The Routledge Handbook of Landscape Ecology

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Scale and hierarchy in landscape ecology

James D.A. Millington

Introduction

What is the landscape of a beetle? How does it differ from the landscape of a white-tailed deer? When is vegetation in a landscape considered fragmented? How do we identify and understand feedbacks between vegetation, physical substrate, and ecological disturbance? Underlying these questions are issues of *scale*, whether we are considering how the beetle and deer perceive their landscapes, how ecologists observe the beetle and deer to investigate how they interact with the world around them, or how ecologists use data collected at one scale to understand processes operating at another. Although scale refers to the physical dimensions of the world, organisms (including humans) perceive and respond to patterns and processes differently. Consequently, it is vital that when describing or investigating landscapes and the environment, we think carefully about our scales of observation and the range of scales that are of particular relevance to the organisms and processes being examined (Wiens 1989; Levin 1992). The emphasis throughout this chapter is on spatial dimensions because of the close links between spatial ecology and landscape ecology, but considerations of scale are equally important in the temporal dimension, and the two are often related and interact to shape ecological systems (Wolkovich et al. 2014; Ryo et al. 2019). The chapter starts with some definitions, first considering components of scale and then examining the differences between 'scale' and hierarchical 'level'. Issues of scale selection and scale dependence are then discussed before the challenges and opportunities of scaling and multi-scale analysis are outlined.

What is 'scale'?

Components of scale

A primary distinction to be made when thinking about scale is the conceptual difference between the *intrinsic scales* and the *imposed* scales of an object, pattern, or process (Wu and Li 2006). The difference enables us to consider the importance of observation and measurement; intrinsic scales might be thought of as independent of observation or measurement, whereas imposed scales depend on – and vary with – outside observers, measurement devices, and study objectives. Intrinsic scales are thus inherent in a phenomenon, characterizing their behavior and dynamics (e.g. typical spatial extent or event frequency). We use scale in the plural here, as multiple scales are often important for a phenomenon of interest independently of any observation of it. In contrast to intrinsic scales, imposed scales are due to the observer rather than the phenomenon being observed itself. However, for all organisms other than humans, these imposed scales are determined in some way by the intrinsic scale of the observer (see Section 3.3). For example, the phenomena a beetle can sense through its antennae on the ground are very different from those that an eagle soaring in the sky can observe with its eyes. However, humans have developed ways to observe phenomena at a variety of imposed scales and independently of our own intrinsic (human) scale. For example, microscopes allow humans to see things that are far smaller than we would otherwise be able to see given our intrinsic human scale (i.e. the properties of our eyes and visual cognition), and aerial photography allows us to view the world in ways that we would not otherwise be able to (contributing to the establishment of landscape ecology itself; see Chapters 1 and 12). Thus, the terms *observational* scale, *experimental* scale, *analysis* scale, and *policy* scale are usually used directly in association with human investigation and can be independent of the intrinsic scale of the phenomenon being studied. All are closely related, and it could be argued that observational scale – the scale at which measurements or samples are made – provides the basis for all the other imposed scale types (experiments, analysis, and policy all relying in some way on observation).

Imposed (e.g. observational) scales have a variety of components, including *cartographic scale*, *grain*, and *extent* (Wu and Li 2006; Wu 2007). The *cartographic scale* component is possibly the most widely understood in general terms and refers to the ratio of the size of an object in the empirical world to the size of the object as represented on the map. In cartographic terms, 'small scale' means many units in the real world for every unit on the map, and vice versa for large scale. Thus, a map with scale 1:1,000,000 (1 cm on the map represents 1,000,000 cm – or 10 km – on the Earth) is smaller scale than a map with scale 1:1000 (1 cm on the map represents 10 m on the Earth). Correspondingly, this nomenclature means that for the same size of map (e.g. printed on paper 1 m square), 'small-scale' maps provide less detail than 'large-scale' maps, but the area they represent is greater. These cartographic scale terms refer to the detail *of the map*; the map is a representation of data about the landscape with the cartographic scale determining what can be represented on it. In contrast, for landscape ecologists, scale terms are usually used to refer directly to *the data themselves* (potentially confusingly), meaning that an ecologist's 'small-scale' data would be plotted on a 'large-scale' cartographic map.

In landscape ecology, the scale components of *grain* and *extent* are more important than the scale elements of a map. Grain refers to the resolution of data, which in turn, is the smallest unit (whether spatial or temporal) within which measured values are assumed to be homogeneous (i.e. constant). For example, even though rainfall may vary during an hour, if the grain of a time series is 1 hour, then each measurement will represent an entire hour (e.g. total rainfall during an hour). Extent refers to the total measurement area (space) or duration (time) of a data set. Just as the cartographic scale determines what is represented on a map (in terms of detail and area), the grain and extent of data influence what is observed and what information can be gained. As demonstrated in Figure 3.1, landscape ecologists generally use 'fine scale' to refer to data that are collected at fine (or high) resolution (i.e. small grain, often over a small extent) and 'broad scale' to refer to data that are collected over a large extent (often with large, or 'coarse', grain). The grain and extent of data are often co-dependent (small grain with small extent, coarse grain with large extent) because of logistical constraints of measurement and the information content of the data. Generally, fine-resolution data require more effort or technical resource to collect, thereby limiting the extent to which they can feasibly be collected. Furthermore, as fine-grain

