

Experimental Design at the Landscape Scale

ROBERT D. HOLT AND MICHAEL A. BOWERS*

Introduction

The identification of key hypotheses and the systematic testing and rejecting of these using well-scripted methodology and experimentation is one of the most powerful tools scientists have of learning about nature. In fact, the objective application of this paradigm is the essence of the scientific method (Hairston 1989) that is credited with much of the tremendous scientific advances of the past 100 years. The link between theory and test is venerable in the field of ecology and related disciplines. Indeed, the genesis for what now is known as experimental design and statistics is found in the work of biometricians like Galton, who developed a quantitative means of comparing variability within and between (statistical) populations, and Fisher, who created analysis-of-variance as a means of addressing questions in agriculture (Levin et al. 1997).

In recent decades, population and community ecologists have wholeheartedly embraced experimentation as a primary means of understanding how organisms interact with their environment (Underwood 1997). The class of phenomena subjected to inquiry, however, has changed over the past two decades, from tests of processes such as density-dependence and interspecific interactions operating at a small scale and within homogeneous spatial areas increasingly to larger-scale studies, where spatial variation and heterogeneity are the factors of interest. The focus has also changed from tests of equilibrational processes to tests of nonequilibrational conditions dictated by nonlinear spatial and temporal processes. At an extreme, experiments are performed at a scale approaching that of entire ecosystems and whole landscapes.

The underlying premise of landscape ecology is that the configuration, types, and spatial arrangement of component habitat elements (e.g., patches, corridors, and matrix) affect ecological systems in spatially explicit ways (Turner 1989, Wiens 1995). All ecological systems, however, necessarily ex-

* Order of authorship determined by chance.

ist in a defined spatial context: Space is inescapable and hierarchically structured. The whole notion of conducting scientific inquiry at the landscape scale is a difficult one, as science progresses through the testing and rejecting of directed hypotheses via experimentation—typically, all variables are held constant but one, and a systematic manipulation of one variable at a time or the careful cross-manipulation of several, can yield definitive information about process–pattern relationships. Landscapes, however, are spatially expansive, complex hierarchical systems that incorporate individuals within populations, populations within communities, communities within ecosystems, and ecosystems within an ecosystem mosaic (O'Neill et al. 1986, Barrett et al. 1997). The reason we perform experiments at all is to control for extraneous variables, such that the dimensionality of the system is reduced, permitting key processes to be isolated and identified with some degree of rigor (Hairston 1989, Underwood 1997). By definition, however, landscapes are highly integrated systems where precise predictions can be difficult to make and where multiple causation often obscures definitive results. The lack of a clear focus that comes from the absence of a general, coherent theory of landscape ecology does little to help the situation.

Classical experimentation always invokes a number of design criteria: control, manipulation, replication, randomization, and independence. In turn, these affect or are affected by inferential domain, units of observation, and falsifiability. In general, classical experimentation begins with a well-defined, targeted process, conceptually sharpened in importance by theoretical studies aimed at mechanistic understanding. In population and community ecology, key casual factors are typically identified in terms of a particular process and studied in “bottom-up” reductionist fashion. Progress is made through the sequential testing and rejecting of null hypotheses, falsifiability being a necessary component. For instance, it is relatively straightforward in principle to perform an experiment to test to what degree a local population is limited by food, by competitors and, in some cases, even by predators.

When testing for processes that operate at larger spatial scales, however, both the conceptual basis on which experimentation is based and the inferential domain for interpreting the results are more difficult to characterize in simple form (Kareiva and Wennergren 1995). To be specific, many questions in landscape or regional population ecology revolve around the relative and combined impact of the four principal demographic processes (birth, death, immigration, emigration) and how these processes are affected by—and become integrated over—the habitat template. In landscape ecology, however, spatial features, not particular processes, typically provide key factors for directed experimentation (Pickett and Cadenasso 1995). Part of the problem is that landscape ecologists tend to label patches, patch networks, and whole landscapes in an arbitrary way and without firm linkage to any particular process or mechanism (Kotliar and Wiens 1990); at best, the manipulation of spatial elements provides an indirect proxy for processes underlying measured responses.

The typical experiment in landscape ecology revolves around the creation of an experimental landscape mosaic in which "treatment factors" are patches of different sizes, different geometries, or different dispersion patterns. Space, however, is a crucible within which singular responses often become subsumed in a multivariate or cumulative manner. In experiments that purportedly measure landscape-scale effects, and where landscape elements are the treatment factor, it is not clear which of many simultaneously operating processes might be producing treatment differences. It does not help that different species often show very different responses to the same landscape (see Chapters 4, 8). Moreover, the larger the spatial scale of the patch system considered, the more likely it is that responses may involve a multiplicity of distinct processes working at different scales, contributing further to the uncertainty of making strong inferences about pattern-process linkages.

Because large-scale responses may involve a suite of different processes working at different scales, and these can be difficult to disentangle, a "top-down" holistic approach that highlights general responses may be a more appropriate approach than one focused on unitary hypothesis rejection (Carpenter et al. 1995). In many ways, this suggestion echos the difference between the inductive approach of landscape ecology to date and the more mechanistic approach typical of classical ecological experimentation.

