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Graduate Student Perspectives on Scale and Hierarchy in Ecology

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KEYWORDS—*scale, hierarchy, ecology, graduate students*

INTRODUCTION—Scale and hierarchy are unifying themes that span a broad range of ecological disciplines (Levin 1992). These themes received considerable attention and went through major conceptual developments in the 1980s and early 1990s, when advances in computing enabled theoretical development through mathematical modeling. Scale is the spatial or temporal space in which a study takes place, while hierarchy refers to the organization of organisms relative to one another. Scale and hierarchy offer a framework for organizing the complexity that characterizes ecological patterns, processes, and dynamics. Underlying the appeal of scale and hierarchy to ecologists is the potential to enhance a mechanistic understanding of how patterns manifested at one scale or level of organization can be explained by processes occurring at another scale or level of organization. Such an understanding can reduce ecological complexity by boiling down the multitude of processes and interactions into a few measurable and meaningful variables. The appeal and allure of scale and hierarchy are still as pervasive now as they were a few decades ago. However, questions remain on how these concepts have developed in both application and, perhaps more importantly, in their intellectual accessibility to early career ecologist in graduate school.

We participated in a semester-long graduate seminar that focused on the development and application of scale and hierarchy in ecology. Our research interests and experiences span a variety of ecological disciplines and range of spatial and temporal domains (FIG 1). They also reflect our status as early career scientists and the limitations imposed by two-year studies and short funding cycles. Despite this, our interests and educational experiences collectively provide a much broader basis with which to assess recent advances and applications of scale and hierarchy to ecological research.

Collectively, we developed a list including some of the major themes and concepts in scale and hierarchy after reading and discussing seminal works on topics (Allen & Hoekstra 1992; Levin 1992; O'Neil & King 1996). We reduced this list to a manageable number of terms that are central to understanding concepts of scale and hierarchy in an ecological context (TABLE 1, TABLE S1). These terms generally apply to integrating or predicting across scales of hierarchical levels (e.g., cross-scale interactions, aggregation, emergent properties), but also include ecological properties relating to stability and equilibrium dynamics (e.g., resistance, resilience). We then performed literature reviews using these terms in conjunction with four ecological disciplines reflecting our collective research and intellectual experiences.

Our synthesis focuses on four distinct ecological disciplines than span marine and terrestrial systems, include plants, animals, and fungi as organisms of interest, and even integrates an evolutionary perspective. Our major objective was to synthesize existing literature in our own

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respective ecological disciplines, then compare among disciplines. Given time constraints, we acknowledge that literature reviews may be far from exhaustive. However, we provide a common framework for synthesizing the collective knowledge on scale and hierarchy, as well as how it has developed over the last three decades.

SCALE AND HIERARCHY IN THE MYCORRHIZAL SYMBIOSIS—The mycorrhizal symbiosis is arguably one of the most important symbioses to life on land. Behind the scenes of the emergence of vascular plants onto land some 450 million years ago (Morris et al. 2018), mycorrhizal fungi were providing essential nutrients to plants that were slowly figuring out how to live on land. In present times, the plant-fungal mutualism remains cosmopolitan, forming in 80% of land plants worldwide (Wang & Qiu 2006). In this mutualism, fungi exchange water and soil nutrients for carbohydrates produced by the plant through photosynthesis (Smith & Read 1996). The mutualism presents itself in many forms, including arbuscular mycorrhizae, which penetrate host root cells, ectomycorrhizae, which operate through extracellular contact, and mycorrhizae that are specific to ericoid plants and to orchids (Smith & Read 1996). For this analysis, I will focus particularly on ectomycorrhizae, which wrap around their host roots and share resources via cell to cell contact with the outer cells of the host roots. The mutualism is pervasive and is undeniably important to the ecology of land plants and ectomycorrhizal (ECM) fungi alike.

