

attention is paid to scale appropriateness and scale translations. The predominance of ecological studies at the scale of the field plot and the three-year research grant is now less than it was in the 1980s (Kareiva and Anderson 1988; Tilman 1989). The traditional ecological 'plot' came out of a legacy of manual measurement in agriculture and forestry, which is now being superseded by automated, machine-assisted and remotely sensed measurements freed of those logistic constraints. Many ecological studies are now conducted at landscape, regional, and global scales, and increasingly, simultaneously at several linked scales. The acknowledged need for a longer time perspective has resulted in a growing international network of Long-Term Ecological Research sites and datasets (Magnuson 1990; Lindenmayer and others 2012). Where working at landscape and larger scales is not yet feasible, the extrapolation of smaller-scale studies to the appropriate interpretation or action scale is now much more systematically undertaken (Scholes 2009). However, a range of complex systems effects, including environmental inhomogeneities and non-linearities of ecological processes due to spatial and temporal interactions, including feedbacks, make the rules for scaling up non-obvious in many cases (see Box 1).

The equally important problem of downscaling has received less prominence in the ecological literature. Upscaling, as a many-to-one problem, is in principle deterministic, though in practice it is usually statistical because the underlying sampling is typically sparse. Downscaling, on the other hand, is an unavoidably one-to-many problem. It is therefore a probabilistic allocation question: if the aggregated result is known, how can the contributions to it by various non-homogeneous subclasses be assigned, and with what confidence? Climate system downscaling has driven much technical progress over the past decades (Flint and Flint 2012).

Addressing the effects of scale and scale transitions in ecology is not only of academic interest. There are urgent and critically important problems to be addressed at a range of scales substantially larger than that of the individual organism. Many of these problems result from processes, such as atmospheric, oceanic, and climatic changes that operate at regional to global scale. Others, like population collapses and biodiversity loss, are driven by more local pressures but accumulate at landscape and regional scales, and manifest worldwide. Furthermore, interventions aimed at addressing these large-scale problems, on which the wellbeing of humans and countless other species depend, occur at a range of *human* scales: the scope of authority of a resource user or custodian, local government, national government, and international institutions. It is necessary to translate the interventions needed to steer the systems onto more sustainable paths into actions at scales that match those of jurisdiction and management, and where necessary point out where those scales are inappropriate for the nature of the problem (Cumming and others 2006).

The past three decades have seen great advances in our capacity to study ecological phenomena at scales in space and time approaching those at which they operate, and at a range of scales and organizational levels simultaneously (Chave 2013). The breakthrough technologies have been computational power, molecular genetics, and autonomous environmental sensing. Techniques such as eddy covariance on land and automated unmanned submersible vehicles in the oceans integrate process measurements over kilometers and seasons. Satellite remote sensing provides spatial details at resolutions from meters to kilometers over the whole globe, while achieving time resolutions from weeks down to minutes for a duration that now spans three decades. The ongoing exponential increase in computational power allows the prolific and multi-scaled data to be assimilated, interrogated, and simulated. Ecologists have for decades been challenged by problems of unbiased sampling and replication (Edmunds and Bruno 1996; De Kruijter and others 2006). The advent of

'big data' in ecology allows this issue to be sidestepped in some cases: analyze the entire population (Soranno and Schimel 2014). Thus, in the contemporary period, there is a fortunate coincidence of the *need* to work at a range of scales and the *capacity* to do so.

This perspective asks two questions: In the field of ecological scaling, have theory, technology, practice, and teaching kept up with each other? What is still missing to form a coherent theory of scale in ecology?

Box 1: A Primer on Why Changing Scales Reveals Ecological Surprises

This box is written for people unfamiliar with the topic of ecological scaling. It serves as an introduction to some of the key concepts.

The word 'scale' has different meanings in geography, landscape ecology, and other fields. Here, we use it to mean the extent in space and duration in time of an object of study, while the word 'resolution' (also called 'grain') refers to the smallest measurement unit in either time or space (O'Neill and others 1986).

When translating a result (y_1) obtained at one scale, with dimension x_1, to another scale with dimension x_2, the simplest assumption is that it is proportional to the ratio of the areas, i.e., $y_2 = y_1 \times (x_2)^2/(x_1)^2$. Thus, if a plot of 10×10 m^2 contains 100 trees, a forest of 100 km $\times$ 100 km would contain $100 \times (10^5)^2/(10)^2 = 10^{10}$ trees, and a plot of 1×1 m^2 would contain, on average, 1 tree. This is simple linear scaling, also sometimes called proportional or additive scaling. It assumes (1) that the process yielding the result is homogeneous over the scale range, or has been representatively sampled over a non-homogeneous area and (2) that the absence of spatial or temporal interactions allows simple proportionality to apply. There are situations where these assumptions are approximately valid, for instance when the scale interval of extrapolation is small, and the spatial distribution of process drivers is very even.