There is a whole suite of more practical problems involved with performing experimentation at large spatial scales, which we will address in some depth later. For example, there are trade-offs between spatial extent, replication, and duration. It simply is not possible to perform detailed study of population processes at large spatial scales. One consequence of such pragmatic constraints is that as one scales-up, both the theory and the mensurative data become increasingly coarse. At an extreme, organismal responses to large-scale spatial pattern may be reported in terms of presence or absence (see Chapter 12). There is also the practical problem of replication and the extent of habitat heterogeneity considered. Given that there is a limited amount of resources to dedicate to a project, does one design a study to include habitat heterogeneity at the largest possible scale, but with few replicates, or, instead, compromise the scale of the study to increase replication? Part of the answer to this revolves around which processes are considered central and what the inferential domain is thought to be. Are populations within patches the subject, or is it the use of multiple patches by the same individual? Finally, can one really replicate spatial treatment factors at large spatial scales?

Nonetheless, experimental studies of landscape-level phenomena are being called for (Kareiva 1989), and for some systems and landscape phenomena, inquiry is being conducted running the gamut of the whole hypothetical-deductive sequence, from observation to hypothesis generation to prediction to experimentation. There are not many of these, but those that have been conducted (including a number in this book) represent examples of how reductionism and inference can work together to broaden our understanding of large-scale pattern-process relationships in landscapes. Such empirical sys-

tems fall somewhere between the real world and the theoretical abstractions of modelers; hence, they play an important role not only in model parameterization and validation, but also in fundamental model design and formulation. The question we address here is whether (and how) one can use a mesocosm, experimental approach (Odum 1984) to study macrocosm, landscape-scale phenomena (Barrett et al. 1995). Our intent is not to treat formal issues relating to experimental design, statistical power, and the like; rather, it is to focus on the conceptual and pragmatic issues that need to be resolved before formal statistical analyses can be performed.

What Is an "Experiment" at the Landscape Scale?

An experiment at the landscape scale, in the broadest sense, involves the deliberate manipulation of habitats in order to examine the influence of one or more aspects of landscape composition or structure on an ecological pattern or process (the experimental model system of Ims et al. 1993, Wiens et al 1993; henceforth referred to as an EMS). Landscape ecology emphasizes that nature is patchy and heterogeneous at a wide range of spatial scales and that the shape and arrangement of patches may be a key determinant of ecological dynamics (e.g., Turner 1989, Harper et al. 1993, Pickett and Cadenasso 1995). Key landscape parameters include the sizes of habitat patches, their shapes, their connectivity, and the juxtaposition of different landscape elements (Wiens 1995). A landscape experiment could in principle vary one to several landscape parameters (though, as will be discussed later there are often necessary, or at least hard-to-avoid, correlations between landscape parameters). Before discussing design features in detail, we will reflect on general methodological difficulties and intrinsic complexities that bedevil all landscape experiments.

Habitat Heterogeneity

There is an element of complexity that characterizes many landscape experiments, compared with other kinds of ecological experiments, particularly smaller-scale "microcosm" experiments. EMS typically feature such treatment factors as spatial blocks of habitat. By its very nature, a unit of "habitat" typically encompasses many aspects of ecological variability all at once—vegetation composition, thermal environment, natural enemy abundance, and so on. Space or habitats are physical areas within which many singular responses become subsumed in a multivariate or cumulative manner. In experiments that are purportedly designed to measure landscape-scale effects, and where landscape elements are the treatment factor, it is not clear which of many processes might be producing treatment differences. This leads to a number of complexities in the design and interpretation of experiments.

Several landscape experiments have been conducted that attempt to control for some processes while varying others, such as effects of patch size upon move-

ments in small mammal species, say relative to a model about how edges and area modulate intraspecific interactions (e.g., Collins and Barrett 1997). In such studies, to reduce heterogeneity, patches are sown with a predefined species complex of plants (e.g., Chapters 7–9) or fenced to exclude interacting species (e.g., predators, competitors). Rarefied designs using sowing can help minimize sources of variability within, and among patches, leaving the manipulated feature of the habitat as the key factor for analysis. Reducing the complexity of the system, however, has difficulties. In particular, one problem with this design is that it may be rather far removed from the natural landscapes one wishes to understand with the EMS. If animal movement behavior evolved in the context of a complex, heterogeneous landscape, then it is possible that those behaviors evoked in a homogeneous but patchy experimental landscape might give a distorted view of behaviors in the natural setting.

An alternative and much more commonly employed design is to take naturally existing vegetation and create patches from this. This too has problems. A truism about communities is that they are heterogeneous at almost all spatial scales and overall, more variable the larger the sample size. Large experimental patches, therefore, are almost always more heterogeneous internally, compared with small experimental patches. Separating patch-size effects per se from ones that involve responses to a more complex vegetation backdrop can then be tricky indeed.

Multifaceted Responses to Experimentation

Ecological communities are dynamic, and changing them, in almost any way can create surprising cascading effects. Creating patches in a preexisting continuous stand of habitat will almost surely change vegetation dynamics, perhaps to differing degrees in small and large patches (see Schweiger et al., Chapter 9). A striking early finding of the Manaus rainforest fragmentation project was that there was considerable blow-down and vine growth on edges, with substantial effects hundreds of meters into the forest, which changed greatly through time. In such studies, patch size treatments would be completely confounded with a host of possible edge effects. Vegetation dynamics, which are affected by both abiotic and biotic factors, may change over time and in response to manipulated features of experimental landscapes, thus creating complex axes of heterogeneity even in monoculture studies that initially use a “sown” template. Moreover, there is the complicating issue of triumvirate feedbacks among focal organisms, manipulated features of the landscape, and vegetation. To be specific, each inhabitant of a patch or corridor exploits resources, thus often making the site less suitable for conspecifics and, possibly, even affecting long-term vegetation make-up (Holt et al. 1995). If population responses to manipulated landscape features involve marked differences in abundance or density, then density-dependent effects on the resource base may work in opposition to those initiating the response in the first place. A longer-term dynamic involving feedbacks between local habitat quality and larger-scale features of the experimental landscape can then complicate interpretation of the results.