Given how prevalent the ECM symbiosis is phylogenetically and geographically, it is unsurprising that scientists have homed in on its ecological scale. While the symbiosis itself forms at the cellular level, emergent properties of the symbiosis can have consequences for populations, communities, ecosystems, and even global-scale processes. The symbiosis has incredible importance on the individual plant-fungus level—most plants and fungi that form the symbiosis do so obligately and can't survive alone (Smith & Read 1996). On an ecosystem scale, ECM fungi are responsible for replenishing nitrogen into the soil environment and helping to reabsorb nutrients into plants; they are pivotal to nutrient cycling in forest ecosystems (Fogel 1980).

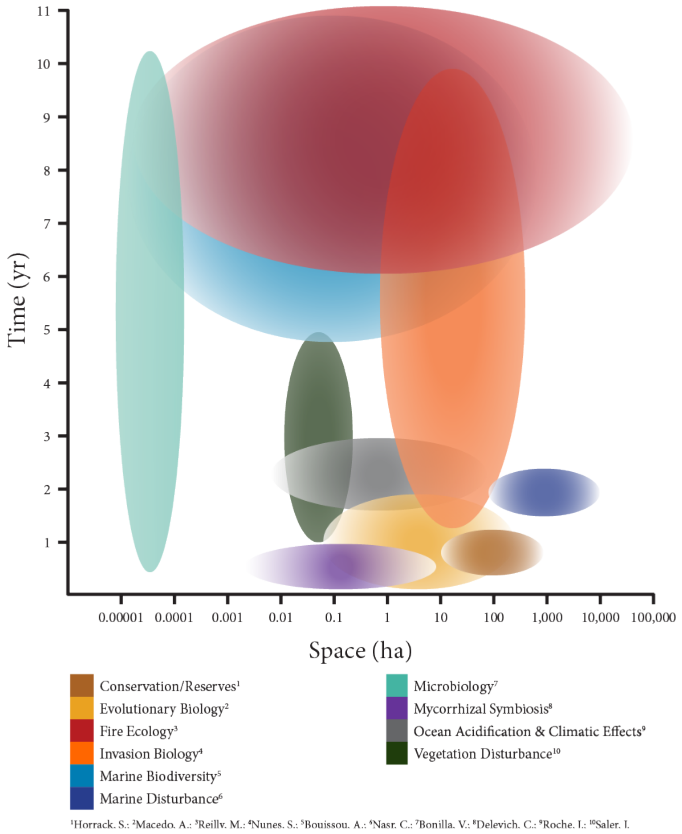

FIGURE 1. A space-time diagram displaying the various areas of focus of master's student thesis projects from the Department of Wildlife and the Department of Biological Sciences at Humboldt State University.

Many studies of the interactions between plants and their ECM fungi rely on laboratory-based manipulation. The feasibility of conducting laboratory-based studies becomes more and more difficult when we are looking to answer large-scale questions. Novel techniques in the field-based study of the ECM symbiosis are quickly emerging, allowing us to begin to integrate across scales using empirical techniques. Perhaps one of the biggest breakthroughs in larger-scale field studies is the use of isotope analysis in studying common mycorrhizal networks (CMNs). Common mycorrhizal networks are underground systems whereby the fungal organ (mycelium) connects roots of different trees, allowing a pathway for sharing soil nutrients, water, and photosynthates. While the concept of CMNs is nothing new, developments in isotope analysis have allowed us to look deeper into these connections and see that they link not just related trees, but entire forest communities through source-sink relationships (Simard et al. 1997). Within these networks, fungi can preferentially allocate their nutrients to plants that provide more photosynthates, elucidating an element of competition in these systems (Fellbaum et al. 2014). By continuing to bolster techniques for field-based

TABLE 1. List of the major concepts and terms related to scale and hierarchy and the prevalence of each in different ecological disciplines. Cells are coded with qualitative ratings on the prevalence of each in the respective discipline. Darker shading indicates less term usage and letter codes are as follows: R = Rare, O = Occasional, C = Common, U = Ubiquitous.