Most ecological scale upscaling and downscaling is more complex than this, with the consequence that the true value at the projected scale is materially less—or more—than simple proportional extrapolation would suggest. The two main reasons for deviation from simple proportionality are as follows: (1) that ecological fields are seldom homogeneous at scales of more than a few meters and days and (2) that factor interactions in time and space cause the scaling rule to be non-linear. Power laws (for example, $\log(y) = k \times \log(x)$) are often suggested for such scaling situations, and there are both theoretical and empirical reasons why they are a common empirical form for ecological scaling. The scaling of animal metabolic rate as a function of body mass to the power 0.75 is a well-known example.

A complication occurs at 'scale transitions.' There are certain critical scales, which may correspond to levels of self-organization, where the form of the scaling law itself changes. Very frequently, the key determinants of the process change as well. An example is the way the process of transpiration scales from leaf to region. At the leaf scale, the process is dominated by stomatal conductance and the vapor pressure gradient. At regional scale, these factors have virtually no effect: the transpiration rate is controlled by the energy available to drive evaporation, which is principally net radiation (Jarvis and McNaughton 1986).

The State of Ecological Scaling Science

There has been considerable progress towards the 'science of scaling' called for by Meentemeyer and Box (1987). Here follows a brief review of some of the key developments.

Hierarchy Theory

Hierarchy theory (Allen and Starr 1982) formally extended the full or partial nestedness of biological systems above the level of the individual organism. Borrowing ideas of 'self-organising criticality' from thermodynamics suggested that populations, communities, ecosystems, and ultimately the biosphere were coherent and repeatable entities, with the higher levels constraining the range of possibilities which could be exhibited by the structures nested within them. A useful heuristic 'stopping rule' arising from hierarchy theory is that causality at one level can mostly be explained by dropping down a single level, and does not require a progression down to some fundamental scale. This is a 'rule-of-thumb' rather than an absolute law, akin to using a Taylor expansion to find the first-order effects of a complex mathematic function, because processes at one scale are often determined by a range of determinants, some of which may be scale-independent or skip some intermediate scales. The possibilities for and limits to the spatial extrapolation of ecological pattern and process are explored by Miller and others (2004), whereas Peters and others (2004) apply the increasing understanding of non-linear system dynamics to

point to the mechanisms that may underlie abrupt scale transitions.

Landscape Ecology and Patch Dynamics

Landscape ecology is conceptually related to hierarchy theory, but less abstract, because it uses the revealed spatial structure of the landscape to define scale domains. It exploits spatial discontinuities such as land cover patches, geomorphological landscapes, and home ranges as physical proxies for the hierarchical levels (Turner and others 1989, Forman 1995, for a modern treatment see Turner and others 2015). Landscape ecology, in particular, has benefitted greatly from the reliable and affordable availability of spatially continuous and temporally repeated remotely sensed datasets, initially from earth observation satellites, but increasingly provided by drones. The development of powerful spatial statistical techniques (for example, geostatistics, edge detection, and object classifiers) has greatly assisted in the analysis of these data (Wagner and Fortin 2005). The use of Geographical Information Systems is now a skill routinely taught to graduate students in ecology.

Patch dynamics models (also called patch mosaic models and gap models) have proven a useful way to scale fine-grained population processes to the ecosystem scale. In particular, they are useful for scaling the effects of disturbances on biodiversity. They have also proven capable of scaling processes such as primary production and harvestable yield. Although they originated in the study of intertidal communities (Levin and Paine 1974), and have been applied in grasslands (Coffin and Lauenroth 1988), their greatest adoption has been in forest ecology (Shugart and Smith 1996). The hierarchical Patch Dynamics Paradigm unifies elements of hierarchy theory with patch dynamics (Wu and Loucks 1995).