By their very nature, landscape experiments are typically "whole system" experiments, where an entire community of interacting organisms and a suite of abiotic factors respond to the imposed spatial design. Given that consumers need resources and cover, typically provided by other species, and that consumers may have to contend with predators, parasites, and competitors, shifts in the behavior or abundance of any of these species in response to the landscape manipulation will likely influence the response of a focal species to the spatial treatment. Many ecological experiments aim at elucidating the impact of a particular ecological factor (e.g., influence of a predator species upon the abundance of its prey; see Hairston 1989). Landscape experiments are by contrast inherently multifactorial, examining how a complex of ecological forces are modulated by changes in the spatial architecture of a landscape.

An analogy with physics may be useful here. A standard model in physics has three necessary components: a set of dynamical equations, which describe the forces operating to change the state variables of the system; initial conditions, which describe the state of the system at a particular point in time; and boundary conditions, which describe the domain within which the forces are carried out. In a sense, landscape experiments modify (usually in an unknown way) the entire suite of forces that operate on an ecological system, while also imposing novel boundary conditions that may or may not correspond to the "natural" scale of forces operating in the system.

Why Landscape-Scale Experiments Are Needed

First, we will note one tangible benefit of conducting experiments at the landscape scale. Because EMS represent empirical systems that fall somewhere between the real world and the theoretical abstractions of modelers, they play an important role in model building, parameterization, and validation (Kareiva 1989). Most models in landscape ecology are abstract, focus on singular processes, and, more often than not, are gross simplifications of the real world. Experience has shown that it often takes some very creative science to link such theory with real-world phenomena. By contrast, real landscapes are by definition complex entities that defy the partitioning of singular effects. Because experimental landscapes fall somewhere between these two extremes, they provide a conceptual bridge between existing theory and the dynamics of real landscapes, and between standard microcosm studies of particular processes and pattern analyses at broad, macrocosm spatial scales. In fact, in the absence of a general, robust theory on how populations respond to heterogeneity at the mesoscale, the EMS approach represents the most direct way of linking processes and patterns at the local level to that at the larger scales.

Having admitted certain generic difficulties of landscape experiments, it is useful to recall major benefits of experimentation. After all, many of the

problems noted above bedevil strictly observational studies of landscapes, too. In the course of discussing some potential advantages of landscape experiments, we will touch on parallel difficulties and constraints; then, in the next section, we will focus on some major design difficulties that must be faced in landscape experimental studies.

Knowledge of Initial Conditions

Observational studies have to contend with the historical vagaries that created a particular landscape. It is typically rather difficult to discern the species or habitat composition of a landscape prior to the creation of the current landscape (e.g., due to habitat fragmentation). Reconstructing prior land-use patterns (e.g., using tree rings or soil analyses) is often a major research project in its own right.

By contrast, a landscape experiment permits an investigator to conduct pretreatment studies in order to ascertain the initial conditions of the system with some precision. This survey may reveal heterogeneities (e.g., differences in soil type) that can be built into an experimental design as covariates, blocked out by systematic means, or deliberately avoided. Many observational studies of landscapes involve "synchronic" analyses, such as documenting species-area relationships—patterns within landscapes at a given snapshot in time. If one is interested in dynamics ("diachronic" analyses) then it is highly desirable to have a precise knowledge of initial conditions in a system. Of course, it may be difficult in an experiment to ascertain initial conditions, but it will surely be even more difficult in a comparable observational study of a preexisting landscape.

Controls

A standard aim in establishing a sound experimental design is to include controls, which permit one to have a yardstick against which to measure treatment effects. Most research using experimental landscapes has focused on fragment size, shape or degree of isolation (e.g., Fahrig and Merriam 1985, Foster and Gaines 1991, Verboom et al. 1991, Robinson et al. 1992, Harper et al. 1993). Such single-scale, patch-based studies typically make inference via correlative relationships among fragments or use larger habitat patches as ad hoc controls for smaller ones, the assumption being that large patches are more representative of conditions in a continuous (unfragmented) habitat than are smaller fragments. Either way, large fragments provide a baseline for evaluating effects of habitat fragmentation.

Habitat fragmentation, however, is a landscape-level perturbation that undoubtedly has landscape-level effects (Forman and Godron 1986, Bowers et al. 1996a). Whereas single-scale studies that use individual fragments as the unit of observation can yield information relating to general features of

fragments, they are limited when it comes to detailing responses to habitat fragmentation at larger scales.

One can argue that the appropriate scale over which habitat fragmentation effects should be evaluated is at the scale of whole landscapes (not patches); in such cases, landscapes are the experimental units (Bowers et al. 1996b, Dooley and Bowers 1998). There are two types of such controls: a temporal comparison of the same area pre- and postfragmentation (e.g., Lovejoy et al. 1986) and a simultaneous spatial control where a fragmented landscape is compared with an unfragmented one (e.g., Margules et al. 1986, Bowers and Dooley, Chapter 8). There are problems with both approaches. For example, when using spatial contrasts, differences between fragmented and continuous habitat landscapes may reflect the effects of fragmentation or, alternatively, differences in microclimate, vegetation, or a number of other factors that are likely to vary at large spatial scales. Such factors are eliminated when pre-versus postcontrasts are used, but an additional set of factors involving temporal, seasonal, or yearly effects can confound the results. Despite these problems, there is great conceptual appeal in using treatment-control landscape contrasts in examinations of habitat fragmentation, and the chapters in this volume document how major advances in understanding the impact of fragmentation upon small mammal population dynamics has come from this approach.