Concepts and Terms	Terrestrial Disturbance	Evolutionary Biology	Conservation and Reserve Design	Mycorrhizal Symbiosis	Ocean Acidification
Scale	O	U	C	U	C
Hierarchy	C	O	U	O	O
Cross-scale Interactions	O	C	O	O	C
Aggregation	R	R	R	R	R
Emergent Properties	R	C	O	O	C
Integration	O	O	R	C	R
Stability	C	C	C	R	O
Ecological Incorporation	O	O	O	O	O
Bottom-up/ Top-down	O	R	O	O	C
Resistance	C	C	C	O	C
Resilience	C	C	C	O	C
Importance of Scale Widely Recognized and Used in Analysis	C	U	U	C	C
Hierarchy Used as a Framework	R	C	C	R	R
Integration Across Scales	O	O	R	O	R

experimentation and observation, we will be able to fill in the gaps in our understanding of the scale and hierarchy of the mycorrhizal symbiosis.

As a proxy for larger field-based experimentation, mathematical models can serve as a mechanism by which we can integrate our understanding of the mycorrhizal symbiosis across scales. Johnson et al. (2006) identifies seven models that vary in their scale of ecological response, from individual to ecosystem-wide responses: functional equilibrium, economic, integrative agent-based, community feedback, coevolutionary mosaic, trophic food webs, and pedogenesis. Take for example the pedogenesis model. Mycorrhizal fungi are important to the formation of soil (pedogenesis) in that they create conditions that support the formation and stabilization of soil aggregates. ¬Physical variation in the mycorrhizal organ has been shown to alter soil aggregation development (Miller & Jastrow 1990). Research on small-scale processes within the mycorrhizal symbiosis has given us pathways to model and scale-up these effects. The pedogenesis model attempts to predict how microscopic interactions between mycorrhizae and their soil environment may lead to drastic bottom-up effects, impacting entire soil food webs. Although empirical studies alone usually lack integration across scales, data from these studies have been used to shape these models, allowing us to theorize how small-scale interactions can affect ecosystem processes.

SCALE AND HIERARCHY IN THE ECOLOGY OF TERRESTRIAL DISTURBANCE—Although imagery of terrestrial disturbances, such as treefalls and wild fires, often communicate devastation and death, such disturbances are crucial ecological events, creating heterogenous landscapes that ultimately promote biodiversity. The success and survival of a vast array of species are dependent on a landscape that is dynamic and subject to change. Decades of research has continually reinforced the idea that disturbance is necessary in order to create a mosaic of habitat types and stand ages that increases species diversity. However, there is a paucity of research that investigates the effects of disturbance across scales and hierarchical levels. Small-scale disturbances, such as treefalls, have far different implications than region-wide disturbances like wildfires. Furthermore, global disturbance events such as climate change are likely to have even more varied implications than small- and regional-scale disturbance. The effect of disturbance on an individual, a population, or species interactions highlights the need for the study of terrestrial disturbance within the context of hierarchy.

Pickett et al. (1989) attempted a system of concepts aimed to help ecologist deal with hierarchies in disturbance. Their system relies on a "minimal structure," consisting of the ecological entity of focus and its interacting components that allow this entity to persist. The authors provide an example of two ecologists wanting to study a population of southern pine: one studies productivity and the other pine beetle outbreak. The ecologist studying productivity would create a minimal structure model that includes energy fluxes as interactions and trophic levels as entities. The one studying pine beetle outbreak would model their minimal structure with canopy characteristics and soil resources as the entities, and phloem transport (which connects soil to canopy) as the interaction that connects the two, creating a persistent structure; the bark beetle population would then be external to this minimal structure and disturb the minimal structure. The development of this minimal structure model is exemplary of the importance of understanding hierarchy in disturbance ecology and provides ways in which we can integrate across scales.