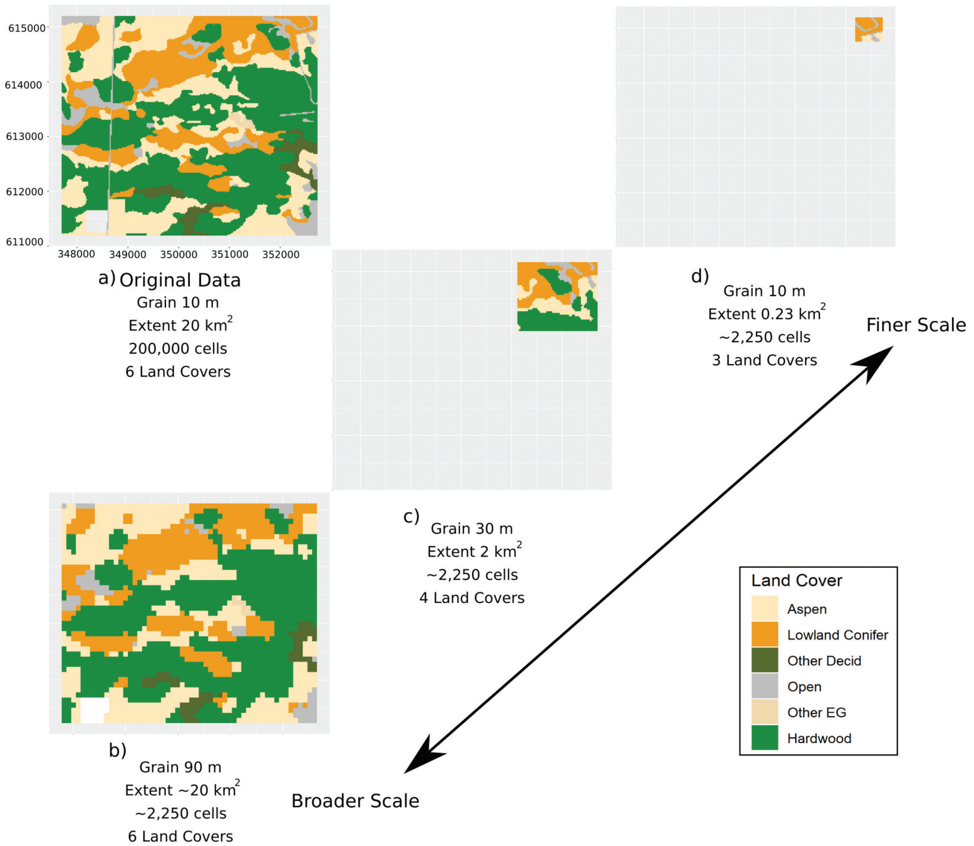

Figure 3.1 Varying scales of data for a forest study area. The original data in (a) from Millington et al. (2010) have been aggregated to a coarser grain but with identical extent to create data in (b). The number of map cells is maintained in (c) and (d), which have a progressively finer scale (i.e. smaller grain and smaller extent). Note how the number of land covers decreases with finer scale; this is by chance in this example, but in general, the number of discrete classes is expected to decrease (Wiens 1989).

data accumulate over large extents, they can contain huge amounts of information, which in turn, produce challenges for data storage, transmission, and analysis. As technical and analytical limits are pushed back, these logistical constraints are being diminished, but challenges do still remain.

The grain and extent of data depend on the measurement tools being used. For example, remotely sensed satellite image data are widely used in landscape ecology because they can be collected automatically, globally, and regularly, providing a unique perspective on biophysical characteristics at the Earth's surface that we would not otherwise have access to (Fassnacht et al. 2006; Kennedy et al. 2014; Chapter 12). Images from satellite remote sensing are raster data; that is, they are a grid of pixels each with a value indicating some property at the Earth's surface (e.g. reflectance of radiation at a given wavelength). Raw satellite image data may be 'classified' so that each pixel is assigned to a single land cover (or other categorical variables) based on characteristics of the reflected radiation (Giri 2012), or pixels may be assigned numerical measures of characteristics such as elevation, canopy height, or productivity, for example, in the area represented by the pixel (Chapter 12). For raster data, grain refers to the length of one side of a pixel and spatial extent to the total area of all pixels in the image (e.g. Figure 3.1). For satellite imagery, temporal grain (resolution) is the time interval between image retrievals, and temporal extent is the duration of time across which a series of images cover from start to finish.

Other components of scale are *coverage* and *spacing*. Coverage is the proportion of the study area or time duration under study that is actually measured or sampled and is also known as the sampling density or sampling intensity. Coverage is a relative measure (e.g. areal extent of measurement as a proportion of total study area) and is a more subjective component of scale than extent, given that an investigator must specify the wider study area of interest (whereas extent is an absolute measurement of area or time). Spacing is the distance between two immediately adjacent (i.e. neighboring) measurement locations or sampling points, whether in space or in time. Spacing is known as the sampling interval or lag. Spacing is similar to grain but does not require that unmeasured values between sampling points are the same as those identified at the sampling points. All the components of imposed scale briefly defined here lead to important constraints on what patterns are observed and identified. However, as discussed in Section 3.3, intrinsic and theoretical considerations of what patterns can be observed at different scales may be more important than any observational or technological constraints that exist.

Hierarchical 'level' is distinct from 'scale'

The terms 'scale' and 'level' may seem to imply similar concepts, but they are not the same thing, and their distinction must be recognized (King 2005). 'Scale' (including the components of scale discussed earlier) is distinct from 'level', which implies a position in a hierarchically organized system (e.g. O'Neill et al. 1986). A hierarchically organized system is one that can be divided into distinct sub-systems that interact with one another to compose other sub-systems. A sub-system is at the same level in the hierarchy as those sub-systems with which it functionally interacts but in a lower level than the sub-system within which it is embedded. Conversely, sub-systems have a higher position (level) in the hierarchy than those embedded within them (e.g. see Figure 3.2). Sub-systems at the same hierarchical level interact at faster rates with one another than with sub-systems in other hierarchical levels, potentially with orders-of-magnitude differences in rates between levels (Simon 1962; Wu 2013). To demonstrate the possible evolutionary roots for why ecological systems are hierarchically organized like this – and how using this organization can be useful for understanding system properties – Simon (1962, p. 470) presented the parable of two watchmakers. There is not room here to re-present the parable (and see Wu 1999 for a further exposition), but the key point is that the watchmaker taking a hierarchical approach to construct her watches (constructing sub-units from individual components that are then coupled with other sub-units to compose the final product) has a greater chance of completing a watch before an interruption can disrupt the process than the other watchmaker not taking a hierarchical approach (i.e. who tries coupling all components individually to create the final product without creating sub-units). The implication is that the development of biologically complex organisms through a hierarchical evolutionary process (e.g. cells composing organs composing humans, etc.) had a greater chance of succeeding than a non-hierarchical one.

