Current Landscape Ecology Reports (2020) 5:12–24
https://doi.org/10.1007/s40823-019-00047-3

SPATIAL SCALE-MEASUREMENT, INFLUENCE, AND INTEGRATION (A MARTIN AND J HOLLAND, SECTION EDITORS)

Assessing the Relative Importance of Factors at Multiple Spatial Scales Affecting Terrestrial and Aquatic Wildlife

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Published online: 20 November 2019

Abstract

Purpose of Review We reviewed recent studies focused on assessing the relative roles of factors operating at different scales in shaping animal populations, species, communities, and individual behaviors. Our goal was to summarize the current state of the science by documenting trends and advances in approaches used to weigh the relative impact of drivers at different scales.

Recent Findings We identify several recent advances in remote sensing–based data collection, such as unmanned aerial vehicles and terrestrial laser scanning, that have the potential to increase the range of scales over which more detailed measurements of the composition and structure of environments can be made. We also highlight the promise of experimental studies and specific statistical approaches for providing a more solid understanding of the relative importance of factors operating at different spatial scales.

Summary We found that after nearly three decades of studies focused on the relative importance of factors operating at different scales, no general pattern has emerged. There is no clear evidence that one scale or one set of scales consistently plays a larger role than others. Nonetheless, it is clear from this research that ecological processes are indeed affected by processes operating at multiple spatial scales. We conclude that a more productive line of questioning might focus not on the relative importance of factors operating at different scales, but on understanding which factors affect a given process, at what scales they operate, and how they interact.

Keywords Multiscale · Hierarchy · Habitat · Scale · Fish · Wildlife

Introduction

The concept of scale, the spatial or temporal dimensions of an object or event, continues to rise in the consciousness of ecologists—recently capturing the attention of more general audiences [1, 2]. In fact, awareness of the importance of scale for understanding complexity across disciplines has reached an all-time high [3]. This fascination with scale arises from its potential to provide unified principles for understanding and predicting patterns (e.g., species richness) and processes (e.g., population dynamics) in a highly complex world [4, 5]. Ecologists have recognized problems of pattern and scale at least as far back as the 1930s [6], but it was the theoretical foundation laid in the 1980s and 1990s [4, 5, 7, 8] and the initial applications of quantitative tools for addressing questions of scale in the 1990s [9–11] that helped establish the field of landscape ecology.

The knowledge that processes operate at different spatial and temporal scales is critical to our understanding of ecological systems [7, 8]. Our ability to understand a given process depends on the scales at which we choose to observe it. For example, a study designed to better understand plant-pollinator interactions would need to focus on much finer

This article is part of the Topical Collection on *Spatial Scale-Measurement, Influence, and Integration;*

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s40823-019-00047-3) contains supplementary material, which is available to authorized users.

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scales than a study focused on ungulate migrations. Fortunately, we do have a basic understanding that processes tend to link temporal and spatial scales—with slower processes occurring over larger extents and faster processes operating at smaller extents. However, we also know that the processes operating at a given scale do not do so in isolation but are affected by patterns and processes operating at both finer and broader spatial and temporal scales—reflecting the hierarchical nature of ecological systems [5, 12–14] (Fig. 1). Each level of biological organization from the organism to the ecosystem is associated with a domain of processes that operate over a range of scales in space and time which includes everything that is below it in the hierarchy. Constraints imposed by processes operating at finer spatial scales can be seen as initiating conditions, which limit the potential of processes at broader scales (higher levels in the hierarchy) [15]. Similarly, lower levels in a hierarchy can be constrained by higher level processes generating environmental limits [16].

Armed with this understanding of the importance of scale and the knowledge that processes and patterns at a given scale are affected by those at broader and finer scales, ecologists began to ask about the relative importance of the factors operating at different scales. Are the processes and patterns in question—e.g., habitat selection, population dynamics, community composition—driven more strongly by higher level processes operating at broader scales or by lower level constraints from finer scales?

Developments over the last decade have made it more possible than ever before to explore ecological questions from a multiscale perspective. Ecologists have developed a number of theoretical and quantitative approaches to assess the relative importance of factors at multiple spatial scales affecting animal populations, species, communities, and individuals. Recent reviews and syntheses that compare and classify different multiscale approaches in wildlife ecology have been particularly helpful for (1) establishing a foundation for understanding habitat selection and (2) highlighting recent quantitative advances [17, 18]. However, the majority of reviews have focused on studies of habitat selection or habitat modeling. Furthermore, there have not been any recent reviews since Mayor et al. [19] that span both terrestrial and aquatic systems.

Here, we review recent efforts to understand the relative influence on wildlife of factors operating at different scales. We do so across both terrestrial and aquatic studies with the hope that reviewing work in both realms in one place might facilitate what is often an elusive cross-pollination of ideas and approaches. We start with a brief overview of the way in which these studies have defined scales. We then discuss the ways researchers have been measuring the drivers of ecological processes at these different scales and where recent advances have been made. Next, we review trends and advances in approaches that have been used to compare the relative influence of factors at different scales. Finally, we explore how future progress in this area could be made by reformulating our questions and implementing what could potentially be considered best practices in study design and data analysis.