Multiple studies in terrestrial disturbance ecology demonstrate that disturbance effects can vary depending on the scale of observation as well. Chaneton and Facelli (1991) evaluated the effect of disturbance on plant community diversity along a 5-m transect and a 1-ha (100 x 100 m) area. They found that comparisons among grassland conditions appeared scale-dependent. This may parallel meaningful changes in the relative importance of factors controlling species coexistence and community organization. In another multiscale study, Reed et al. (1993) examined the effects of spatial scale on the relationship between vegetation composition and underlying environmental variables. They found that as scale increased, so did the correlation with the physical environment, and confirmed that the results of vegetation analyses can depend greatly on the grain and extent of the samples employed.

Kotliar and Wiens (1990) explored how each level of hierarchical patch structure was influenced by the contrast among patches as well as the degree of aggregation of patches at lower levels in the hierarchy. The results of the study have wider implications in the study of habitat selection, population dynamics, and habitat fragmentation, and look to expand the realm of landscape ecology beyond the current focus on anthropocentric scales. Whittaker, Willis, and Field (2001) discuss the implications of considering multiple scale effects on the conclusions of narrowly focused studies. They state that one scale is not independent of other scales—a study narrowly focused on one scale may entirely miss the mechanism for what is observed. Additional studies that use scale and hierarchy as a framework continue to reinforce the idea that scale and hierarchy are essential when designing a study and interpreting its results, as one scale or level of hierarchy is not independent of those above and below the scale or level of hierarchy containing the study.

In the future it is essential to integrate scale and hierarchy into more studies involving terrestrial disturbance. This will be a daunting task to complete that will require more time and additional small-scale case studies with which to test generalizations among ecological systems. Integrating these findings into comprehensive meta-analyses across multiple scales and hierarchical levels can make more definitive conclusions about their effects and implications on ecological systems, as well as predictions for how these effects may vary in the future. This could greatly help conservation of biodiversity and mitigating economic and social losses when inevitable disturbance events occur.

OCEAN ACIDIFICATION: IMPLICATIONS OF SCALE AND HIERARCHY—Ocean acidification (OA) is a hot topic in marine research, as human activity continues to produce exorbitant amounts of atmospheric carbon dioxide (CO_2), which is absorbed by the ocean and ultimately increases acidity of oceans worldwide. This extremely harmful phenomenon affects the early life history of many marine organisms and even influences predator-prey dynamics (Dupont et al. 2008; Ferrari et al. 2011). Such observations of the impact of OA may reveal a cascade of effects on key trophic systems and other important mechanisms in ecology, but requires marine ecologists to consider these impacts in the frame of scale and hierarchy.

Scale and hierarchy are inherent in modern marine ecology due to the systematic interactions between species as well as spatial and temporal variation in marine systems. Marine ecosystems are being influenced globally, and with increased intensity, by large-scale top-down drivers such as OA. Key climatic processes occur both within short-term and long-term time scales. Over time, climatic effects that drive OA span globally and can carry effects from a single population up to the entire biosphere. A changing climate and transitions in localized weather patterns can lead to shifts in species distributions, disruption of match-mismatch systems, changes in migratory patterns, and other, largely undiscovered, effects.

Contemporary marine research attempts to quantify the effects of OA on marine ecosystems in the present, as well as the future, since the effects of OA vary with the time scale of study. The effects of global warming, OA, and their interactions are difficult to detect in short-term studies, but may manifest over time through changes in growth and behavior of organisms. These delayed effects may in turn affect ecosystem processes and structure (Godbold & Solan 2013). Feely et al. (2009) examined the uptake of anthropogenic CO_2 by the global ocean and its projected effects on seawater chemistry by the year 2100. They suggest that oceanic saturation of aragonite and calcite, which are crucial carbonate minerals, will be greatly reduced from current conditions. This will likely have detrimental effects on the ability of shell-building organisms and other marine calcifiers to sequester different forms of calcium carbonate.