Macrosystems Ecology: Ecology at Large Scales

The phrase 'macrosystems ecology' is a recent coinage, sometimes contracted to macroecology (see volume 12(1) of Frontiers in Ecology, especially Heffernan and others 2014 and Levy and others 2014). It refers to ecological studies conducted at fundamentally large scales, as opposed to being extrapolated to large scales, though the issues of scale translation and cross-scale interactions are important in this field (Soranno and others 2014). An example was the SAFARI 92 and SAFARI 2000 campaigns, which used the atmospheric gyre over southern Africa as an integrator of fine-grained emissions from vegetation fires (Lindesay and others 1996; Annegarn and others 2002). Motivated by the need to address large-scale issues such as climate change and regional land use change, macrosystems ecology has been enabled by advances in ecological observation technology, such as micrometeorology and remote sensing. In particular, it exploits the opportunities provided by 'big data' to quantify processes and patterns at scales of whole regions or continents (Soranno and Schimel 2014).

Meta-Populations, Networks, Dispersal, and Community Ecology

The concept of meta-populations (populations of genetically related individuals, spatially linked with variable strength to other related populations) has the potential to unify the fields of ecology and evolution in a spatially and temporally explicit way (Hubbell 2001; Leibold and others 2004; Holyoak and others 2005). It has applications in biodiversity conservation, particularly in a changing and increasingly fragmented environment. Understanding the rate and spatial dynamics of organism dispersal is a key to addressing the adaptation of communities to climate change (Settele and others 2014). The advent of affordable, multi-allele genetic sequencing makes it practical to trace genetic flows, and provides a common thread to link biodiversity concepts all the way from the gene to the ecosystem (Pereira and others 2013). Network theory, borrowed from information science and applied to ecological interactions, has confirmed the ubiquity of modularity at all scales; thus, the principle and pattern of decomposability is scale-independent, even if the particulars are not (Borenstein and others 2008).

Sampling Theory

Even where spatial interactions are not thought to be very strong (for instance, when aggregating quantities of material where the rules of conservation of mass apply), accurate upscaling still requires a representative sample. Obtaining such representivity usually requires either an unreasonably large sample size or sufficiently detailed a priori knowledge to allow stratification. One approach, when it is possible to remotely sense the property to be scaled, is to forego sampling and just measure the whole population: the quantification of land cover and ocean surface conditions are already at this point, and the measurement of ter-

restrial aboveground biomass is fast approaching it. For attributes that are likely to resist cost-effective comprehensive remote sensing for the foreseeable future (such as belowground properties), a useful and efficient approach is to quantify the factors associated with variation between the sample plots, and use a statistical model driven by a continuous field of those factors or their proxies (which can if necessary be derived a posteriori) to do the upscaling or downscaling (De Kruijter and others 2006). This represents a break from the classical stratified random sampling frame, so entrenched in ecology and many other fields.

Fractals, Power Laws, Allometry, and Stoichiometry

Fractal concepts (self-similarity at a range of scales: Mandelbrot 1977) have been quite seductive in ecology. They have found practical applications as well as misuses (Halley and others 2004). Allometric 'laws,' which relate aspects of organismic biology to scale were once purely empirical; for instance, the various power laws. Increasingly they have a foundation in mechanism, making them more robust and generalizable. This trend is apparent in the scaling rules for animal metabolism (Savage and others 2008) and in botany, where universal forms have emerged to relate tree size to tree biomass (Chave and others 2014). Using the organismal scaling laws and stoichiometry, both robust over many orders of magnitude of body mass, to cross the scale transition to the ecosystem level has been somewhat less successful, judging from the decreased fraction of variance explained when extrapolated to that scale (Brown and others 2004; Helton and others 2015).

Process-Based Models

Process-based models are the most robust way to deal with the spatial and temporal interactions that underlie most complex scaling behaviors. The gold standard for a process-based model is one that is able to achieve scale transitions seamlessly: this is a very challenging test. Physical processes of ecological interest, such as atmospheric and oceanic circulation, have been able to use the same fundamental equations of conservation of mass, momentum, and energy across a very wide range of scales, but computational constraints and instabilities mean that when circulation models are run at global scale they remain unable to resolve certain critical local scale features, such as the formation of clouds or eddies. They therefore apply a statistical 'fix' (called a parameterization) to represent the local phenomena. Nesting models within models (or applying variable-resolution grids) has been a key to downscaling climate projections to ecologically relevant scales (for example, Engelbrecht and others 2013).