What follows is not a quantitative, systematic review. Conducting a comprehensive search for all studies that have compared the relative effects of factors at different scales and interpreting differences across response types, scale definitions, and approaches made such a comparison difficult, if not impossible. Nonetheless, to answer the specific question of whether factors at larger or smaller scales tend to have larger effects on animal responses, we conducted a targeted search and quantified the results of those studies.

Defining Scales of Inquiry

To help build a meaningful understanding of the relative importance of drivers of ecological patterns and processes at different scales, studies need to use adequately defined,

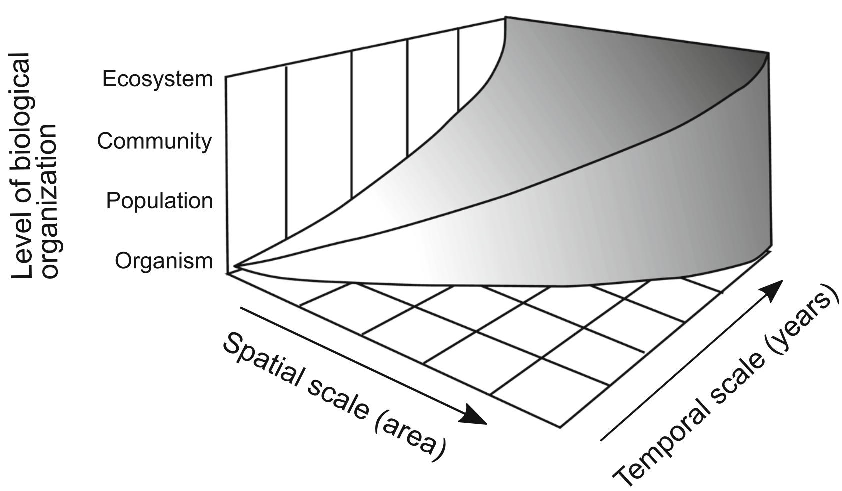

Fig. 1 Hierarchical levels of biological organization in relation to spatial and temporal scales of ecological processes. Scales of ecological processes increase from the level of an individual organism to an entire ecosystem, but the domains of processes for a given level of biological organization operate over a range of scales in space and time that includes everything that is below it in the hierarchy [adapted from 107–109]

ecologically meaningful scales. The selection of ecologically meaningful scales is perhaps the most critical aspect of designing a study to explore the relative impacts of factors at different scales. For example, if one selects the appropriate scale at which to explore fine scale drivers and an inappropriate scale at which to explore broad scale drivers, one might conclude that finer scale drivers are more important whether they are or are not. In a 2009 review, Wheatley and Johnson [20] found that the selection of scalers in many of the studies that explore the role of drivers of ecological process across scales is often arbitrary with little to no declared relationship to biology or ecological process. This is generally true of the studies that have been conducted between 2009 and 2019 as well. Nonetheless, a number of studies either explicitly or implicitly acknowledge a lack of understanding of the appropriate scale at which to measure one or more variables [21•, 22]. One study that explicitly explored the linkage between process and scale is Chiavacci et al. [23•] who explored nest predation and found different landscape correlates of predation rates at different scales for different species.

Whereas all studies are faced with the challenge of selecting ecologically meaningful scales, terrestrial studies appear to struggle with this more than do aquatic studies. The majority of comparative multiscale studies we encountered used scale labels of plot, local, landscape, and regional. Many of these studies do provide an ecological justification for the dimensions of the scales, but plot, local, landscape, and regional are all human constructs and could be of any size. For example, Mitchell et al. [24] used a 1-m^2 local scale to explore environmental drivers of soil microarthropod communities, whereas Martin and Fahrig [21•], studying habitat relationships for three mid-sized mammals, used a local scale of 70,650 m^2. Other terrestrial studies define scales based on an ecological unit, such as a stand, a piece of dead wood, or a plant cluster [25–27]. Studies focused on movement or space often use temporal extent to define scales of observation. For example, Northrup et al. [28] defined spatiotemporal scales based on activity patterns over 5-, 10-, 25-, and 170-h time periods. In almost all cases, the scales used in terrestrial studies define a spatial extent, although, particularly in the case of the ecologically defined scales, they may not be the same across all observations. By contrast, relatively few studies focus on different grains [29, 30].