When referring to hierarchically organized systems, embedded means 'faster than' and/or 'constrained by', such that the functioning of a lower-level sub-system may be faster than and/or constrained by a higher-level sub-system. However, for the more general concept of 'a hierarchy', embedded can mean 'smaller than' and/or 'contained within', such that a lower-level sub-system may be physically smaller and physically contained within a higher-level sub-system. Note that the key difference between these ideas is that in hierarchically organized systems, sub-systems

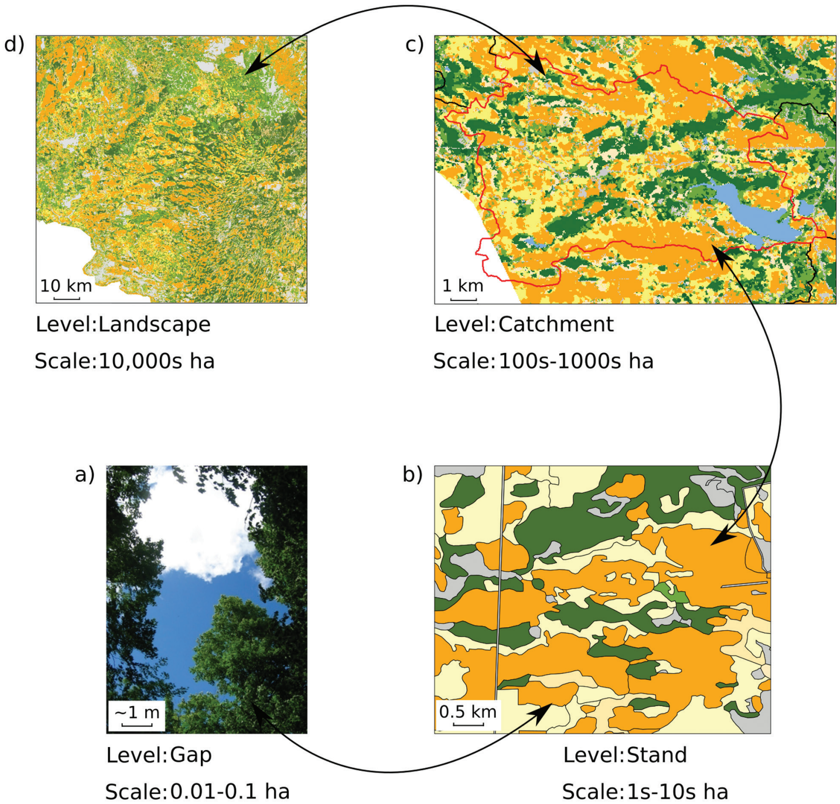

Figure 3.2 Four levels in a (nested) forest hierarchy. At the lowest level, *Gaps* (a) in the forest canopy are defined by the influence of large trees. Multiple gaps will be found in *Stands* (b) at the next level, defined by species composition and age structure. Many stands will be found within *Catchments* (c) at the next level, defined by local drainage basins. In turn, multiple catchments may be found at the *landscape* level (d), which may be defined by changes in land use and disturbance regime. (After Urban, D.L., et al., *BioScience*, 37, 119, 1987.)

at the same level *interact functionally* to compose the next higher sub-system (see Holland 1998 for how this relates to the concept of 'emergence' in complex systems). Furthermore, where sub-systems are physically contained within one another, the hierarchy is said to be 'nested' (e.g. see Wu 2013). Most of the hierarchically organized systems considered in landscape ecology are 'nested' in this way and thus have both sets of attributes. That is, sub-systems lower in the hierarchy are both functionally 'faster than' and 'constrained by' and physically 'smaller than' and 'contained within' sub-systems higher in the hierarchy. It is the combination of both sets of attributes, due to the nested character of physical environments (MacArthur 1972), that can lead to confusion about the meaning and usage of the terms 'level' and 'scale' in landscape ecology.

An archetypal example of a nested, hierarchically organized system in landscape ecology, concerning forest landscapes, is described by Urban et al. (1987). In particular, they outline a hierarchy to describe species-composition dynamics in deciduous forests of the eastern United States (Figure 3.2). The hierarchy ranges from forest gaps at the lowest level, through forest 'stands' or seral stages and river catchments, to the forest landscape itself. In these forests, when large, old trees die, they fall to leave a gap in the canopy (characteristically 0.01–0.1 ha in extent).

This gap subsequently provides smaller, subordinate trees that had been struggling beneath the larger tree (or even seeds waiting in the soil) with greater resources (e.g. light), which allows them to thrive. These trees then compete with one another until one or a few of them manage to dominate the others, thereby winning the competition for the gap. Interactions between trees mark the functional and spatial boundary of the gap – those surrounding trees that are not influenced by the change in resources (due to the fallen tree) are not 'in' the gap. Those trees are, however, in the next level of organization up the hierarchy established by Urban et al. (1987) – the forest 'stand' or seral stage.

This next level in the hierarchy is composed of mosaics of gaps and their surrounding trees, which interact (for example via seed and nutrient exchange) and which are similar in terms of their species composition, density, and size-class distribution (characteristically 1–10s ha in extent). Foresters use the term 'stand' to define these areas and often focus their management plans at this level, for example by aiming to mimic the natural processes of gap creation (by harvesting individual large trees) and subsequent tree regeneration in the stand. Where forest management is minimal or non-existent, and processes of ecological succession dominate, natural processes and conditions – including gap creation and competition, seed dispersal, local soil types, topography, and disturbances (e.g. windthrow events) – produce mosaics of gaps and surrounding trees that can be considered to be in the same seral stage. The boundary between these areas is determined by the processes that make them internally similar (i.e. human activity, local soil, topography and local disturbances, etc.).