It is often both useful and computationally efficient to derive reduced-form models (also called 'lumped parameter' models) above critical scale transitions, based on or calibrated against more detailed models with finer resolution (Rastetter and others 2003.) This approach has been successfully applied to the problem of scaling photosynthesis from the cell to the biosphere, a key ecological issue for the global carbon budget. The cell-to-leaf scale is handled by an enzyme kinetics-diffusion rate model (Farquhar and von Caemmerer 1982), the leaf-to-landscape scale by canopy interception models (for example, Williams and others 1996), and the landscape-to-world scale by photosynthetic efficiency models driven by remotely sensed absorbed photosynthetic radiation (for example, Landsberg and Waring 1997). In Table 2, I use the phrase 'scale-related process-morphing' as shorthand for the phenomenon of the changing balance of key drivers of a single process as the scale of analysis changes, illustrated by this example and the transpiration example in Box 1.

Model Inversions for Downscaling

In non-mathematical terms, the inversion of a scaling rule means running the 'forward' model that accumulates outcomes as you upscale them in reverse. In other words, starting with observed large scale outcomes, such as the carbon dioxide concentration of the atmosphere at set of known global locations and times, the approach infers the spatial and temporal distribution of the sources and sinks of carbon dioxide that could plausibly have led to that outcome (Bousquet and others 1999; Gurney and others 2002). This is only possible by constraining the problem with multiple observations, known covariates, and an underlying process understanding (in this case, the process of gas transport and measurements of wind fields). A key attribute is that model inversion can be performed such that it delivers explicit uncertainties associated with the downscaled estimates (Ciais and others 2010). We can expect to see many more applications of model inversion approaches to a range of ecological inference problems, including downscaling.

Natural Scales and the Limits of Reasonable Extrapolation

The problem of scaling can be simplified to three sub-problems. The first is to determine the scale domains over which a scaling law is valid. Techniques such as spatial statistics, fractal mathematics, and spectral and wavelet analysis in the time domain can help determine the ranges over which scaling law homogeneity should apply. A complication is that scale domains in the real world are fuzzy-edged rather than clear-cut. In most cases, the fractal breakpoints or peaks in variance that reveal the change in domain occur over a broad scale range. Thus, it is possible that the scaling rules that work over the middle of a domain break down towards its edges, but the rules for the next domain are not yet applicable.

The second sub-problem is to scale the process within a domain. There are two main approaches as follows: full (wall-to-wall and start-to-finish) integration using a process-based model appropriate to that scale and resolution and calibration of a domain-specific empirical model, such as a power law, to fit over the range of scales within the domain. The large expansion of the scope of ecological studies (scope is the extent divided by the resolution) afforded by multi-resolution satellites and long-term ecological research has made it possible to obtain data over the full-domain scale range. A hybrid approach is widely applied: use the process-based models to simulate patterns at a range of scales, and then fit a parsimonious response surface to it (Rastetter and others 2003).

The third sub-problem is how to navigate the transition between scaling domains—what information to keep, what to discard, and what new information to incorporate? One approach is to apply brute computational force to the transition, using a process-based model with detail at a scale finer than the transition, and hoping that the higher-scale patterns will emerge. However, adding more and more mechanistic detail to ecosystem models is generally not helpful in either understanding the observed phenomena at larger or smaller scales, nor in managing them (Hilborn and Ludwig 1993). This is particularly true where the errors in assigning parameters to express those multiple fine details exceed the benefits of better representation of processes. A preferred alternative is to derive a reduced-form model incorporating only the essential variables, to deal with the next scale domain. This mimics what is thought to happen in nature: the scale transition acts as an information filter (Poff 1997).

Applying these three sub-procedures in principle allows any number of scale domains to be bridged, as if climbing a ladder, step by step (Wu 1999). Each step observes the 'hierarchy triad' of outcomes at a focal level, mechanisms at a lower level, and constraints at a higher level. Does this procedure have to be applied from scratch for every ecological scaling problem, or are there natural scale steps that are broadly applicable to many processes, and perhaps to many ecosystems? If the latter is true, how do you recognize them? Results from complexity theory suggest that some features of self-organization, such as modularity, are so advantageous at all scales that they result in scale-invariant patterns. It is important to remember that the principles of hierarchy theory apply to scale hierarchies, rather than the definitional hierarchy of levels of ecological organizational level (individual–population–community–ecosystem). The two types of hierarchy are only loosely related: an ecosystem is likely to be larger and more persistent than the communities of which it is composed, and so on down; but there are ecosystems at a huge range of time and space scales (from a small, ephemeral puddle to the whole biosphere), and a single ecosystem will incorporate subsystems operating at a wide range of scales (microbial communities at minutes and less than a meter, mega-herbivores at centuries a tens of kilometers). Nevertheless, there is reason to believe that the scales of various ecological processes will often share breakpoints, because they respond to common underlying patterns such as geomorphology, biogeochemistry, climate, and genetic composition. The production of high-resolution bioclimate and ecosystem maps of the world (Metzger and others 2013; Sayre and others 2014) set out to provide a shared spatial template for sampling and scaling.