In aquatic ecology, the hierarchical structure of hydrologic drainage basins provides a template for conceptualizing the physical processes that drive riverine ecosystems at multiple scales in space and time [31]. The nomenclature for the hierarchical organization of riverine habitat is relatively standardized because the physical environment of streams imposes a structure that is visually apparent. For example, basins (i.e., watersheds) contain sub-basins with tributaries that flow into larger streams and accumulate in size downstream. The stream network draining a hydrologic basin is divided into sections (i.e., portions of stream between tributary junctions) that are composed of reaches, which contain channel units (i.e., pools and riffles). A channel unit can be further subdivided into subunits and microhabitats. This schema forms the basis on which factors influencing biological and physical responses in streams can be quantified at multiple spatial scales [32]. The influence of the surrounding landscape on a given point in a stream network, thus, can be measured at any of the aforementioned levels (e.g., channel unit, reach, section, sub-basin, basin) and at various distances extending laterally from the stream in riparian buffers of various widths. It is important to note that the various levels in the hierarchy of stream habitat represent relative differences in spatial scale and technically require quantification to be interpretable [33]. For example, a pool in a small headwater stream that is 1 m in width is likely to be less than 10 m long, but a pool in a river 10 m in width will be tens of meters long.

Measuring Drivers

Although some studies explore the same drivers across multiple scales, many explore different sets of potential drivers at different spatial scales. We define “drivers” as the factors that influence a given ecological response, i.e., population density, occurrence, or habitat selection. In terrestrial ecology, typical drivers that are measured at multiple scales include elevation, aspect, slope, vegetation type, and land use (i.e., forest, agriculture, urban). In freshwater environments, drivers are usually quantified both on land and in the water. Land-based drivers are similar to those in terrestrial ecology (see above). Aquatic drivers, however, include water quality metrics (temperature, pH, turbidity), underwater habitat type (pool, riffle), water depth, and substratum type (sand, gravel, boulder). In general, studies often rely on field data to describe patterns at finer grains and smaller extents. Conversely, at broader scales, these same studies tend to rely on remotely sensed data to describe patterns and represent potential processes. Although this generalization tends to apply to both terrestrial and aquatic systems, there are, nonetheless, informative differences in the types of drivers measured in the two realms.

Terrestrial

At finer spatial scales, multiscale terrestrial studies tend to focus on the elements that structure an animal’s immediate environment including plant species composition and structure—factors affecting food availability, microclimatic conditions, and predation risk—microclimates, and more rarely interspecific interactions e.g., [34, 35]. At broader spatial scales, these studies often focus on the impacts of landscape composition—the elements that make up a landscape—

climatic factors, and anthropogenic changes—e.g., land-use, road density e.g., [36, 37]. That is not to say that some aspects of landscape configuration—the way that elements that make up the landscape are arranged—are not measured at broader spatial scales. Fragmentation, distance to roads, patch sizes, and edge densities are often explored at broader scales e.g., [38, 39•]. The factors at these broader scales often influence larger scale movements and resource use on seasonal or annual time scales, and also influence finer scale processes like predation and local climatic conditions.

Advances in remote sensing are providing better estimates of environmental patterns at broader scales as well as making it easier to measure finer scale aspects of environmental structure across larger extents. For example, lidar (light detection and ranging) can be used to measure structural aspects of vegetation remotely over larger extents, in ways that would traditionally require extensive and intensive ground-based sampling [40]. More recent developments have allowed researchers to start to assess composition with lidar [41]. There have also been advances in mapping various aspects of the environment including land cover [42], vegetation structure [43], and biomass [44] using combinations of lidar and passive remote sensing products. Recent advances in the application of lidar itself also provide the opportunities for increasing our understanding of multiscale drivers. Ground-based lidar—or terrestrial laser scanning (TLS)—can potentially be used to more quickly and easily define vegetation structure [45, 46] and the use of laser return intensity (LRI) information from lidar could help resolve vegetation structure over larger extents [47].

Unmanned aerial vehicles (UAVs) have the potential to increase our ability to explore the drivers of ecological processes at multiple scales [48]. UAVs can be used to, among other things, survey animal populations [49], measure vegetation structure [43, 50], and map topography [51]. As with advances in remote sensing products, UAVs can facilitate detailed measurements of the terrestrial environment at broader extents than is possible with ground-based sampling—allowing researchers to more easily explore patterns at multiple spatial scales.