Urban et al. (1987) propose that river catchments (characteristically 100–1000 ha) define the next higher level, both because stands in the same catchment will share a similar resource base (water availability, soils) and because they will interact more with one another than with those in other catchments. Interactions between stands might include seed dispersal and nutrient flux, and the boundary between different catchments is delineated functionally by the watershed defining them. Finally, at the highest level in this hierarchy, the landscape is defined as a mosaic of interacting river catchments (with a spatial extent of 10,000s ha). The boundary of the landscape is indicated by areas with non-interacting catchments and different physiographic characteristics, disturbance regimes, and/or human activity and land use conditions.

This example helps explain why the terms 'level' and 'scale' are often confused and (incorrectly) used interchangeably in (landscape) ecology. As in this example, hierarchies in landscapes (and biological systems in general; e.g. Berry and Kindlmann 2008) are usually nested – with components of the different levels contained, physically, within one another – meaning that it is inevitable that components in a lower level of the hierarchy also have a smaller spatial extent than those in higher levels (see King 1997). What is not inevitable is that functional interactions exist at each of these levels. For example, as King (2005) highlights, if interactions at the level below the landscape (in the preceding example, the catchments) do not produce 'emergent, holistic, aggregate' properties that would not otherwise exist, there is no 'landscape level' – there is simply a landscape (the definition of which is organism dependent). Of course, the 'landscape scale' might still be referred to in this case, but 'scale' refers only to the physical extent of the area that encompasses the mosaic of catchments. Consequently, the terms 'level' and 'scale' can be differentiated; 'level' is a position in a hierarchy which, if enumerated, is unitless and simply reflects the rank ordering relative to other levels in the hierarchy, whereas 'scale' refers to the spatial and/or temporal dimensions of an entity or event and in contrast to 'level', can be enumerated as a quantity with units of space (e.g. m^2) or time (e.g. s). Furthermore, if entities in a hierarchy do not depend on the functional interactions of entities at lower levels, 'level' should not be used as a descriptor (e.g. we should simply refer to the landscape and not the landscape level). And finally, we should only refer to the 'landscape scale' if we are willing to define its spatial extent and the characteristic duration of temporal processes.

One of the primary benefits of taking a hierarchical perspective – and being concerned with distinguishing different levels – is that it helps to simplify complex systems for analysis and understanding (Simon 1962). For example, a hierarchical perspective facilitates the use of a 'triadic approach' in which a focal level (often designated 'level 0') is selected, and then adjacent levels are considered: the embedded (faster/smaller, 'level −1') for understanding dynamics influencing the focal level, and embedding (slower/larger, 'level 1') for understanding constraints on processes within the focal level (O'Neill 1989). In the hierarchical forest landscape structure outlined here, for instance, treating stands as level 0 facilitates understanding about not only gap dynamics (level −1) to investigate stand processes and patterns, but also how those processes and patterns are constrained by the hydrological balance and position of the stand within the catchment (level 1). A hierarchical approach may also be useful when developing disaggregated, 'bottom-up' models that represent fine-scale elements to investigate ecosystem dynamics (e.g. individual- and agent-based models). The 'pattern-oriented modelling' suggested by Grimm et al. (2005) argues that such a model is useful if the processes specified at one level are able to produce patterns observed at other levels of organization. For example, continuing to use the hierarchical forest landscape as a case, a model of gap dynamics should be able to reproduce the age structure of a stand when simulated over time to provide confidence that mechanisms are appropriately represented (e.g. Rademacher et al. 2004). General criticisms of the hierarchy perspective have been argued, including a lack of clear definitions and principles (e.g. Wilby 1994), and in reality, multiple hierarchies often exist and overlap one another. But the successes of applications across multiple disciplines indicates that a hierarchical perspective provides analytic tractability in the types of complex systems that landscape ecology is concerned with, and its continuing use is expected (e.g. Wu 2013).

Scale dependence and selection

There is no single 'correct' scale

Possibly the most important scale concept in ecology is the understanding that there is no single 'correct' scale at which ecological phenomena should be studied (Levin 1992, 2000). This is because patterns and heterogeneity (see Chapter 15) are scale dependent, varying with the scale of observation (Turner 1989). Although humans have developed techniques and technologies to observe and measure the physical world at different grains and extents (e.g. from microscopes to satellite imagery), other organisms' perceptions of the physical world are dictated by their intrinsic (characteristic) scale. The difference between intrinsic and imposed scales (as discussed in Section 3.2) has been described by Mac Nally (2005) as the difference between *organism-centric* scale problems and *probing* scale problems. Organism-centric scale problems arise from the influence of organisms' intrinsic scale on their perception and response to the physical world, while probing scale problems arise from the different possible scales at which humans can observe and measure that world (using tools that are independent of our own intrinsic scale). Interactions between probing and organism-centric scale problems are inherent in how humans understand the relationships of organisms (including ourselves!) to pattern and heterogeneity in the physical world.

Organism-centric scale problems can thus dictate how an organism's 'landscape' should be defined. Heterogeneity and pattern in a beetle's landscape may be created by clumps of grass (e.g. tens of centimeters in diameter) in a matrix of unvegetated ground, as the difference between these two land covers can influence their movements greatly Wiens and Milne (1989). But for a larger organism, the white-tailed deer, for example, this same area will be perceived differently. Patterns and heterogeneity at a broader scale, for example between areas of grassland, shrubland, and forest (e.g. hundreds of meters in diameter), will be more important for the deer than for the beetle. It is patterns at this broader scale that influence deer movement and other behaviors (e.g. winter sheltering; Millington et al. 2010), much more so than fine-grained differences (such as between clumps of grass and a bare ground matrix) that influence the beetle. From the perspective of the habitat-forming vegetation in these examples, it is the scale of fragmentation that is key to defining landscape. Analogous to grain, 'dispersion' is a measure of the spatial arrangement of fragments of vegetation that lies on a continuum from 'geographical' (broad scale with greater isolation of fragments) to 'structural' (finer scale with less isolation; Lord and Norton 1990). Detecting critical scales in fragmented landscapes is important for understanding how organisms with differing dispersal behavior perceive the connectivity of a landscape (Keitt et al. 1997).