Underlying hierarchical structure of marine systems has been examined in context of top-down effects triggered by OA. Shifts in the trophic structure of marine communities and changes in species dominances may occur, which could lead to the simplification of food webs (Kroeker et al. 2011). Ocean acidification has also been shown to decrease diversity, biomass, and trophic complexity of marine communities, suggesting that biodiversity and ecosystem function are likely to suffer as the effects of OA intensify (Kroeker et al. 2011). In contrast, bottom-up effects of OA are commonly considered a challenge to study, as responses at large-scales are often caused by events at much smaller scales, like the organismal level. However, we argue that large-scale effects are often not limited to individual-scale causes, as is denoted in FIG 2; events at higher-order hierarchical levels may also cause repercussions on global scales. Given the perceived limitations of cross-scale integration, attempts to predict the impacts of OA have been relatively limited to local or global scales, despite community or mesoscale

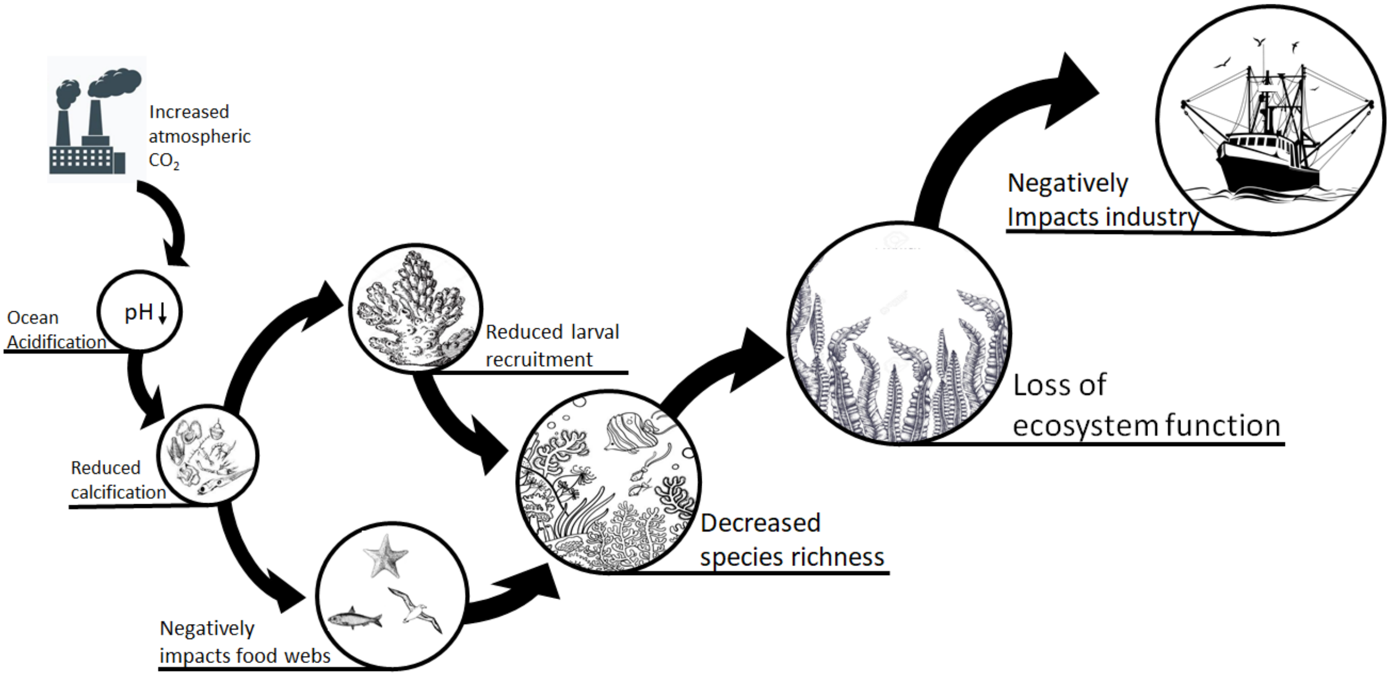

FIGURE 2. Ocean acidification as a conceptual framework.

studies being more meaningful for ecosystem management and resource use. Models that integrate sampling methods used in both larger- and smaller-scale analyses can help fill the sampling gap at intermediary scales. For example, Van Gennip et al. (2017) employed assimilative models to simulate and forecast animal movement patterns at a regional scale. If coupled with field experiments, investigators may predict community changes caused by stressors from large-scale sources such as OA.