Aquatic

In freshwater environments, drivers of ecological response are measured both on land and in the water itself. On-land measurements of drivers in aquatic ecology are generally made in a similar manner as in terrestrial ecology (i.e., through direct sampling or remote sensing), except that the spatial boundaries encompassing the area of influence for a given driver are demarcated by the watershed. This is an important distinction because aquatic response at a given point in a hydrologic drainage network is influenced by the cumulative effects of upstream factors on land and in the water. Measuring drivers below the water surface presents a whole new set of challenges for visual observation, sampling, and aerial assessment. Lakes, streams, and ponds are essentially opaque to the terrestrial observer because the physical properties of the water obstruct, limit, or at best, distort one's view of the underwater environment. Turbidity, surface roughness, and water depth all add layers of uncertainty and logistical complexity to the process of quantifying influences of environmental factors at multiple spatial scales. This difficulty in sampling systems that are essentially invisible to the human eye is widely recognized in marine ecology and limnology [9] and particularly in soil sciences [52]. Compared with the open ocean and subterranean environments, however, rivers, streams, and lakes have an advantage in that they are relatively accessible. Nevertheless, riverine ecologists interested in multiscale analysis of aquatic habitat must adapt their methods to the constraints imposed by the unique aspects of a flowing aqueous environment [53]. Underwater techniques for habitat assessment such as snorkeling, scuba, and remote cameras are effective only where turbidity is low and turbulence is limited [54]. Aquatic ecologists have attempted to resolve this problem by using increasingly sophisticated remote sensing methods to map rivers and streams in a manner that characterizes the "riverscape" [55]. Remote sensing and in situ approaches for quantifying riverine habitat at multiple spatial scales have developed rapidly in the last decade, and it is now feasible to map water temperature [56, 57], water depth and velocity [58], substratum type (e.g., gravel, cobble, boulder) [55], and stream geomorphology [59] at a very fine spatial resolution over tens of kilometers.

Recent advances in remote sensing of freshwaters are making it possible to explore drivers of ecological patterns at multiple spatial scales. However, these data are limited compared with publicly available satellite and aerial imagery used by terrestrial ecologists and collecting data with fixed-wing aircraft or helicopters is often cost prohibitive. Unmanned aerial vehicles have potential for application in some freshwater systems [60], but the extensive linear nature of rivers and streams constrain the line-of-sight distance required by federal aviation regulations. Furthermore, the sensor technology for drones may not have the precision required for aquatic applications [61].

Where it is not feasible or cost-effective to use remote-sensing approaches to quantify spatial patterns, field data can be collected intensively and extensively to quantify drivers at multiple scales. In contrast to terrestrial environments, the linear structure of rivers and streams makes this approach more tractable because the spatial extent of interest is only along the linear "riverscape" as opposed to across an entire two-dimensional landscape [62]. For example, Brenkman et al. [63] mapped aquatic habitat for fish at a very high-resolution (i.e., every pool and riffle) over 65 km, and

McGuire et al. [64] analyzed multiscale patterns of streamwater chemistry samples collected every 100 m throughout an entire headwater stream network (32 tributaries). Developments in low-cost stream temperature sensor networks and spatial modeling have also increased the spatial extent and resolution of data available to freshwater scientists and practitioners, facilitating the investigation of temperature effects over tens to hundreds of kilometers [65]. Fiber optic–distributed temperature sensing has been applied at a finer spatial extent of kilometers, but with a resolution of meters, to characterize hydrogeological factors and their influences on the spawning behavior of brook trout overa range of scales [66].

Study Designs and Analytical Approaches

Although many ecological processes have been explored across a range of spatial scales, a true understanding of the relative impact of factors at different scales can only be obtained from a multiscale study explicitly designed to compare drivers at different scales. Choices in the design process include whether the ecological process of interest (the response) is measured at a single or at multiple scales, whether the drivers (explanatory variables) are the same or different across scales, and whether the grain of explanatory variables changes with the extent of measurement. Some approaches require the a priori definition of scales of observation whereas others are more flexible, allowing the relevant drivers to emerge at the relevant scale.

Studies have taken a variety of approaches to determining the relative contribution of factors at different scales to ecological processes. Wheatley and Johnson [20] created a typology of multiscale habitat studies that captures the range of the study designs used to date. Here, we adapt that typology to (1) better reflect both the types of studies that have explicitly explored the relative influence of different factors at different spatial scales, (2) provide more detail about specific study designs, and (3) be more inclusive of aquatic studies. The important distinction to make between the typology outlined by Wheatley and Johnson [20] and the simple classification provided here is that Wheatley and Johnson were particularly interested in calling out differences between studies focused on the effects of changing the spatial scale of observation (e.g., how processes scale) and the multitude of other multiscale studies.

Varying the Scale of Explanatory Variables but Not the Response

The most commonly applied design across studies aimed at determining the relative influence of factors operating at different scales is one in which a response at one scale is analyzed in relation to drivers at multiple scales. The pattern or process of interest (e.g., bird nest locations, amphibian community composition, fish abundances) is measured at a single spatial extent. The potential predictors or drivers are then measured at multiple spatial extents. Simple model comparison (e.g., comparing the fit of models built at different scales and/or with multiscale predictors) is a common approach of analysis for studies of this type [25]. For example, Duan et al. [67] modeled insect community composition in 400-m^2 plots in response to explanatory factors measured at a plot scale (400 m^2), a “landscape scale” (1 ha), and a regional scale. Wendt and Johnson [37] measured occupancy at the scale of a nest box and modeled it as a function of box attributes, local (17,660 m^2), and home range (3.14 km^2) scale patterns.