What is meant by "control" needs to be dealt with cautiously in landscape-level experiments. Consider a more standard kind of ecological experiment, namely, to assess the importance of a predator in regulating prey abundance. A proper experimental design would include three kinds of sites: cages without the predator; cages, permitting predator access [to examine artifactual effects of caging, per se]; and open sites, exposed to ambient levels of predation. The problem with a landscape experiment is that there is no such thing as a control without a particular landscape structure: *All ecological systems exist in a landscape*. A landscape experiment can at best contrast the effects of different landscape structures. It is often difficult, therefore, to ensure appropriate controls in landscape experiments, partly for reasons of scale. Even partial controls, however, are better than none at all.

Control over Landscape Structure

In descriptive studies, there will be a great deal of heterogeneity in the sizes, position, and juxtaposition of landscape elements. In a landscape experiment, there can be some control over these design elements, thus reducing variability in the data. Defining a restricted set of landscape elements for inquiry has the effect of reducing the dimensionality of the system, thus eliminating some of the extraneous confounding factors and leaving a reduced set of key features for analysis. As will be discussed later in more detail, however, various elements of landscape structure are often strongly related, and, so, it may be difficult to disentangle their effects.

Replication

Along with controls, another desideratum of good experimental design is replication, which is essential to discern true treatment effects and to avoid pseudoreplication (Hurlbert 1984). In descriptive surveys, it is often quite difficult to find patches of nearly the same size, much less patches with the same size, equivalent land use and geomorphological histories, similar soils, comparable vegetation, and similar surrounding matrix habitat. In an experiment, however, one can ensure replication of landscape features of particular interest (e.g., patch size, presence of corridors). As we will see later, however, there are pragmatic difficulties in replication at appropriate scales in landscape experiments. Replication in some sense is easier in observational studies, but at the expense of precision in comparability of the "replicate" units.

Synchronicity in Patch Initiation

One aspect of replication is that one can ensure that habitat units were created at a given time. In natural or anthropogenic landscapes, different habitat units are likely to be of different, unknown ages, as in successional mosaics. Because ecological communities often change in their composition through time, differences among habitat units may often reflect differing histories or successional stages rather than landscape-level effects. In some ecosystems or landscapes, the conditions present at the time a patch or habitat unit was created can have a large effect on its subsequent history.

Randomization Across the Landscape

A key element of experimental design is the spatial interspersal of different treatments. Ignoring such interspersal can lead to the problem of "pseudoreplication" (Hurlbert 1984). For instance, in the experiment sketched earlier to assess the impact of a predator upon its prey, if the caged treatments were all on one side of a field, and the uncaged controls were all on the other, there might be differences between treatment and control because of systematic spatial differences across the field, say in resource abundance. One could similarly imagine an experiment where organismal responses were compared pre- versus postfragmentation. The problem is again one of pseudoreplication, but this time in a temporal sense.

This leads to serious problems in interpreting patterns in natural or anthropogenic landscapes. For instance, consider studies of habitat fragmentation, where the fragments have been created by human land-use practices. It is highly unlikely that humans utilize the landscape in a random manner. Rather, for economic, social, and logistic reasons, some areas are a priori likely to be intensively used, with other areas utilized to only a limited degree, only much later. On the island of Honshu (Japan), for instance, essentially all flat terrain is occupied by human-made structures or intensively cultivated; rem-

nant forests in such terrain are just tiny, scattered patches. The remaining forests, some quite substantial in extent, are nearly all on the steep slopes of volcanic mountains where the soil is highly unstable and prone to landslides. A study of patch size effects, per se, on plant community structure is greatly confounded by the presence of such systematic physical differences between small, isolated forest remnants and large areas of forest. In an experimental study of habitat fragmentation, one can reduce this problem by spatially interspersing patches differing in size, either randomly across a landscape, or blocked with respect to known gradients or the distribution of habitat types.

Given these potential advantages of landscape experiments over strictly descriptive studies, we will now turn to difficulties that arise in the design and interpretation of such experiments. For the purpose of discussion, it is useful to have a particular landscape in mind. The most frequent design in the literature to date involves habitat fragmentation and effects of patch size.

What Is the Unit of Observation?

It is often not clear what the basic unit of observation should be in a landscape experiment. Imagine that one could do the following thought experiment: We select a landscape comprised of various habitat patches and then impose invisible force fields around each one, precluding movement in and out (Holt 1993). One would then have an experiment focused, say, on patch size per se, by habitat type, but stripped of landscape context.

Landscape experiments involving "open" habitat units are necessarily much more complex because mobile organisms can move among habitat units. It may be simpler to begin with stationary individuals, and then to contrast these analyses with more highly mobile organisms. What counts as a "stationary" organism must be scaled against patterns of mobility of individuals in the context of the spatial structure of the landscape. We will sketch several possible ways one can treat data from such an experiment.