With regard to probing scale, a raster, categorical land-cover data set with a larger pixel size (i.e. larger grain) will likely represent fewer distinct patches of habitat (e.g. clumps of grass for the beetle or forest stands for the deer) across a given area of the Earth's surface than a raster data set with smaller pixel size. This is because habitat patches with area smaller than an individual pixel may be dominated by other land surface categories (in terms of area), and so that pixel will not be classified as habitat (assuming categories of land cover are either viable habitat or not, as in the patch-mosaic model of landscape ecology; see Chapter 2). The larger pixels get, the more often this will happen, and so the fewer pixels will be classified as habitat (as shown, for example, in Figure 3.1). If habitat patches are evenly distributed spatially across the area, the extent of the image will also influence both the number of habitat types and the number of individual patches observed; an image with smaller extent will observe fewer habitat patches, as more will lie outside the image boundary. Wiens (1989) formalized this pattern by saying that as grain increases (i.e. pixel size increases) for a constant extent, the proportion of spatial heterogeneity in the observed landscape contained within a sample (i.e. pixel) increases and is lost to the observer (Figure 3.3). For a raster land-cover map, this means that larger pixels are more likely

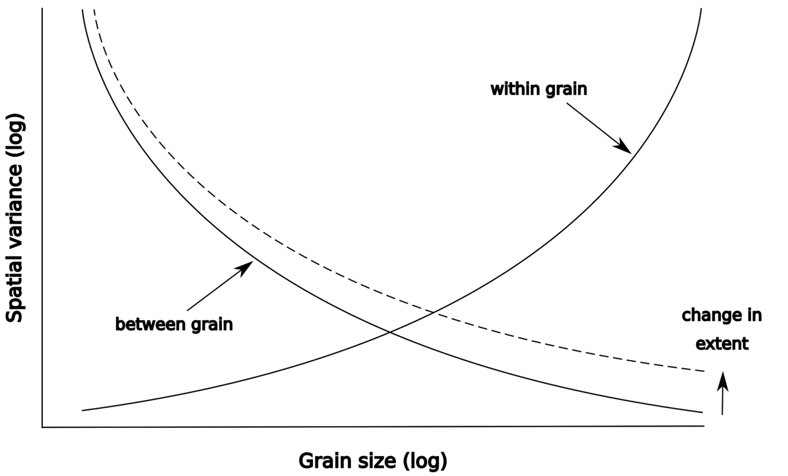

Figure 3.3 The effect of changing grain and extent on spatial variance. As grain increases, more spatial variance is included within samples (e.g. pixels), and vice versa. A lower effect, increasing extent, may increase the number of classes (hence, spatial variance). (After Wiens, J.A., *Functional Ecology*, 3, 385, 1989.)

to contain multiple land-cover types, which we are unable to see (because they are classified as a single type). Conversely, between-sample heterogeneity (i.e. pixel variance) decreases as grain increases for a constant extent, because spatial heterogeneity in the landscape becomes 'averaged out' (i.e. fewer land-cover types are represented in the final map). Finally, as extent increases (i.e. if we look at a larger landscape), between-sample variance will increase, but within-sample variance will likely remain unchanged. That is, more land-cover types will be present in the final map, but each pixel will likely contain just as many different land-cover types (but we are unable to see these, as in the final map, each pixel is assigned to only a single type). These issues contribute, in part, to land-cover classification errors in remotely sensed satellite imagery (Moody and Woodcock 1995; Foody 2002) and have become known as the Modifiable Areal Unit Problem (MAUP; Gehlke and Biehl 1934; Openshaw 1984; Wu 2004; Bissonette 2017). The MAUP recognizes that statistical analysis of data for aggregated units of areas (e.g. 'pixels') can be affected not only by grain size but also by the different ways units of a given grain size might be configured (e.g. triangular vs. square vs. hexagonal pixels).

Beyond influencing patterns in raster data, scale dependence means that the imposed scale of observation can influence our understanding of relationships that are due to the intrinsic scale of organisms or patterns being observed. For example, the relationship between the body size of an animal species and its geographic range (i.e. the spatial extent over which that species is found) is generally expected to be positive (as one increases, so does the other), but some studies have reported a negative or no relationship (Gaston and Blackburn 1996). Examining multiple studies, Gaston and Blackburn (1996) showed how studies that examined comprehensive (i.e. full) coverage of species' geographic ranges did indeed usually find positive body size–geographic range relationships, and that it was mainly those with only partial coverage that found negative or variable relationships. Similarly, Palmer and White (1994) examined the importance of scale dependence on the relationship between the number of species found in a region and the absolute area of that region. Palmer and White found that both grain and extent of observation were important in identifying species diversity hotspots (hotspots increase as a function of both grain and extent) and that diversity hotspots are observable over a wide range of grains.

Thus, when observing, measuring, monitoring, or experimenting to investigate questions in landscape ecology, we must remember not only that is there no single correct scale to adopt (because of organism-centric scale problems) but also that the scale we use may artifactually influence results (because of probing scale problems). So, how do we establish what scale or scales we should use to collect and analyze data? Ultimately, the scale or scales we work at will be dictated by the motivations of our study's research questions and practical limitations of data and other factors. Considerations include (Meentmeyer 1989; Bissonette 2017) the size and speed (i.e. rate) of phenomena (e.g. organisms) and processes being studied, the amount of observed variance or heterogeneity (e.g. in land covers) in the landscape, the size of spatial units within a given organizational level (e.g. gap, patch, etc.), scales of existing data and data collection sources (e.g. remotely sensing), and technological constraints on data collection (e.g. data logger capacity). Generalizing this still further, approaches for selecting a scale or set of scales to work at might be thought of as 'process oriented', 'pattern oriented', and 'data oriented'.