Measuring a pattern or process at a single spatial scale and the potential drivers at multiple scales generally makes intuitive sense. For example, it would be reasonable to explore the potential effects of climate over larger spatial extents but to study species interactions, food resources, or nesting substrates over smaller extents. In fact, a hierarchical structuring of habitat selection and resource use in which decisions at finer scales are determined by decisions made first at broader scales has long been proposed [68–70]. For example, as it applies to avian habitat, at broader scales, processes and patterns that affect activities occurring across a home range might drive habitat selection—e.g., access to water and availability of vegetation types suitable for nesting or foraging. At a finer scale, however, the structure of vegetation might be important for concealing movements or placing a nest.

However, there are also reasons for assessing the potential impact of the same drivers across multiple spatial extents. For instance, when little is known about the scales at which particular processes operate, it may be difficult to assign specific processes to particular spatial extents. Studies that explore the same explanatory variables across a range of spatial extents tend to do so at larger spatial scales e.g., [21•, 35, 71]. This may be because data used at larger extents is often remotely sensed and, thus, is readily available for analysis at multiple spatial extents, whereas finer sale patterns—e.g., in vegetation structure—must be laboriously sampled to produce multiple sampling extents. Alternatively, it may be that researchers have a better understanding—or at least believe they have a better understanding—of the extents over which finer scale processes operate than they do of the extents at which broader scale processes operate.

A number of different analytical techniques have been used to compare the relative impact of factors at different spatial scales on patterns or processes occurring at a single spatial scale. Each of these approaches, in its own way, addresses the critical challenge of cross-scale correlations in explanatory factors and in so doing isolates the variation in the pattern or process of interest associated with each spatial scale. Multicollinearity can be a problem in any observational study but is particularly prevalent in multiscale studies given the hierarchal structure of ecological systems. That is, drivers at finer spatial scales influence factors at broader scales and factors, at broader scales constrain factors at finer scales. Battin and Lawler [72] provided some examples of approaches that could be used to tease apart contributions of factors operating at different spatial scales. They focused on simulation modeling, variance partitioning, and hierarchical models. Since then, significant progress has been made in these areas as well as with other approaches. Below, we provide a brief review of the approaches that have been used to date.

Variance Decomposition

One of the most widely used approaches to exploring the relative contribution of factors at different spatial scales involves decomposing or partitioning the variance explained by the multiple factors into different elements based on the spatial scale at which they were measured. Whittaker [73] introduced this statistical approach as a means of isolating the components of variation in a multivariate data set that could be solely attributed to individual explanatory factors and those that could not be attributed to individual factors but were, instead, shared components of variation. Borcard et al. [74] extended the approach to spatial analyses and Cushman and McGarigal [75] first used the approach to explore multiscale relationships between bird community composition and environmental drivers at multiple spatial scales. They partitioned the variance in bird community composition into components that could be explained solely by factors at the plot level, the patch level, and the landscape level—i.e., "pure" components—as well as components that were shared by each pair of levels and all three levels, respectively. Later studies applied the approach to individual species to explain the relative contribution of drivers of abundance or presence at different spatial extents [76].

The strength of variance decomposition lies in the ability to isolate the components of variation explained by factors at different scales. However, doing so does not always reveal a clear hierarchy of influence. An isolated pure component of variation can be solely attributed to the factor, or set of factors, in question. However, the components of variation that are shared across scales, which are the product of correlations and/or interactions, cannot be solely attributed to a single scale. When the pure components of variation from each of the scales are large relative to the shared components of variation, it may be possible to rank the relative contributions of the factors at the different scales. Conversely, when the shared components of variation are large compared with to pure contributions of the scales, any clear ordering of the influences of the scales are likely to be obscured [76].

A number of recent studies have used variance partitioning to explore the relative importance of factors at different spatial scales. These studies have focused on owl nesting habitat [37], Lepidoptera assemblages [22], soil fauna composition [77], stream fish assemblages [78], riverine macroinvertebrate community composition in response to damming [79], drivers of lake phytoplankton species richness [80], and many other relationships. Although many studies using variance partitioning are able to draw clear conclusions about the relative influences of factors at different scales, some are more challenged by cross-scale correlations [22, 80, 81]. Interpreting the cause of the shared variance in these studies is critical [80].

Hierarchical Models

Graham [82] described an approach to using sequential or residual regression to address multicollinearity. Although there are several ways to apply the approach to the analysis of multiscale associations, each of these involves an implicit assumption about the hierarchical structure of the relationship. In the simplest application, a model is used to explore the relationship between the response variable and a set of explanatory variables that are all measured at the same scale. The residuals from this analysis are used as the response variable in a model with the explanatory variables from a different spatial scale. Again, this assumes a hierarchical structuring of the system in question with relationships at a given scale (often the broadest scale) constraining the relationships at finer scales. Battin and Lawler [72] demonstrated such an approach using classification trees, and McMahon and Diez [83] provide a thorough description of hierarchical linear models and two examples—using plants in this case.