Individuals Within a Patch Mosaic: Stationary Case

One can examine individual traits (e.g., survival or demography, or morphometric traits) as a function of, say, patch size, or distance to edge of a habitat unit. At first glance, this may seem unproblematic. Recall from earlier, however, that the landscape treatment affects the entire suite of ecological processes that impinge on individuals. This can lead to serious problems in interpretation. For instance, many individual-level parameters are sensitive to local density. If local density is affected by the landscape-level treatment, then these parameters may regularly vary as a function of the landscape treatment, regardless of direct effects of landscape on the individual variables.

Individuals Within a Patch Mosaic: Mobile Case

If individuals are mobile, then they will often experience a number of distinct habitat units in the course of their movements. Individual properties thus reflect integration over a number of spatial units, not just a given patch type or distance to edge. This means that there may be an ambiguous assignment of individuals to treatment units.

It is quite clear that mobility confounds interpretations of landscape effects, and working out the details is rather challenging. In the case of very high mobility, with indiscriminate habitat use, each individual over some time period may experience conditions that exist in all habitat units, regardless of the habitat in which they are found at the moment of capture or observation, which results in a landscape-level average (Vance 1984). In the case of very low mobility, individuals will usually live out their lives in a single habitat unit, converging on the stationary case discussed earlier, resulting in a response that is largely patch-specific. Individuals that show intermediate levels of mobility may exhibit a complex combination of both patch- and landscape-level responses (Fahrig and Paloheimo 1988). In a single study, responses by a suite of organisms of differing mobilities are often measured (e.g., Diffendorfer et al., Chapter 4; Bowers and Dooley, Chapter 8). Such studies offer a broader conceptual basis for making inferences than those provided by single-scale, single-species studies.

Populations Within Patches

The definition of *population* always contains a shade of ambiguity. The simplest definition is the number of individuals found within a defined area in a small interval of time. This is not a problem if individuals are stationary (but see later). If individuals are mobile, then samples taken within very short time intervals can be viewed as estimates of intensity of use. If one has mark-recapture data, then Nichols and Coffman (Chapter 14) recommend the use of multistate models to estimate local demographic parameters and transitions among habitat units.

There is a sampling problem that arises, even with stationary individuals, in estimating densities. Let us say one wishes to compare densities of a plant, or "plantlike" mammal (e.g., pocket gopher) on small and large patches using standard quadrat samples. To characterize a large patch, one would need to sample multiple quadrats, placed at random or in accord with some stratified design across the patch. A similar number of quadrats placed within a single small patch, however, would necessarily end up with a shorter average distance between quadrats. A basic truism about the earth's surface is that at all spatial scales, heterogeneity of all sorts (e.g., differences in soil types or plant community composition) increases with area, so nearby quadrats should be more similar to each other than are more distant quadrats. The only obvious

way around this is to sample from a number of small patches; however, this in turn raises the issue of how to arrange these small patches in space. In our experience, if one takes a given area of habitat and subdivides it among n patches, the convex polygon containing those patches typically spans a much larger collective area than does the original, unfragmented area. Hence, there is a trade-off of sorts between having equal intensity of sampling, with different-sized habitat units, and introducing additional sources of variance, which are expected to exist on a priori grounds (see also below).

The goal is often to compare an average per-unit measure of abundance across treatment categories (e.g., of different size). This is often accomplished through some means of standardization. For example, if one is testing for patch size effects and small patches are 1/16 ha and large patches 1 ha, then to express densities in terms of a 1-ha standard would require multiplying abundances in small patches by 16. By the law of large numbers and central tendency, one might expect the smaller the area sampled, the poorer the estimate, and the greater the between-subject variation in estimates of abundance. Higher variation in smaller than larger patches would be further exacerbated when using multiplication to achieve standardization. One result of such standardization is that standard errors would increase with decreasing patch size for even highly replicated designs, thereby affecting the power of statistical contrasts. One way around this problem is to include more smaller than larger patches, so that the areas sampled are the same, but then the problems of introducing additional sources of spatial variability (see earlier) becomes an issue.

Metapopulations Within Landscapes

If rates of movement among habitat units are sufficiently great, then the utility of viewing samples taken within each unit as a distinct "population" loses its utility. The proper unit may instead be an entire landscape, or portions of a landscape. For instance, the Kansas fragmentation experiment (Robinson et al. 1992, see Chapters 4, 9) devised a spatial design in which "large" patches (0.5 ha) could be compared with clusters of "medium" and "small" patches, where the outer perimeter of the cluster also spanned 0.5 ha; this permitted plant sampling quadrats to be laid out with equal intensity, with equivalent spacing among quadrats within both large patches, and clusters of small patches. The disadvantage with this scheme is that now the unit of analysis might properly be viewed as an entire ensemble of small patches, and not just a single patch. For statistical analyses, this requires replication of the entire ensemble, thus greatly increasing the size and cost of the experiment.

Because of vagility, a given individual may be observed in different landscape units, or in the same unit multiple times. This can imply nonindependence among observations, amounting to "pseudoreplication" (Hurlbert 1984) if observations from a single individual are treated as if they were from multiple, independent individuals. Whether or not this is a problem depends upon the question

at hand. For instance, consider observations of a long-lived predator foraging in an experimental patch array. If the focal question has to do with patch choice by the predator, counting multiple observations of a single predator in one patch inflates sample size. If the question has to do with the likely risk of predation experienced by prey instead, then the appropriate measure might be "predator-hours," and multiple observations of a single predator in a patch might indeed imply a higher estimated predation risk.