Process-oriented scale selection

The process-oriented approach to scale selection starts by considering the intrinsic scale of the process or organism of interest. This approach includes considering, for example, the rate at which a process characteristically operates (e.g. a landscape fire burning over days) or the characteristic size of an organism (e.g. a 30 m tall pine tree). In turn, characteristic rates and sizes can help to establish the scales of patterns or environmental heterogeneity that are likely to influence the function of the process or organism. For example, Mac Nally (2005) suggests an organism-centric approach that uses the somatic size and lifetime of an organism to estimate a characteristic measure of scale, λ:

$$\lambda = O(\alpha\delta)$$

where α is the characteristic length of the organism, δ is the characteristic lifetime of the organism, and O means 'on the order of'. In turn, the total distance moved by the organism over its entire lifetime, stated as a multiple of λ, provides a measure that can be understood as the 'experience' (E) of the organism. For example, for the endangered Australian swift parrot (*Lathamus discolor*), Mac Nally (2005) estimates $\lambda \sim 5$ m/yr, as the birds are about 0.25 m in length and live for around 20 years. The swift parrot migrates from Tasmania to central Victoria for the winter each year, moving around 1,000 km in the 6 months it is on the mainland, giving an estimate for E of $2 \times 10^6\ \lambda$ on the mainland. The perception of the organism can then be related to measures of spatial landscape variation (e.g. distance between patches of potential habitat) and temporal resource fluctuation (e.g. quality of those habitat patches for breeding), also scaled in units of λ and denoted L. For instance, the swift parrot forages on flowering eucalyptus, which Mac Nally (2005) estimates to vary at spatial extents of tens of kilometers over 3–6 months, giving an estimate of L of $1\text{–}2 \times 10^3\ \lambda$. It is important to understand that L is a measure of *variation* in the landscape and that E and L are measures of space *and* time. These measures can be used to identify theoretical scales of landscape that the organism can perceive and respond to. An organism should be readily able to perceive and respond to the landscape variation when $E \sim L$ (the scales are concordant) and when $E > L$ (although not as well). However, this theory predicts that when $L > E$, the organism will find it difficult to perceive and will be unable to respond to the landscape variation (and landscape resources at this scale will be 'unreachable'), and when $E >> L$ and $L >> E$, the organism will be unable to perceive the landscape variation. Thus, the quoted values of E and L mean that the swift parrot is likely able to perceive and respond to the flowering eucalyptus but not to resources with smaller extent but with longer availability. For human investigators and managers, it also implies that measurements and management might be best targeted in the concordant zone where $E \sim L$.

Pattern-oriented scale selection

A good understanding of the processes (and/or organisms) to be studied is needed for process-oriented approaches to scale selection, as the approach described by Mac Nally (2005) illustrates. Thus, the process-oriented approach is less appropriate when previous understanding and data about the process or organism of interest are unavailable or when processes are initially inferred from pattern. A pattern-oriented approach seeks to identify the scales at which the spatial (or temporal) variability of an attribute or phenomenon is maximized (Meentmeyer 1989), based on the relationships shown in Figure 3.3. For example, if a spatial pattern in vegetation cover is believed to be regularly spaced, blocking techniques or an analysis of spatial lags can be performed (Turner et al. 1991; Dale 1999). This approach compares within- and between-block variance for blocks of varying size (uniformly located across a landscape) to identify the grain at which variance is maximized. When pattern is irregular, moving window analyses are more appropriate (Turner et al. 1991). These work in a similar fashion to blocking but compare variance between halves of a block (window) that is moved across the landscape; variance is maximized where patch edges are found, potentially allowing identification of characteristic patch sizes. Similarly, pattern-oriented approaches are appropriate when processes operating within a particular level of a hierarchy are of concern. For example, if forest gap processes (e.g. tree regeneration) are of interest, the characteristic size of the gap will govern the choice of scale (primarily grain, but also possibly extent to ensure that a sufficient number of gaps is included in data collection and analysis). Note that these methods are primarily appropriate for univariate measures of landscape pattern, and other approaches, such as multi-scale pattern analysis (Jombart et al. 2009) or wavelet analysis (e.g. Carl et al. 2016) are needed in multivariate cases.

Beyond identifying appropriate grain, other approaches are useful for identifying appropriate landscape extents or distances between study units in a landscape (Holland and Yang 2016). For example, Amici et al. (2015) examined the importance of landscape extent empirically for forest plant species richness by examining regression models and variance partitioning for landscapes of different sizes. Autocorrelation methods are frequently useful to identify the lag distance beyond which independence can be assumed, which is often important for appropriate statistical sampling (e.g. Millington et al. 2007). Similarly, Pasher et al. (2013) considered a fixed landscape size (100 ha), but locations of these landscapes in a broader region were selected to maximize heterogeneity (in the sample of landscapes) and such that the distance between landscapes meant they were not spatially autocorrelated. Regardless of the specific approaches employed, some preliminary analysis of pattern will often be useful to help guide the scale or scales of study most appropriate for the research questions in hand.