The process of scaling by climbing the hierarchical ladder is quite demanding. There is thus an argument for stretching the scale steps as far as you can, thereby minimizing the algorithmic steps. But as you cross scale transitions, there is the risk of accumulation of errors rather than filtering of noise. Is there a stretch too far? Based on my three decades of working across scales from the plot to the biosphere, in research programs such as the International Geosphere-Biosphere program and assessment efforts such as the Intergovernmental Panel on Climate Change, the Millennium Ecosystem Assessment, and the Intergovernmental Platform on Biodiversity and Ecosystem Services, I offer the following postulate: it is possible to scale from the patch to the biosphere in three steps (but no less) while conserving relative error. Those steps

are patch to landscape, landscape to region, and region to globe (see Table 1 and Figure 1 for the definitions, methods, and reasoning). A corollary is that you cannot go from global to local without at least one intermediate step. An example is the upscaling of agricultural production data from the field to the globe, for purposes of assessing food security now and in the future. Yields and their relation to environmental drivers such as soils, inputs, and climate are determined at the farm field scale. These are accumulated to regions (agroecological zones) with consistent patterns of species–soil–environment–management combinations, which are then accumulated globally (often first by national reporting, but that is a step imposed by institutional arrangements rather than necessity).

Taking the Voodoo Out of Scale-Linked Emergence

Scaling theory can be thought of as the playing out of complex systems theories of emergence in the spatial and temporal domains. The concept of an 'ecosystem' was introduced by Tansley 90 years ago to counter what was perceived as a worrying tendency towards mysticism in the young science of ecology (Rastetter and Vallino 2015). He proposed that the creation of order in systems composed of many parts involved no mysterious force; it simply required that those parts be fully understood, along with their interactions. The field of ecology may be growing out of some of its early insecurities. I remember, as an undergraduate three decades ago, being warned of the intellectual sin of super-organismal notions. Today, we routinely and without criticism invoke ideas such as the 'planetary metabolism.'

Rastetter and Villino's (2015) classification of theories of emergence into ''mechanistic,'' ''chaotic,'' and ''teleological'' varieties is helpful. It is true that automatic acceptance of teleological emergence, which is based on the inference that the emergent phenomenon has a purpose, can lead to a tautological shutting down of enquiry; but it is premature to always dismiss it as unscientific. Teleological emergence (and notions that accompany it, such as ecosystems as super-organisms) is distrusted by biologists because it seems to require undefined forces from outside the system, *deus ex machina*. But what if the purpose is internal to the system? Various authors (Simon 1962; O'Neill and others 1986) have suggested that the hierarchical structure of biological systems is ubiquitous be-

Table 1. Suggested Natural Scales in Ecology and Techniques Used to Bridge Scale Transitions

Scale name	Characteristics	Scaling tools
Individual organismal	Range of influence of an individual organism	Ecosystem process models, population models, allometric laws, stoichiometry, single-commodity production models
Patch plot, stand	A more-or-less ecologically homogeneous unit with a shared disturbance history	Patch dynamics models, meta-population models, statistically designed sampling frames, high-resolution (1–20 m) imagery
Landscape local' human scale, lowest ecosystem scale, marine gyre, or coastal type	A predictably repeating or structured pattern of environments, with a characteristic geomorphology, species pool and disturbance regime and set of uses	Propagule dispersion models, watershed-scale hydrological models, moderate-resolution (0.1–1 km) maps of ecosystem types, land cover and ocean regions (based on color, temperature, and salinity), nested atmosphere or ocean circulation models
Region biome, large marine biogeochemical province	A set of contiguous landscapes which share broad climatic constraints and evolutionary histories. A region is tightly coupled by trade, human cultural system or oceanic or atmospheric circulation	
Biosphere global	The oceans, terrestrial mass including freshwater ecosystems, cryosphere, and troposphere	Global atmospheric and ocean circulation models, economic or trade models, large-scale migration models, downscaling by atmospheric transport inversions

Corresponding spatial and temporal domains are shown in Figure 1.

cause this architecture allows stability, and is thus selected for not just at the evolutionary level of individuals in populations, but at all hierarchical scales. There are many examples, ranging from the tight collaboration of metabolic processes within a cell (Wolkenhauer and Hofmeyr 2007), through the coordinated and self-sacrificing behavior of unicellular organisms when they form multicellular colonies (Berelman and Kirby 2009), to altruism in populations (Fletcher and Doebeli 2009), where the emergent phenomenon can be considered to have a purpose without assuming an external designer. In the age of the Anthropocene, ecologists recognize that virtually no ecosystem is independent of linked and powerful social systems. It is clear that social systems can be motivated and shaped by purpose; therefore, contemporary social–ecological systems can also show teleological emergence.