Problems with Landscape Experiments

Scaling of Species and Questions to Artificial Landscapes

The issue of identifying appropriate "units" for analysis is also a problem for interpretations of descriptive surveys of landscape patterns, not just landscape experiments. The problem, however, may be somewhat more severe in experiments than it is in surveys because of differences in scale.

As noted earlier, the problem of identifying appropriate "units" for analysis becomes more severe the more "open" a system is. For an organism with a fixed vagility, the smaller the experimental system, the more likely this will be a significant problem. Communities are comprised of species that experience the world spatially in radically different ways (Holt 1993). Any experimental landscape is likely to have taxa present for which habitat units are large relative to home-range size and average dispersal distance, and others for which the units are small, so that single individuals encounter multiple landscape units, even on a daily basis.

If one does not have an appropriate measure of vagility, then one may pose an inappropriate question with respect to the processes operating to produce a spatial pattern in the landscape. In an experimental patch array, for instance, one could use a time series of presence-absence data to estimate local extinction probabilities and rates of colonization (e.g., Chapter 4). If the organism moves frequently among all the patches in the array, however, then "extinctions" might reflect individual decisions regarding patch utilization, leading to the abandonment of certain patches in favor of others, rather than meaningful extinctions at the population level. In this case, the research question should focus on issues of individual patch use and habitat selection, instead of population-level colonization-extinction dynamics.

This problem has been promulgated by the way ecologists label landscape features (Kotliar and Wiens 1990). "Patches" and "landscapes" are not entities with set processes; rather, they are spatial abstractions over which different processes operate at different scales. There may be thresholds that affect responses to patches, such that at the small end of the scale continuum a fundamentally different set of processes (i.e., habitat selection by individuals) may be involved than at larger scales (population persistence via colonization and extinction; see Bowers and Matter 1997).

Moreover, these thresholds can be different for different species. Confounding of processes, such as habitat selection and rates of colonization, has made it difficult to advance landscape ecology to a more mechanistically based and predictive science. This is an important concern because, out of methodological necessity, EMS systems tend to fall toward the small-scale end of the patch-scale continuum. The value of EMS studies to landscape ecology ultimately rests with how findings at a small scale can be extrapolated to discern processes and account for patterns at larger scales. This means that in practice microlandscape designs need to be precisely oriented toward the measurement of specified responses of model species. There is no prescription for achieving this goal except that understanding the biology of the targeted species is paramount, and the questions addressed must be well thought out. Because the basic biology and life histories of small mammals are well-understood (at least as compared against many other taxa), this group again represents an excellent model for addressing landscape-level questions.

Limitations of Scale and Feasibility

A scaling problem arises, in part, because there are logistical, economic, and societal limitations imposed on the spatial and temporal scales at which landscape experiments can be realistically carried out. A landscape experiment by definition requires land, the cost of which in any given region scales roughly with area. To be successful, the land in such an experiment must be protected from interference. In practice, this means that landscape experiments will usually be conducted within the confines of land owned or controlled by institutions, such as university field stations, or by the federal government, such as national laboratories.

One example of the kind of problem that arises in the absence of institutional control over a landscape is provided by the famous fragmentation experiment in tropical rainforest near Manaus, Brazil, initiated by Thomas Lovejoy in the early 1980s (C. Gascon, pers. comm.). The patches were created by ranchers clearing forest, leaving behind patches of forest surrounded by pasture. This protocol was feasible because the Brazilian government subsidized ranching in the region and had a legal requirement on the books that a certain fraction of the forest should be left uncut. Due to changes in administrative policies, ranching became less profitable, and some ranchers allowed the interstitial habitat separating the patches from contiguous forest to re-enter succession, which in this region leads rapidly to tall secondary forest. This introduced an entirely new dimension of heterogeneity among the original experimental patches that was not part of the original design.

As another example of how these pragmatic issues constrain landscape experiments, consider the Kansas fragmentation experiment (Robinson et al. 1992, Holt et al. 1995), which was designed to examine the long-term conse-

quences of patch size and landscape position on secondary succession in both the producer and consumer communities (see Fig. 13.1 for experimental patches in later stages of secondary succession). The University of Kansas Endowment Association owns roughly 1500 acres of contiguous land available for ecological research. Some of this is designated as a "reserve," which can be used for observational studies, but is not to be deliberately manipulated. In the early 1980s a substantial fraction of the remaining land (the Nelson Environmental Study Area) was already involved in various (nonlandscape) experimental studies. This left a few tracts potentially available for landscape experiments. The tract chosen was the largest such tract that had a homogeneous land-use history over the previous decade. Having made this choice, the size and shape (roughly, rectangular) of the tract immediately imposed design constraints on the range of patch sizes that were feasible, and how they could be arranged. Moreover, because the surrounding landscape itself was heterogeneous, the arrangement of patches had to ensure randomization with respect to likely preexisting gradients. In turn, these spatial constraints determined which species might be expected to show population-level responses to patch size (e.g., herbaceous plants, small mammals)



FIGURE 13.1. Photograph of the long-term University of Kansas fragmentation study showing experimental patches in the later stages of secondary succession.

and which might not (e.g., vertebrate predators). We suspect such constraints are endemic to landscape experiments.

Another pragmatic issue is that the cost of maintaining and sampling a landscape experiment at a given level of spatial resolution scales roughly with area. Given a fixed budget, the larger the area, the coarser the spatial resolution in any resultant data set is likely to be. This leads to constraints on the kinds of questions that can be addressed within any given landscape experiment.