Here, we highlight three examples of the application of hierarchically structured statistical models to multiscale questions. Ranius et al. [26] used hierarchical Bayesian regression to explore the relative importance of multiscaled factors in structuring distributions of saproxylic beetles. Cuffney et al. [84] used multilevel hierarchical models to explore the potential effects of regional scale influences on the effects of finer basin-scale drivers on aquatic invertebrates and algal communities. Finally, Fenoglio et al. [85] used a multilevel Bayesian model to explore the potential drivers of parasitoid density at scales defined by a leaf, plant patch, and a city neighborhood.

Structural Equation Modeling

Graham [82] also recommended structural equation modeling for addressing multicollinearity. Through a set of linked models, structural equation modeling facilitates the application of specific theories to empirical data by defining the relationships between the various potential causal factors in a system [86, 87]. As applied to multiscale studies, structural equation modeling allows one to specify the potential causal relationships between the factors at different spatial scales. Stoner and Joern [38] used structural equation modeling to explore the relative impacts of fragmentation and patch size at a broader scale both directly and indirectly through impacts on the plant and predator communities, on insect communities. Villeneuve et al. [88] used path analysis to explore the direct and indirect impacts of watershed-, reach-, and site-scale factors on macroinvertebrate communities across France. Morante-Filho et al. [39•] used a similar approach to look at the direct and indirect effects of forest cover and edge density at broad scales both directly, and indirectly through effects on fruit abundance and vegetation complexity at a finer scale, on the frugivorous bird community in the Atlantic forest of Brazil.

Experimental Studies

Another strategy for exploring the relationships between responses at a single scale and potential drivers at multiple scales is the use of experimental approaches. Using an experimental approach, the researcher "applies" the hypothesized drivers as treatments, combining drivers from different spatial scales to explore interactions. For example, Chacin and Stallings [89] tethered fish to plots of artificial seagrass of different densities in different locations to compare the relative effects of broader scale drivers (turbidity, salinity, predator community) and finer scale drivers (vegetative cover). Similarly, Haynes et al. [90] attempted to tease apart the relative impacts on planthopper dispersal and distributions of patch quality at a finer scale and matrix composition at a broader scale. Finally, Frey et al. [91•] explored the impacts of woody habitat heterogeneity at multiple spatial scales on predation rates. They used artificial caterpillars to explore the effects of vegetation structure at a finer scale of home gardens to those at broader scales.

Varying the Scale of Both the Response and Explanatory Variables

The studies discussed above that hold the spatial extent of the response variable constant and vary the spatial scale of the explanatory variables ask how factors at different scales affect a single pattern or process. By contrast, studies that vary both the extent of the sampling of the process or pattern of interest and the extent of the potential predictors or drivers ask a slightly different question. By varying the extent of both the response and the explanatory variables, it is possible to explore a broader range of ecological questions about a pattern or process of interest. For example, the factors influencing the population density of a given animal enumerated in a 1-km^2 sampling area may be completely different from the factors affecting population density in a 10-km^2 sampling area. Thus, predicting response (i.e., population density) in 1 km^2 is not the same as predicting response in 10 km^2 because population density itself varies systematically with spatial scale. Mayor and Schaefer [92] eloquently demonstrated this phenomenon by analyzing census data for three species of mammals (squirrel dreys, beaver lodges, and moose) and illustrating that population density was negatively correlated with the area over which animals were counted. Furthermore, the landscape attributes that were correlated with population density also varied depending on the spatial scale (i.e., area) at which density was calculated. Similar results have been shown for the population density of Atlantic salmon in streams [93].

Examples of census data for animals over spatial extents spanning tens of kilometers are limited, as are studies that quantify ecological response at multiple scales. Such approaches have much to offer for understanding the relative importance of drivers of species abundance at multiple scales. However, collecting high-resolution data over large areas or even data at more than one spatial scale has been cost prohibitive in ecological studies despite its novelty and potential for advancing ecological understanding and addressing resource management questions. In the following paragraphs, we provide some notable terrestrial and aquatic examples of these approaches and emphasize the sampling designs and ecological questions of the studies as opposed to specific analytical approaches, as were outlined in the preceding section on varying the scale of explanatory variables but not the response. Our rationale is that (1) varying the scale of both the response and explanatory variables is still in its infancy and there are not many examples of this type of analysis, and (2) analytical methods outlined in the preceding section (e.g., variance decomposition, hierarchical models, and structural equation modeling) can also be applied to studies that vary the scale of both the response and explanatory variables, except that multiple iterations of these approaches will be required in order to analyze responses at multiple scales.

In terrestrial wildlife ecology, it is particularly challenging to collect census data or to measure ecological responses at multiple scales because it is difficult to locate and map species that are cryptic and mobile. LaForge et al. [94] compared the factors influencing population dynamics of feral horses at multiple spatial scales by conducting a census of an entire island in Canada. They analyzed the population density of foals at three different spatial extents to determine the most important predictors of mortality. The drivers of mortality differed depending on the spatial scale at which density was calculated.

