

When is a Landscape Perspective Important?

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What is Landscape Ecology?

Although the definition of landscape ecology has been dealt with extensively (some would say ad nauseam) in the landscape ecological literature, there remains confusion among other ecologists as to exactly what landscape ecology is and, particularly, what its unique contribution is to ecology as a whole.

Ecology is the study of the interrelationships between organisms and their environment (Ricklefs 1979). The goal of ecological research is to understand how the environment, including biotic and abiotic patterns and processes, affects the abundance and distribution of organisms (Figure 1). This includes indirect effects such as the effect of an abiotic process (e.g., fire) on a biotic process (e.g., germination), which in turn affects the abundance and/or distribution of an organism. Processes considered are typically at a "local" scale, that is, at the same scale or smaller than the scale of the abundance/distribution pattern of interest.

Landscape ecology, a subdiscipline of ecology, is the study of how landscape structure affects the abundance and distribution of organisms (Figure 2). Landscape ecology has also been defined as the study of the effect of pattern on process (Turner 1989), where "pattern" here refers specifically to landscape structure. The full definition of landscape ecology is then: the study of how landscape structure affects (the processes that determine) the abundance and distribution of organisms. In statistical parlance, the "response" variables in landscape ecology are abundance/distribution/process variables, and the "predictors" are variables that describe landscape structure. Again, this includes indirect effects such as the effect of a biotic process (e.g., herbivory) on landscape structure, which in turn affects the abundance and/or distribution of the organisms of interest.

What is Landscape Structure?

The above definition begs the question, "what is landscape structure or pattern?" "Structure" and "pattern" imply spatial heterogeneity. Spatial heterogeneity has two components: the amounts of different possible entities (e.g., different habitat types), and their spatial arrangements. In landscape ecology these have been labelled landscape "composition" and "configuration" respectively. The amount of forest or wetland, the length of forest edge, or the density of roads are aspects of landscape composition. The juxtaposition of different landscape elements, and measures of habitat fragmentation *per se* (independent of habitat amount) are aspects of landscape configuration (McGarigal and McComb 1995).

What is a Landscape-Scale Study?

A landscape ecological study asks how landscape structure affects the (processes that determine) the abundance and/or distribution of organisms. To answer this, the response variable (process/abundance/distribution) must be compared across different landscapes having different structures (Brennan et al. 2002). This imposes a fundamentally different design on a landscape-scale study than on a traditional ecological study. Each data point in a landscape-scale study is a single landscape. The entire study is comprised of several non-overlapping landscapes having different structures (Figure 3).

A landscape-scale study therefore has the following attributes: (i) individual data points in the study represent individual landscapes, i.e., the landscape is the observational unit, and (ii) the size of a landscape depends on the scale at which the response variable responds to landscape structure. This typically depends on the scale at which the organism(s) in question move about on the landscape, or the typical scale of the process of interest. Note that the landscape is not a level of biological organization (King 1999). In fact, a landscape-scale study can be conducted at the individual, population, community, or ecosystem level of biological organization. In the following I provide two hypothetical examples of landscape-scale studies; the first is at the individual level and the second is at the population level.

Example 1. Individual-scale Study

Consider a researcher who is interested in identifying the factors that determine fledging success rate of a particular species of bird. The usual approach to this would be to locate a number of nests and their associated territories. For each nest, response variables measured might be the number of young fledged or proportion of eggs taken by predators, and the predictor variables might be availability of food in the territory, or density of predators in the territory.

To include a landscape perspective in this study, the researcher would determine whether the landscape context of a territory, i.e., the landscape structure of the region surrounding each territory, affects the number of young fledged or the proportion of eggs taken by predators in that territory. This will require a completely different study design.

First the researcher must determine a reasonable maximum size for individual landscapes. This is done by asking at what scale (s)he expects no effect of landscape structure on the response variables. This will generally depend on movement scales of the organisms in the study. For example, if the predator has a daily movement range of 3 km then each landscape should be at least 3 km in radius. The researcher must then locate individual territories that are spaced far enough apart such that non-overlapping landscapes of this size can be delineated around them.

Predictor variables in the study will then include both the original predictor variables (local availability of food, local density of predators), and new predictor variables that

describe the structure of the landscape surrounding each territory. These variables might include compositional variables (e.g., amount of wetland, amount of forest), and configurational variables (e.g., fragmentation and juxtaposition of habitat types). Optimally, the landscape structural variables should be measured at several different scales to determine the size of landscape unit that has the greatest effect on the response variables.

Example 2. Population-scale Study

In the above example the researcher is interested in the factors that determine a process (fledging success), which has an assumed effect on bird abundance/distribution. An ecologist may also examine directly the factors determining abundance/distribution at a population level. For example, one might ask, "what factors determine presence/absence of this frog species in different ponds?" Variables such as pond size, or presence/absence of fish in the ponds might be considered.