Choice of Experimental Organisms

The whole point of conducting a landscape experiment is to examine processes believed to be important in a wider universe (i.e., processes that transcend levels of organization, Barrett et al. 1997). If one is interested primarily in a particular taxon, then an experiment may be relatively easy to relate to nonexperimental studies of that taxon. For instance, the observation that small mammals in experimental patch studies are often actually less abundant on larger patches within the experimental range of patch sizes, whereas the reverse is true when one examines a much larger range of patch sizes in observational studies (Bowers and Matter 1997), provides pointers as to mechanisms that may be operating on small mammals at different spatial scales.

Because there are inevitable constraints on spatial scale in landscape experiments, however, one can also view them as "experimental model systems," wherein small organisms are studied at relatively modest spatial scales, yet provide insights that bear on the dynamics of other organisms that operate at much larger scales. Although we feel this is a valuable approach, it is important to keep in mind limitations in extrapolation from small-scale landscape experiments on small organisms, to larger-scale patterns that involve different taxa. There are several distinct limitations.

First, the taxa chosen for experimental analyses tend to be those that are relatively abundant in the first place. It is likely that there are a wide range of systematic effects of abundance or rarity on behavior, demography, and so on (see Kunin and Gaston 1996 for examples). Abundant species may not be good "surrogates" of rare species, even if they have the same body size (Murphy et al. 1990).

Second, because home-range size and vagility tend to increase with body size, experimental landscape studies tend to concentrate on smaller animals. It is too simplistic to assume that one can translate the dynamical consequences observed for a mouse species that resides in a landscape with a given array of patch sizes onto a moose population that resides in a formally similarly structured landscape of patches (scaled up by the body size ratio moose:mouse). Many ecological traits tend to vary allometrically with body size, including life history traits, rates of resource utilization, the allocation

of resources among competing needs, and the risk of mortality due to predation. These traits help determine how organisms translate spatiotemporal variation in the environment into demographic responses. For instance, small-bodied organisms traversing unsuitable habitat as they move among suitable patches must run the gauntlet of a large range of predator species. Large-bodied organisms often have many fewer predators to fear. This suggests that the mortality risk of dispersal—a crucial ingredient in landscape models of population dynamics—cannot be translated directly across spatial scales when comparing organisms differing in body mass.

Trade-Offs Between Scale and Replication

We noted that landscape experiments almost always operate within spatial constraints. This then leads to a series of interconnected constraints on the design of the experiment. For instance, in experiments focused on patch size (given a fixed total area available for the experiment) the larger the individual patch is on average, the lower the level of replication. Moreover, the greater the distance between patches or between any given patch and the edge of the experimental area, the lower the level of replication. With a low degree of replication comes a reduction in statistical power.

The easiest way to increase power is either to lower the between-subject variability (by methods such as engineering vegetation for homogeneity, e.g. sowing), or by increasing the degree of replication, which means reducing patch size or distance between patches. Both of these latter solutions have their problems. For organisms of a fixed density, absolute population size in a patch scales directly with patch area. In very small patches, the absolute number of individuals expected per patch will be very small. This implies that the dynamics in such patch will be driven largely by the chance vicissitudes of demographic stochasticity (Goodman 1987). Moreover, parameters estimated from small sample sizes will have large confidence intervals.

Decreasing distance between patches permits increased replication, but at a price. If distances are too small, then individuals will be able to move freely among patches, and the system may be one more appropriate for behavioral studies of patch use than for population studies.

Problems of Pseudoreplication and Spatial Arrangement

Many landscape experiments involve habitat units that vary in size. This leads to a practical problem in how to compare such units. If one has a fixed density of sampling units arrayed on the landscape (e.g., live-traps in a grid across an entire site), then there will necessarily be a larger absolute number of samples from a large habitat unit than from any given small unit. Uniform sampling at the landscape scale, therefore, automatically implies an unequal intensity of sampling, on a per patch basis.

There are two ways around this, and neither is entirely satisfactory. First, one could equalize the number of samples taken per landscape unit. This has several undesirable consequences. If one has a single sample per landscape unit, then there will be no measure of the heterogeneity that is almost always present within landscape units (and which typically increases with area). If one instead takes a fixed number of multiple samples within a landscape unit, then the distance between samples will be greater on larger units. Because spatial autocorrelation is ubiquitous in natural communities, multiple samples from small landscape units are not really independent of one another.

The second approach is to increase the number of small landscape units. This leads to a problem in landscape design. For example, take a patch-size experiment. If there is a fixed distance between patches, and between each patch and the edge of the experiment, an increase in the number of small patches, placed at random on the landscape, leads to an increase in the amount of surface area spanned (e.g., by a minimum convex polygon) by those patches, collectively. This implies that a collection of small patches that provides a total of N samples will collectively tend to sample more preexisting spatial heterogeneity than would large patches that also provide N samples. We suggest that the influence of area on variance in measured quantities, within and among patches, is a particularly important dimension of landscape experiments.

We noted earlier that there may be limited replication because of spatial constraints, particularly of landscape units that are large in size (Hargrove and Pickering 1992). For instance, if the unit of observation is to be a metapopulation distributed across multiple patches in a fragmented landscape, the appropriate control might be a single very large unfragmented area (e.g., because of the spatial constraints discussed earlier). This leads to pseudoreplication if standard statistics are applied to multiple samples within the control and a confounding of site with treatment effects (e.g., because of large-scale spatial gradients transecting the entire study site; see Hargrove and Pickering 1992).