Census approaches have been applied in freshwater aquatic systems, which are inherently difficult to sample. These spatially continuous visual surveys of river fish abundance are conducted over tens of kilometers [63], and the data can be scaled to any grain size [i.e., river segment length; sensu 95] to facilitate analysis over a nearly continuous range of scales [96]. Video and imaging technology have improved in the last decade, and these approaches have been applied to assess fish and habitat data over various spatial scales across a temperate reef [97]. Most commonly, however, sampling of ecological responses in terrestrial and aquatic environments is discontinuous, with measurements made at distinct scales selected by the investigator. For example, Millette and Keyghobadi [27] explored the relative effects of habitat amount and configuration on midge genetic structure at multiple spatial scales. They measured both genetic structure and habitat attributes at scales associated with a plant, a cluster of plants, and a peatland, and they measured corresponding habitat variables at each scale. Wellemeyer et al. [98] similarly aggregated abundance from reach to segment to basin in order to assess fish response at multiple spatial scales without having to conduct a census of entire river basins.

Until recently, the massive quantities of data obtained through radio and satellite telemetry of animals have been beyond the reach of the quantitative toolbox of ecologists. These data are collected at relatively fine intervals in time and provide high-resolution spatial data on species response to multiscale drivers over broad extents [99]. This allows the response of a tagged animal to be examined over a nearly continuous range of scales to determine the domains over which a given driver is ecologically relevant. Optimization techniques can then be used to evaluate the response of species to multiple drivers along a continuum of spatial and temporal scales [17]. Northrup et al. [28] evaluated wildlife responses to land use and resource management at spatial extents that were defined at biologically justified temporal scales. Lipsey et al. [100] used a novel spatially hierarchical approach to integrate songbird response conditionally across scales using Breeding Bird Survey data. They found that species occurrence was more strongly affected by local drivers when landscape context was favorable than when it was unfavorable. Rapid advances in analytical tools and computing power are making it more and more feasible to use high-resolution spatial and temporal data collected over large areas and over long periods of time to conduct multiscale studies that vary both the response and explanatory variables. This is a new frontier in landscape ecology that warrants additional work in both theoretical and applied research.

Which Scales Are the Most Important?

This, of course, is a question that has many answers. If ecologists have learned anything, it is that the answer to any question like this is that it depends. The relative importance of different drivers at different scales will depend on the ecological process being investigated, the drivers being considered, the system, and the spatial and temporal aspects of the study, among other things. Nonetheless, we attempted to discern whether there is any consensus across studies that have compared the relative effects on animals of factors at different spatial scales. We constrained our analysis to studies published in English that used variance partitioning to compare the relative effects of factors at different scales, and that reported the pure and shared components of variation associated with each of the scales being addressed. Constraining the studies in this way meant that we did not have to compare results across analytical techniques and that we did not have to rely on the authors' interpretations of the relative importance of different scales. We searched both the Web of Science and Wildlife and Ecology Worldwide databases using the following search: (*scale* AND relative AND (importance OR effect* OR influence*)) AND (variance partitioning OR variance decomposition).

Our searches highlighted a total of 368 papers, 26 of which compared effects of factors at two or more scales and presented the results in such a way that allowed us to compare the pure and shared components of variation. Because some studies conducted their analyses on multiple groups (e.g., taxonomic groups, individual species, separate biomes), we treated those analyses separately and thus we report on 44 comparisons from the 26 papers. Of these comparisons, roughly half ($n = 21$) compared the effects of factors at two scales, and the other 23 compared the effects at three scales. For each comparison, we recorded whether the largest proportion of variance explained was from the smallest, largest, or intermediate scale.

We found that half of the 44 comparisons reported shared components of variance that were large enough relative to the pure components to preclude definitive conclusions about which scales had the largest effect on the pattern in question. Large shared components of variance can obscure the effects of individual scales because it is impossible to determine what portion of that shared variance is attributable to relationships with factors at a given scale. We considered a pure component of variance large enough to have the dominant effect when, compared with the sum of any other pure component and its associated shared components, the pure component in question was still larger. Of the 22 comparisons from which we were able to conclude that factors from a given scale had larger effects than those from other scales, 64% found the largest effects at the smallest spatial scale, 27% at the largest scale, and 9% at an intermediate scale.

Our analysis indicated that factors at finer scales appear to play a larger role in driving the patterns in question. That said, this simple analysis is limited in a number of ways. First, these studies were trying to explain different ecological patterns—e.g., species richness, community structure, abundance, and presence and absence. Second, several of these studies compared the effects of drivers at a finer scale, drivers at a broader scale, and spatial drivers, whereas other studies did not include spatial location as a separate category of driver. It is possible that had spatial factors not been analyzed separately, at least some of the variance explained by spatial factors would have been explained by the broader scale factors or by factors at an even broader scale. Finally, these studies explored different spatial scales.