It is likely that most ecological emergent behaviors can be sufficiently accounted for by entirely non-purposive causes, operating at finer scales. In practice, however, reproducing complex system outcomes from the properties of their underlying elements plus their interactions (as required by mechanistic emergence) is hard to achieve, especially in the case of ''chaotic emergence,'' and is likely to remain so for some time. Ecologists and other complex systems scientists are still some way from deriving a comprehensive mechanistic understanding of most emergent patterns. Therefore, establishing models of the phenomenon *at the scale of interest*, and empirical rules for translating this to other scales, may be a more practical near-term goal. Such an approach may eventually lead to an ecological 'theory of everything'; in the meantime, it will help to address pressing problems at critical scales, whether they be local, regional, or global.

Some of the reluctance to accept ''phenomenological'' models (in other words, descriptions of pattern and dynamics at a particular scale that are not rooted in mechanisms at finer scales) is based on wishing to mimic the success of highly reductionist approaches in physics and chemistry. It must be noted, however, that these fields were not assembled from the bottom up, rather they proceeded from the observable downward. Early successes were based on finding useful rules at larger scales that only later proved to be generalizations of underlying processes. For example, Boyle's gas laws were empirically derived and successfully used for decades (and continue to be used) before it was shown how they emerged from the interaction between molecules and the walls of their container. This is a comparatively simple case. Despite hubristic claims such as that 'life is nothing but chemistry,' or 'consciousness is nothing but a series of electrical states,' the reconstruction of complex phenomena in biology from first principles has been markedly unsuccessful. Ecologists should therefore not feel inadequate when they describe a pattern at a given scale, but do not yet have a well-established and seamless link to causality at a lower scale. Closing that scale gap can serve as a useful research challenge. It is particularly important that ecologists develop a robust body of theory at each of the several scale levels occupied by 'ecosystems,' that is, the landscape (and its marine equivalent), the region, and the biosphere.

Convergence Between Theory, Practice and Ecological Education

The tools for studying ecosystems at a range of scales, from the molecule to the whole Earth, now exist and are becoming increasingly affordable. They create the possibility of observation-driven

Table 2. The Top Scale-Related Challenges for Ecology Over the Next Two Decades, in the Opinion of the Author

Develop scale-explicit, predictive understanding of the most important ecological processes and patterns at patch, landscape, regional, and global scales
Develop a set of practical and widely accepted upscaling and downscaling procedures, which may be empirical, allowing scale translations to be performed with known uncertainty for given processes and phenomena, for defined scale ranges
For a set of important ecological processes, gain a predictive understanding of the degradation in accuracy and increase in bias as a function of the ratio of the scale of extrapolation to the scale of measurement. This would provide an estimate of scaling error and allow scale discontinuities (scale transitions at which there are relatively abrupt increases in uncertainty) to be identified. These are the points where you need to change to a different scaling rule (that is, a different model)
Explore the origins of scale-related emergent properties, in order to identify the contributions from cross-scale interactions, scale-related process-morphing, statistical aggregation effects and other possible mechanisms, for various processes and circumstances. The objective is to find general rules for emergence

theories and tests of scaling rules, rather than abstractions that later seek observational confirmation. Several promising building blocks for a general theory of ecological scale have been proposed, as reviewed above. Their unification and incorporation into everyday ecological practice appears to be an achievable goal over the next two decades (Table 2). This will require exposing learner ecologists to concepts of scale as a fundamental part of ecology, rather than a somewhat exotic and marginal advanced topic. Their training must also ensure that they have access to the necessary toolbox of observational techniques and spatial and temporal analytical approaches to venture into this field with confidence. Scale is a fundamental issue in ecology and will thus never magically 'go away.' Indeed, it is likely to become into greater focus with continuously improving observation technologies and the emergence of environmental problems at larger and larger scales. The response by ecologists must be to address scale issues explicitly and rigorously wherever they are pertinent.

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