The fact that multiple ponds are studied does not render this a landscape-scale study (Figure 3A). In a landscape-scale study, the landscape context of each pond would need to be determined. A new set of ponds would be identified for the landscape-scale study. These ponds would need to be spaced far enough apart that non-overlapping landscapes could be delineated around them. As above, a reasonable maximum landscape size would need to be determined. This might be based on the maximum between-population dispersal distances of the frog species in question.

Predictor variables in the study again include both the original predictor variables (pond size, presence/absence of fish), and new predictor variables that describe the structure of the landscape surrounding each pond. These variables might include compositional variables (e.g., amount of forest, amount of road surface), and configurational variables (e.g., fragmentation, juxtaposition of various landscape elements). Again, the landscape structural variables should be measured for several different landscape sizes, to determine the size of landscape unit that has the greatest effect on the response variables (e.g., Findlay and Houlihan 1997, Pope et al. 2000).

When is a Landscape Perspective Necessary?

From the preceding it should be clear that a landscape perspective is necessary whenever landscape structure can be expected to have a significant effect on the response variable (abundance/distribution/process) of interest. This leads to the somewhat frustrating Catch-22 that, in order to determine whether a landscape perspective is necessary, one must conduct a landscape-scale study. Practically speaking, this implies that a landscape perspective is always necessary.

However, we expect there must be some, if not many, situations in which landscape structure does not have a large effect on the response variable of interest, which, in retrospect, tells us that a landscape perspective was not necessary for that problem. Avoiding a landscape-scale study when one is not necessary will be time- and money-

saving. Can we delineate some circumstances in which a landscape perspective is not necessary?

When is a Landscape Perspective Not Necessary?

Probably the most straightforward situation in which a landscape perspective is not necessary is when a sufficient proportion of variation in the response variable can be explained with local variables only. The definition of "sufficient" will of course depend on the purpose of the study. One might argue that the rarity of landscape-scale studies (as defined above) in the ecological literature suggests that the proportion of variation explained by local variables is high in most cases. However, we know this is not the case. Reasons for the lack of landscape-scale studies are discussed in the following section.

It may also be possible to identify certain classes of circumstances in which at least certain components of a landscape perspective can be ignored. For example, most studies that have examined the effects of landscape structure on ecological responses have found large effects of landscape composition (reviewed in Fahrig 2003). In contrast, modeling studies suggest that there are many situations in which landscape configuration has little or no effect on abundance and/or distribution of organisms, such as when the landscape structure itself is highly dynamic or when the amount of habitat on the landscape is above a certain level (Fahrig 1992, 1998, Flather and Bevers 2002).

Impediments to Landscape-scale Studies

The impact of landscape structure has been largely ignored in ecology, mainly because of the perceived difficulty of conducting large-scale studies. This constraint is disappearing with the increasing availability of remotely-sensed data, allowing much easier measurement of landscape structural variables.

The main constraints that must now be overcome are cultural constraints within the discipline of ecology. For example, many ecologists view a "landscape-scale" study as simply a study that covers a large area. If a study including several patches of forest is "large" to that researcher (s)he may call it a landscape-scale study; however, it is more correctly termed a "patch-scale" study (Figure 3A). As I argue above, a landscape-scale study is one that examines the effect of landscape context on a response variable. It answers the question, "does the structure of the landscape in which this observation is imbedded affect its value?" This can only be answered by comparing the response variable across several landscapes with different structures (Figure 3B).

Probably a greater hindrance to true landscape-scale studies is the current emphasis in ecology on experimental studies. By definition, landscape ecological studies look at the effect of a pattern (landscape structure) on a response. Judicious choice of landscapes with contrasting structures can result in a pseudo-experimental design, termed a "mensurative experiment" (McGarigal and Cushman 2001; e.g., Trzcinski 1999). In contrast, manipulative experimentation at a landscape scale (i.e., multiple experimental landscapes) is generally not possible. Where landscape-scale studies have been

conducted, large effects of landscape structure (especially landscape composition) have been found. Inability to apply "in vogue" experimental methods to landscape ecological studies is no reason to ignore these effects or to avoid the landscape perspective.

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Figures 1-3 (15KB pdf)

Figure 1. The study of ecology. Solid lines represent ecological interactions. The goal of ecological research is to understand how abiotic and biotic patterns and processes affect the abundance and distribution of organisms.

Figure 2. The study of landscape ecology. Dark solid lines represent landscape ecological interactions. The goal of landscape ecological research is to understand how landscape structure affects the abundance and distribution of organisms.

Figure 3. A. Patch-scale study: each observation represents the information from a single patch (black areas). Only one landscape is studied, so sample size for landscape-scale inferences is one. B. Landscape-scale study: each observation represents the information from a single landscape. Multiple landscapes, with different structures, are studied. Here, sample size for