Data-oriented scale selection

Available existing data and technological constraints often determine the scales of observation and analysis. For example, the spatial and temporal grain and extent of satellite image data (whether raw or classified) has a strong influence on what can be observed when using such data. There is often a trade-off in spatial and temporal scales for satellite remote sensing imagery, as sensors that have high temporal resolution have low spatial resolution (and vice versa). Satellites in geostationary orbit (such as weather satellites) can retrieve images every 15 minutes but are a relatively long way from Earth and so have a low spatial resolution (1 km). Such coarse spatial resolution can make these data inappropriate for studying many organisms or processes. In contrast, polar-orbiting satellites such as Landsat are much closer to Earth and so have a higher spatial resolution (e.g. 30 m), but can only retrieve images for a location on Earth's surface when they pass overhead every 16 days or so. These characteristics again influence what is observed. For example, a large wildfire that burns across a landscape for a short time (e.g. a few days) may be detected multiple times by a geostationary satellite but not at all by a polar-orbiting satellite. Conversely, a small wildfire may go undetected by a geostationary satellite (due to its low spatial resolution) but be detected by a polar-orbiting satellite (with higher spatial resolution). However, as discussed further in Chapter 12, advances in remote sensing technologies that mean such restrictions are now diminishing, for example with the introduction of the Sentinel satellites (10 m spatial resolution with a maximum of 5 days between overpasses) and methods to detect processes acting at sub-pixel scale (e.g. for fire detection; Wooster 2012). Advances in object-based image analysis are also developing useful tools to minimize problems of artificial patch boundaries due to fixed data resolution (Karl and Maurer 2010; Lechner and Rhodes 2016).

Trade-offs may also exist in data collection between spatial and temporal grain and extent due to the power and data constraints of the technology used. Devices used to collect data remotely must be powered in some way (often by an electric battery) and be able to transmit data to a receiving station or store data for later physical retrieval. A smaller grain for any fixed extent will increase the coverage (sampling density) of collected data, decrease the spacing (sample interval) of the data, and result in an overall increase in the amount of data that must be transmitted or stored. Furthermore, if power is used each time a data collection is made, more frequent collection will require more energy. Thus, data collected at a smaller grain (i.e. higher resolution), whether spatial or temporal, often demands increased power and data transmission/storage resources. For example, Webb et al. (2010) used global positioning system (GPS) collars to track the movement of white-tailed deer in Oklahoma, United States, but faced a trade-off between relatively high-frequency data collection (to understand the potential effects of moon phase and short-term weather patterns on movement patterns) against data storage capacity and battery duration of the GPS device (high frequency of data collection consuming the resources more quickly than lower frequency). In some circumstances, such technical restrictions may be a problem (depending on the questions we wish to address), but as with satellite sensing advances in terrestrial sensor networks (e.g. see Chapter 13), power storage/production and other technologies means that such restrictions are diminishing.

Pattern and process across scales

Scaling and extrapolation

The challenges of scale dependence have contributed to landscape ecologists' interest in *scaling* (e.g. Wiens 1989; Ludwig et al. 2000; Denny and Benedetti-Cecchi 2012). Indeed, some have argued that understanding scaling is a foundational challenge for improving scientific understanding; "the problem of relating phenomena across scales is the central problem in biology and in all of science" (Levin 1992, p. 1961). This definition of scaling – the identification of relationships between phenomena at different scales – is closely related to the term *extrapolation*; the adjustment of a value measured at one scale to match what the value would be if measured at another scale. Scaling from fine scale to broad scale, known as 'scaling-up', is important for understanding how regional patterns and processes are produced from fine-scale, local data collection (Turner et al. 1989). Scaling-up is challenged by the expense and logistics of collecting fine-resolution (detailed) data collection across large extents (but see improvements in sensor networks). Local spatial variation can be controlled and accounted for through appropriate sampling and experimental designs, but this becomes increasingly difficult across broader extents. The converse of scaling-up, 'downscaling', is important for understanding how the context of broad-scale patterns constrains local processes and for interpreting the outputs of broad-scale ecosystem and physical (e.g. climate) models at local scales. For example, the position of a tree of a given species in a forest stand (whether near the center or the edge of the stand) may influence its chances of survival (e.g. because of differences in resource availability or browse pressure at the edge of a stand compared with the center). Downscaling is challenging because broad-scale relationships become less coherent (i.e. identifiable) at local scales as fine-grained variation and historical contingencies become more important. These scaling challenges lie at the heart of understanding ecological patterns and processes in landscapes; scaling-up the effects of local processes often does not neatly account for observed landscape patterns, while scaling-down often fails to account for contingencies that affect local patterns and processes (Cushman et al. 2010b).

Because our understanding of patterns and process is so closely related to our data about them, the terms 'scaling-up' and 'downscaling' are often used synonymously for the process of adjusting values between scales. The identification of consistent relationships between values at different scales (i.e. scaling relationships) is desirable to evaluate possible problems in analysis due to the MAUP (e.g. when analyzing wildlife movements; Bissonette 2017), to enable estimation of fine-scale patterns from broad-scale data (e.g. remote sensing; Riiters 2005; Anderson 2018), and for integrating disparate data sets (e.g. at different resolutions; Atkinson 2013). Others have suggested that scaling relationships may be useful as conceptual models in the processes of assessing the robustness of understanding by, for example, comparing the performance of a model against data at multiple scales to identify where, when, and at what scales relationships hold or collapse (Miller et al. 2004). In landscape ecology, more effort has been devoted to developing methods to extrapolate values from fine to broad scales (scaling-up) than vice versa. Turner et al. (2001) attribute this emphasis to the immense data requirements needed to verify the predicted results of scaling relationships from data at larger grain (across large extents) to finer grain in multiple local locations (in contrast, for example, to the downscaling of general circulation model outputs using measurements from a large number of automated weather stations or stream-flow gauges; Wilby and Wigley 1997). Three general methods to extrapolate by aggregating values about patterns and processes from finer to broader scales have been considered (King 1991; Rastetter et al. 1992): linear 'lumping', the statistical expectation operator, and the calibration approach. 'Lumping' is the most straightforward approach, in which estimates of values at the larger grain are simply averaged over the finer-grain data falling within the aggregate area (e.g. total photosynthetic activity for an entire tree calculated from the mean value of a sample of individual leaves). The statistical expectation operator extends 'lumping' by considering the probability density of fine-grain data and using this with weighting to calculate expected values at the larger grain (e.g. accounting for the distribution of photosynthetic activity across a sample of leaves to calculate a weighted sum for total tree photosynthetic activity). The calibration approach uses regression with weighted sums of fine-grain data with data (for other variables; e.g. leaf size in the previous examples) from the larger grain to estimate scaling relationships between the scales. Cushman et al. (2010b) list several difficulties associated with these traditional approaches, many associated with the criticism that they are tied to a hierarchical view (as in Section 3.2) of scaling in which large-grain properties can be readily aggregated from finer-grain data. For example, they argue that aggregating approaches assume that the finer-grain data and processes being extrapolated can be treated as random variables, that none of these methods can account for disequilibrial dynamics, and that these methods result in a loss of information about pattern and processes. More recently, Hamil et al. (2016) have shown how mixed-effect regression models can be used in a calibration-type approach to better account for the varying effects of spatial heterogeneity at different scales.