Due to the large spatial and temporal extent of this topic, OA is largely presented as a conceptual framework. Ocean acidification is a phenomenon that occurs at a large spatial and temporal scale (Godbold & Sloan 2013). Recent literature suggests that the effects of ocean acidification due to atmospheric carbon have been continuously intensifying for the past 21,000 years (Riding et al. 2014). In order to effectively model and manage the effects of OA, we must first develop a similar framework among disciplines so we can begin to integrate scale in research and conservation efforts (Blackford 2010).

THINGS CHANGE: HIERARCHY AND SCALE IN EVOLUTIONARY BIOLOGY—Evolution is incredibly complex, occurring at many different spatial scales and across levels of biological organization. Evolutionary processes have a temporal scale as well, such as the tempo and mode of developmental processes. An understanding of these processes can inform us on changes in organisms through time. The use of scale and hierarchy as a framework in evolutionary biology is largely ambiguous, as evolution is often measured at a specific scale or organizational level. For example, changes in genetic structure are usually studied at the molecular and phenotypic scale, while phenotypic variation is studied at the population level and compared geographically at different spatial scales. This is especially true when describing new species, where both morphological and molecular evidence is used to support differences among populations.

Small-scale changes in an organism's genome can lead to drastic effects across hierarchical levels, affecting individuals and entire populations in positive, as well as negative, ways. Geneticist Dmitry K. Belyaev best described this in his seminal research on the genetic basis of animal domestication. Belyaev found that when select genes in an animal are slightly altered, they can give rise to a wide network of changes in the developmental processes the gene governs (Belyaev 1969). This "small" change at the genetic level led to profound changes at the phenotypic level, such as how tame an animal was likely to be (Belyaev 1969). Genotypic changes during domestication were even similar among mammals from different taxonomic groups, because they all shared similar regulatory mechanisms for hormones and neurochemistry. As a result, many phenotypes are shared among domesticated mammals, such as dwarf and giant varieties, piebald coat color, floppy ears, and changes in reproductive cycles (Belyaev 1969). Belyaev's research was, and still is, an incredible body of work, because it linked small changes at the genetic level to dramatic phenotypic and behavioral changes associated with domestication. Unfortunately, not all genotypic changes lead to desirable phenotypic displays. The loss of genetic diversity and in-breeding often characteristic of endangered animal populations have led to pronounced physical deformities. In endangered Florida Panthers (*Puma concolor coryi*), individuals have been found with bent tails (Roelke et al. 1993). On the other hand, populations of invasive American Bull Frog (*Lithobates catesbeianus*) appear to not be negatively affected by a lack of genetic diversity and inbreeding (Klamath et al. 2016). These studies indicate that our current understanding of the emergent properties of low genetic diversity requires continued research and inquiry.

In addition to the hierarchical framework through which genetic selection operates, selection on life-history traits over ecological timescales can have far-reaching, indirect macroevolutionary effects. A shift in the relative timing between two developmental processes in a descendant ontogeny, also known as heterochrony, can often effect evolutionary processes (Raff & Wray 1989). A good example of heterochrony is displayed in obligate paedomorphic salamanders, which retain larval characteristics into adulthood. Because of this, populations of these salamanders are genetically more distinct from one another than are metamorphosing populations, which fully transform to a terrestrial adult stage and retain no larval characteristics in adulthood (Shaffer 1984). High genetic diversity among populations of obligate paedomorphic salamanders is likely the result of low genetic flow, given that they tend to stay in smaller areas of streams or in isolated ponds. They may then have higher speciation rates compared to salamanders that can metamorphose and travel between ponds. Changes from facultative paedomorphosis to obligate paedomorphosis can occur in descendant ontogeny; therefore, paedomorphosis in salamanders can often result in heterochrony