The Geometry of Landscape Experiments

Landscape experiments are normally conducted within a defined area, set by logistical and legal issues, such as ownership and land management. This implies a series of interlocked spatial constraints, such that a decision regarding one landscape attribute predetermines other attributes of the experimental landscape. The geometry of an experiment in effect defines a set of interlocking landscape characteristics, making it difficult at times to determine the mechanism underlying any observed effect. This is a large and complex topic, elements of which have been touched on earlier. Here, we will simply present some key considerations.

As a hypothetical example, imagine that the total area available for the experiment is a single square block. If one places several large patches within this area, then their edges will necessarily be closer to each other, and to the edge of the

site, compared with a similarly spaced array of small patches. Moreover, the larger the patch, the fewer the number of replicates at any given spacing that can be placed in an experimental field. Decisions regarding replication, thus, constrain the range of sizes that can be contained in an experiment, and this in turn influences the pattern of distances that separate patches. Further constraints arise if the total area available is not a simple square, or if there are gradients in the nonexperimental landscape within which the experiment is embedded.

Because of individual mobility, animals may move among experimental patches. This implies that in effect there is a neighborhood zone of influence around each patch, a spatial "window," that determines local abundances, movement patterns, and so on. Each patch in an array of patches is likely to have a near-unique landscape neighborhood. "Replicate" patches in a complex landscape may not be biologically true replicates at all because of the constraints of geometry and spacing. The geometry of the landscape, as filtered through the movement patterns of the focal taxa, thus, defines what counts as a replicate for statistical purposes. This is a significant consideration in the analysis of data from extant experiments (e.g., see Chapter 9).

Toward a Typology of Landscape Experiments

Most landscape experiments to date have concentrated on effects of patch size, shape, separation, and connection via corridors (see Fahrig and Merriam 1985, Lapolla and Barrett 1993, Holt and Debiniski, 1999). These are obviously fundamental and do highlight features of landscapes most often considered by theory. However, it should be recognized that there are a wider range of potential landscape experiments that in principle would be valuable to perform.

Edges

Most experiments have used patches with sharp edges, defined by logging or mowing. In natural landscapes, many edges are rather fuzzy. Once patches are created, in long-term experiments pronounced edge effects often arise (e.g., the Manaus study). One could imagine experiments that focus on different kinds of edges. For instance, with selective logging one might create open "buffer zones" or ecotones around experimental patches, with the entire unit surrounded by clear-cutting. In fact, there is reason to think that individual organisms may respond differently to "hard" and "soft" patch edges (Wiens et al. 1985), which suggests that patch or landscape responses may vary according to the nature of edges.

Matrix Experiments

The nature of the intervening matrix can be crucially important in determining observed effects in a landscape experiment that involves patches or habi-

tat fragments. The matrix can constrain the rate of movement between patches. Some species, however, may be habitat generalists (see Chapter 3), able to use the matrix facultatively; the vegetation of the matrix influences how important such habitat use is likely to be. Moreover, the matrix can be the source of resource fluxes into habitat patches, harbor reservoirs for pathogens, or otherwise be dynamically important (Polis et al. 1997). We are unaware of any experiments that have deliberately focused on dynamics in arrays of experimental patches, surrounded by different matrix types. Instead, most EMS designs in this book and elsewhere use the simplest possible landscape mosaic: habitatable patches of a single general type embedded in an uninhabitable matrix.

Heterogenous Patches

It would likewise be interesting to conduct experiments in which distinctly different types of habitats are included in the patch array. Theoretical studies suggest that heterogeneity within and among patches (especially relative to overall "quality") can have a major effect on population persistence and stability (Holt 1992, 1993, 1997). A few patches with low rates of extinction can permit the broadly distributed persistence of a species in a landscape. Moreover, there are a number of important landscape mechanisms that have received considerable theoretical attention, but have yet to be experimentally addressed. A particularly striking omission are experiments testing tenets of source-sink dynamics (Holt 1985, Pulliam 1988). Given that much of the relevant theory about landscape-scale patterns focuses on differences in habitat quality and dispersability, it seems that designs like that in Bowers and Dooley (third-generation landscape; Chapter 8) will be particularly useful.

Applications for Management at the Landscape Scale

We have dwelt at some length on some of the problems that arise in the design, implementation, and interpretation of landscape experiments. These lamentations may sound like a counsel of despair, but this is by no means our intent. A clear-headed awareness of potential problems and pitfalls in landscape experimentation is essential to maximize the utility of this class of ecological experiments, which are still relatively rare, compared to other kinds of experimentation (Holt and Debinski 1999). Most of these problems also plague descriptive studies of landscape pattern. Landscape experiments provide a powerful tool which can clarify some of the complex dynamics of heterogeneous landscapes. Unlike single-species manipulations, landscape experiments involve changes in entire systems, containing mixtures of species with radically different responses to any landscape feature (e.g., patch size); therefore, such experiments will necessarily often be complex and difficult to interpret. The partial control provided by an experiment, however, over such features as range of patch sizes, position in a landscape, and so

forth, may help keep such complexity within manageable bounds, at least compared with descriptive studies. Insights from such experiments are vital if we are to increase our understanding regarding how threatened species, perturbed communities, and agroecosystems are to be managed and sustained for future generations. An awareness of both the strengths and weaknesses of different aspects of landscape experimental design is essential to making firm management decisions based on information gleaned from these difficult and still all-too-rare ecological experiments.

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