Given their criticisms of the scaling challenges that emerge from the patch-mosaic model of landscape structure (which assumes that discrete patches of land or habitat are categorically defined), Cushman et al. (2010b) argued for a different approach they call the 'gradient perspective'. This approach does not require a hierarchical perspective for examining landscapes across different scales and instead, emphasizes the depiction and analysis of continuously varying ecological phenomena (McGarigal and Cushman 2005; Cushman 2010a). The gradient perspective considers direct measurements of variables and processes, meaning that redefinition (of entities, variables, or units of observation) is not needed when moving between two different scales; Cushman et al. (2010b, p. 60) argue that this enables better consideration of non-linear and multivariate interactions, thereby 'greatly simplifying the task of robustly linking patterns with processes across scale[s]'. One area where the consequences of these differences in perspective for scaling are readily apparent is in a comparison of scaling categorical pattern metrics (e.g. Wu et al. 2002; Wu 2004) against the more recent scaling of gradient surface models (e.g. Frazier 2016; Frazier and Kedron 2017). As discussed in detail in Chapter 15, landscape pattern metrics enable the identification, quantification, and interpretation of spatial heterogeneity and its change. In their classic studies of categorical pattern metrics, Wu et al. (2002) and Wu (2004) demonstrated a range of responses of pattern metrics with changing map grain and extent: no clear scaling response; simple scaling functions; and 'stepped' or 'staircase' behavior. In contrast, taking a gradient perspective, Frazier (2016) found that polynomial functions were appropriate for extrapolating in many cases and argued that (continuous) surface metrics might be better suited than (categorical) pattern metrics for scaling from broad to finer scales. However, Kedron et al. (2018) highlight that finding appropriate analogues between pattern and surface metrics may not be possible in many cases (meaning that both are needed), and once again, we are reminded that the appropriate method or perspective will depend not only on the questions and organisms in hand but also on the scale or scales at which they might most appropriately be studied.

The continuing need for multi-scale research

If process or pattern are not considered when selecting the scale at which to observe or collect data, scale is essentially being selected arbitrarily. Unfortunately, this arbitrariness seems too frequent in landscape ecology studies. For example, in a review of wildlife-habitat research from 1993 to 2007, Wheatley and Johnson (2009) found that 70% of observational studies used an arbitrarily chosen scale with no apparent biological rationale. In their review of papers on habitat selection between 2009 and 2014, McGarigal et al. (2016) reported that only 5% explicitly examined multiple scales and levels. And in a review of 348 studies published between 2004 and 2014, Estes et al. (2018) found that most studies did not even clearly report the scale they were working at. Despite clear recognition of the importance of scale by ecologists since the late 1980s, it appears that comprehensive consideration of scale remains an outstanding challenge. Furthermore, continuing improvements in our understanding of scale dependence, observational/MAUP issues, and scaling challenges mean that intentionally identifying a *single* scale of study may prove inadequate. For example, Martin (2018) argued that we cannot assume that species respond to their landscape context at a single scale and that different biological responses may need to be examined at different scales. Others have argued that because the pressing challenges of the Anthropocene are caused by human influence on physical systems at multiple scales, improved understanding of ecological scaling is imperative (Scholes 2017). Improvements in technology mean that multi-method approaches to multi-scale research should prove fruitful in this regard (Bissonette 2017), and multi-hypothesis and multi-model approaches (e.g. Miguet et al. 2016) may facilitate thoughtful and systematic understanding of scale effects.

Multi-scale research will be particularly important if multiple processes or organisms occur in a landscape (which seems inevitable), as each will likely have its own set of intrinsic scales, which will be further compounded in studies that involve human–environment interactions. Data for human phenomena are often not available at the same spatial and temporal resolution, with human data frequently aggregated to political or other administrative units that have no, or limited, correspondence to the scale of physical data or processes (e.g. Millington et al. 2007). Such situations result in a scale mismatch between the scale of social organization and the scale of ecological processes, with potentially detrimental impacts on ecological and social function and resilience (Cumming et al. 2006). Furthermore, notwithstanding the problem of whether social data aggregated to political and administrative units suffer from problems associated with the MAUP, different people interpret and understand the world based on different perspectives of what constitutes scale, including those different from the definitions of scale offered here (what Manson 2008 termed the 'epistemological scale continuum'). For example, to reflect the representative nature of social structures, sociologists might add 'representational' and 'organizational' to the spatial and temporal dimensions of scale (Cumming et al. 2006). If social and natural sciences are to become integrated to ensure sustainability and resilience, there is still work to be done in improving our understanding of how different disciplines perceive space and scale (Vogt et al. 2002; Higgins 2012), and the ecological perspective presented here should be seen as only one of many.

Summary

1. There is no single 'correct' scale in landscape ecology.
2. The notion of 'scale' is not the same as 'level of organization', although in landscape ecology, the two are often closely related.
3. Patterns in time and space are scale dependent.
4. Scaling is the identification of relationships between phenomena at different scales.
5. There are different ways to establish the appropriate scale to work at depending on process, pattern, data, and perspectives.
6. Multi-scale analyses will increasingly be needed in future to understand landscapes in the Anthropocene.

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