(Gould 1977). Interestingly, heterochrony at one hierarchical scale doesn't necessarily lead to heterochrony at other hierarchical scales. For example, the molecular basis of paedomorphosis in salamanders can vary among individuals and is not always related to shifts in timescale. In some salamanders, paedomorphosis is triggered by the disabling of the production or reception of a specific hormone, which is more related to turning a gene on or off rather than changing the timing of hormone production. While macromorphologically we see evidence of heterochrony in the form of delayed adult features, it was not triggered by a delayed molecular event. Therefore, changes in timing at the molecular or cellular level need not produce heterochronic patterns at the whole-organism level, and heterochrony at the organismal level need not involve changes in the timing of molecular events.

Evolutionary biologists frequently use hierarchy and scale as a framework, especially when understanding how changes at the genetic level can have long-term effects on individuals, populations, and even the persistence and conservation of entire species. Heterochrony and domestication are just a few examples that have employed integration across scales and hierarchies to better understand and explain complex evolutionary processes. With the advent of more robust genetic and molecular tools, we may uncover new information to help us integrate more intensively across hierarchical levels, therefore demystifying the complex and often enigmatic processes that collectively lead to evolution. As we enter the Earth's sixth mass extinction, the goal for future integration is to question how these effects spanning hierarchical levels and spatial scales interact and become linked or decoupled on ecological and evolutionary timescales.

USE OF SCALE AND HIERARCHY CONCEPTS IN RESERVE DESIGN RESEARCH—As the world population of humans continues to grow, ecological reserves play a major role in limiting human encroachment into important natural habitats that are home to sensitive wildlife. In many parts of the world, reserves represent the only places that natural biodiversity is maintained and natural processes are allowed to play out. Reserves must be designed for maximum conservation efficacy if they are to have a significant impact on maintaining biodiversity. Reserves that are too small and isolated can function essentially as ecological islands. Just like island systems, they may contain less biodiversity and be more prone to local extinctions (MacArthur & Wilson 1967). The use of scale and hierarchy as a framework for assessing reserve adequacy and efficacy has the potential to inform conservation strategies and policy decisions relating to land-use allocation.

Recognizing the concept of scale-dependency may play a key role in creating effective reserve systems, but logistics and limitations often prevent the integration of this concept into reserve design. Creating a small reserve in a single location may be helpful to species that have limited ranges that are contained within the reserve. However, highly mobile species with ranges that expand beyond the reserve's borders, such as migratory birds, may see little benefit if the entirety of their range is not adequately preserved. Similarly, relatively sedentary species within a small reserve may be well protected on an individual or population level, but their genetic diversity may be severely limited if populations outside of the reserve go extinct or have no contact with the protected population. Baker (1992) noted that a key element of any reserve design is ensuring that reserves are large enough to withstand potential disturbance events. Pickett and Thompson (1978) also argued that reserves should be designed based on a "minimum dynamic area," a size threshold at which there can be enough internal repopulation within a reserve to avoid extinction after a disturbance. By considering scale-dependent effects when designing individual reserves and larger reserve systems, the preservation of biological diversity across all hierarchical levels could be increased significantly. Little work has been done showing how reserve design practices can actually be integrated across scales. Most studies recommend looking at larger scales for more mobile species and smaller scales for more sedentary ones. The few studies that have made recommendations on how to integrate across spatial scales when considering reserve designs cite a lack of comprehensive data as a major limiting factor (Andelman & Willig 2002).