Despite the fact that we cannot conclusively report that factors at one scale play a larger role in structuring ecological patterns than factors at other scales, there are some definitive conclusions that can be drawn from these and all of the other studies we reviewed. Perhaps the most important conclusion that one can draw from the diversity of studies exploring the relative importance of drivers at different scales is that in almost all cases, there are significant relationships with drivers at multiple spatial scales. Although this is by no means surprising, the relative consistency of this finding is impressive. When studies explore drivers at multiple scales, they tend to find relationships at multiple scales. Thus, explanations that come from studies focused on a single scale are almost certainly limited. The results of these multiscale studies provide an impressive volume of evidence for one of the foundational tenets of landscape ecology—that processes operating at a given scale tend to be influenced by processes operating at both finer and broader scales [5, 12, 16].

Given that there will most likely always be drivers at multiple scales affecting a particular ecological process and that the relative importance of these factors will vary with context, one might wonder whether asking about the relative importance of different scales is a worthy pursuit. In some instances, we suggest that it will be. For example, to inform the conservation or management of a particular species or system, one might legitimately need to know where to put one's efforts—whether that be changing land-use practices throughout a watershed or altering structural complexity within a stream reach [101]. However, if the goal is to identify an overarching principle—e.g., that broader scale processes play the largest role in structuring animal communities—an identification of key scales may not be a beneficial use of an investigator's time.

Instead of asking about the relative importance of factors at different spatial scales, it might be more productive to ask questions about the way systems work and how the various components interact. For example, one might ask what drivers affect community composition and at what scales those factors operate. One might also ask how drivers interact and whether some determine or constrain others, or whether they are causal or merely correlated.

In shifting the focus away from searching for the dominant scales of influence or the correct scale at which to study a process, ecologists may want to change the way they approach scale in general. The expectation that "problems of scale" (sensu 8) can actually be solved may get in the way of the understanding that "scale" and "scaling" are ways of thinking about and investigating ecological phenomena [102]. Thus, one must view "scale" as part of the approach and process that unifies concepts and methods of scientific inquiry within and across fields [103]. In this sense, concepts of scale become integrated with the scientific method and are incorporated in the process of ecological understanding [104].

Best Practices for Moving Forward

To treat scale as part of a comprehensive approach to investigating ecological phenomena and to ask questions that focus more on understanding entire systems, ecologists might consider adopting a set of best practices that inform study designs and subsequent analysis. Here, we highlight a few particularly important practices and tools that we selected from some of the more innovative studies covered by this review. First, it will be important to acknowledge our lack of understanding of the scale at which processes operate. This means not assuming that a specific size of plot will be appropriate for a given study—e.g., a 1-km diameter plot for measuring variables representing landscape context, and a 10-m diameter plot for measuring vegetation structure. It means that exploring variables across a continuous range of scales is important e.g., [21]. It also means that looking for relationships at finer and broader scales than we might normally consider is essential. At least one study we reviewed concluded that the relationships of interest were found at a broader scale than had previously been explored [97], supporting the conclusion that ecologists are exploring too narrow a range of spatial scales [105]. Increasing availability of high-resolution remotely sensed data that can detect vegetation composition and structure will make it easier to investigate variables at broader scales than have traditionally been explored.

To better understand how factors at different scales interact, studies will need to adopt designs and analytical approaches that allow the researcher to elucidate causal pathways and to isolate drivers and interactions [106]. Experimental studies provide one route to identifying causal factors and interactions [91•]. Structural equation modeling provides another approach—one that, like an experimental approach, forces the researcher to layout their hypotheses for how the system works and how factors affect one another at different scales [e.g., 39•]. To date, these two approaches have been relatively rarely used compared with simpler model-comparison studies.

From the late 1980s to the present, ecologists' understanding of the implications of the scales at which they observe ecological systems has evolved significantly. The field has moved from the positing of concepts and theories about scale in the 1980s and 1990s to the development of tools and techniques that have facilitated the measurement patterns at multiple spatial scales in the 1990s and early 2000s. The most recent decade has seen the application of these tools to many questions of scale—including the search for the scales at which the most influential drivers of a given ecological process operate. Although this search has yet to reveal any consistent predictions about where higher level or lower level processes should predominate, it has provided a wealth of empirical evidence to support several key suppositions. Ecological systems are indeed influenced by processes operating at different spatial scales which interact in complex ways. We conclude that perhaps the most fruitful line of inquiry moving forward will be to focus on these interactions and to build a better understanding of the entire system in which the processes and patterns of interest are situated.

Acknowledgments We are grateful for discussions with D. C. Schneider for broadening our perspectives and increasing the depth of our understanding of scale in ecology. Constructive reviews from N. Schumaker and an anonymous reviewer on an earlier version of this manuscript helped improve the clarity and precision of the ideas presented in this paper.

Compliance with Ethical Standards

Conflict of Interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

Disclaimer Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. government.

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