There is clear evidence that scale can have significant implications on reserve design plans. Huber et al. (2010) compared algorithmically-generated reserve plans that were based on either local-level (within an individual county) or regional-level (within several neighboring counties) species abundance and distribution data and found the resulting reserves to have little overlap. Local planning seemed to ignore most large-scale ecological processes, but purely regional planning ignored resource specificity and habitat heterogeneity. Hartley and Kunin (2003) highlighted similar issues, noting how extinction risk and other conservation priority factors varied greatly depending on the scale at which they were examined. Both studies make similar recommendations that scale must be considered when making conservation plans and that data from multiple scales should be combined.

In addition to recognizing the importance of scale, some work has focused on choosing the appropriate scale when designing reserves. Schwartz (1999) compared the efficacy of both small- and large-scale reserve designs and recommended that if a single scale is to be considered, larger scales are generally preferred. When it comes to actually integrating multiple scales in a single reserve design, most studies recommend an algorithmic, computer modeling approach (Schwartz 1999; Huber et al. 2010). But not many studies have actually put this approach into use. One study that did use this methodology while making recommendations for reserves to protect Paraguayan bats noted that the major limitation to this method is the lack of large, consistent data sets (Andelman & Willig 2002). While they found the results of the approach promising, they noted that it was only possible because they had access to long-term, comprehensive monitoring data for the bats in question.

If cross-scale integration is to become more common in the field of reserve design, large-scale and consistent data collection should be prioritized in areas of conservation concern. Such datasets would increase the ability of researchers to use computer modeling techniques to design more effective ecological reserves. Until these types of data become more readily available, scientists should at least acknowledge scale in their reserve plans and try to work at the scale most appropriate to their specific conservation goals. While integrating across spatial-scales may not yet be realistic, given the data limitations, the scale-dependence of conservation actions must be recognized when planning new conservation reserves. Reserve plans should focus on creating large enough reserves to maintain sufficient biodiversity, and networks of closely-linked reserves should be created if possible.

CONCLUSIONS—After reviewing the literature in each of the respective ecological disciplines, we developed a simple characterization of three different approaches or applications of scale and hierarchy in each ecological discipline. First, there are those applications that explicitly acknowledge the importance of scale or hierarchy in their discipline. There appears to be a growing number of applications that explicitly incorporate observations at two or more scales. Secondly, there are those papers that apply scale or hierarchy as a framework to help communicate how interactions across scales may be manifested at different hierarchical levels. Finally, there were those studies that integrated across scales or levels of hierarchy in a predictive capacity. Applications that integrate across scales or levels appear to be relatively rare and may still be primarily limited to theoretical studies or modeling exercises. The application of concepts related to scale and hierarchy in empirical studies has lagged compared to the rapid theoretical advances in the 1980s and 1990s. We hope that this paper inspires more thought on the importance of considering scale and hierarchy in ecology, its value as a framework, and the appeal of understanding the integrating ecological processes across scales and hierarchies into a few measurable and meaningful variables.

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SUPPLEMENTARY MATERIAL

TABLE S1. List of terms and concepts related to scale and hierarchy in ecology..

aggregation	Grouping of organisms or biological processes that may affect the quality of information one can extrapolate depending on the scale of the observations.
bottom-up/to-down	Ecosystem structuring driven by nutrient supply, productivity, and type of primary producers (bottom-up) or top predators controlling the structure or population dynamic (top-down).
cross-scale interations	Relationship of organisms or processes across a broad range of space or time.
ecological incorporation	The ability of an ecosystem to adapt to changes.
emergent properties	A property of a system that is not seen at the level of the individuals or characteristics that comprise that system.
hierarchy	The arrangement and relation of organisms to each other.
integration	How various levels of hierarchy relate to and compose other levels.
resilience	The ability to resist damage and recover quickly after disturbance.
resistance	The ability to remain fundamentally unchanged by disturbance.
scale	Spatial and temporal size.
stability	The ability of an ecosystem to return to equilibrium after a disturbance.