
Approximating Nature's Variation: Selecting and Using Reference Information in Restoration Ecology

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Abstract

Restoration ecologists use reference information to define restoration goals, determine the restoration potential of sites, and evaluate the success of restoration efforts. Basic to the selection and use of reference information is the need to understand temporal and spatial variation in nature. This is a challenging task: variation is likely to be scale dependent; ecosystems vary in complex ways at several spatial and temporal scales; and there is an important interaction between spatial and temporal variation. The two most common forms of reference information are historical data from the site to be restored and contemporary data from reference sites (sites chosen as good analogs of the site to be restored). Among the problems of historical data are unmeasured factors that confound the interpretation of historical changes observed. Among the problems of individual reference sites is the difficulty of finding or proving a close match in all relevant ecological dimensions. Approximating and understanding ecological variation will require multiple sources of information. Restoration, by its inherently experimental nature, can further the understanding of the distribution, causes, and functions of nature's variation.

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Introduction

Reference information is used to define restoration goals, determine the restoration potential of sites, and evaluate the success of restoration efforts. Reference information can also contribute to a larger goal—determining the conditions under which restored ecosystems are likely to be self-sustaining and therefore likely to have low costs of management. Even when self-sustaining behavior is not possible (e.g., for an area that is too small for a natural disturbance regime) or even desirable (e.g., for historic communities that require management against natural successional change), reference information helps us determine a site-specific set of feasible restoration goals and forecast the need for management that will replace or counteract natural processes. In essence, selecting and using reference information requires that we address a fundamental issue in ecology: understanding the nature, cause, and function of variation in ecosystems and landscapes. Hence, the selection and use of reference information is a central and defining issue for restoration ecology and will probably play an important role in the development of this field.

All reference information is implicitly time- and space-based: that is, it is about a particular place (a reference site) at a particular time, even if the place and time are broadly or imprecisely defined, the site is no longer an extant natural area, or the historical conditions no longer apply. Selecting and using *extant reference sites* is basic to restoration ecology, but it is only part of the larger problem of using a wide range of historical and contemporary information, including information collected on the site to be restored (Table 1).

Restoration is carried out for a wide range of purposes, including ones that are not centered on restoring natural processes, but rather on direct human uses such as improving water quality or supporting harvestable populations of fish and game. Although our emphasis in this paper is natural area restoration, the issues we raise are broad ones, because all restoration projects require analysis of the same kinds of information. For example, restoration for water quality requires prescriptions appropriate to geology, climate, terrain, history, human influence, and vegetation—that is, it requires the selection and use of reference information.

We begin with an outline of sources of variation in ecosystems. We then discuss the values and limitations of different kinds of reference information and describe how multiple sources of information must be used to understand variation in nature. We conclude our discussion with an overview of topics for future research and application. Although restoration decisions include economic, social, and political criteria (Higgs 1997), we confine our discussion to ecological issues.

Table 1. Types of reference information used to document and infer change in composition (including invasions and extirpations), structure, dynamics, and physical factors.

Current Conditions	Reference Information	
	Historic Records	Legacy and Latency
Climate variables	Data on composition and structure	Fire scars
Topography and hydrology	Written and oral history	Snags and coarse woody debris
Soil and substrate	Historic photos	Dendrochronologies and age structure
Spatial context	Land survey records	Pollen, spores, and microfossils
Composition, structure, and dynamics	Management and land use records	Macrofossils and subfossils
Successional trends	Fire records	Geomorphological features (e.g., meander bends)
	Hydrologic records	Relict distributions
	Weather records	

Variation in Nature

Why is the selection and use of reference information difficult? The simple answer is that nature is variable in time and space. We often must use fragmentary information about this variation to understand current conditions, deduce the potential for restoration, set restoration goals, and propose restoration methods. In this section we expand upon this answer by discussing the effect of observational scale on our interpretations of variation and by outlining sources of temporal and spatial variation in ecosystems.

Scale Dependence in Observations of Variation in Nature. Perceptions of ecological variation depend both on the characteristics of the variation and on the scale of observation. Observational scale has two components: grain and extent (Fig. 1; Wiens 1989; Allen & Hoekstra 1992). Grain is the unit of resolution for an observation, the contiguous area over which one observation is made (e.g., plot, quadrat, or pixel size). Extent is the area over which separate observations are distributed. In sampling an historical record, grain and extent are, respectively, resolution (the time span of the individual sample) and duration (the time span of the set of observations).

Grain and extent affect observations in different ways. For the simplest case—an ecosystem that is relatively homogeneous (e.g., an even-aged stand on a site of uniform topography and substrate)—individual quadrats that are smaller than the size of dominant organisms will vary despite the relatively homogeneous condition. For example, in a forest sampled with small quadrats, one quadrat may contain a tree base, another the forest floor. As the grain size of quadrats increases, the quadrats average across this small-scale variation. Hence, variation among quadrats will likely decrease as grain size increases.

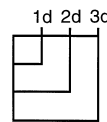
Extent also influences perceived variation. For any grain size and number of quadrats, increasing the extent of a sample (that is, distributing the quadrats over a larger area) is likely to increase the range of environmental conditions sampled. Quadrats that are farther

apart are less likely to be influenced by spatially correlated factors like seed rain. The variation among quadrats will generally increase with increasing extent.

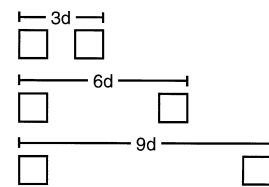
Many ecosystem parameters are scale dependent. For example, Busing and White (1993) showed that the coefficients of variation for density and basal area were dependent on quadrat size in an old growth Southern Appalachian forest. Further, early successional trees had higher coefficients of variation across a series of quad-

A. Components of scale: grain and extent

Three grain sizes:



Three extents:



B. Expected variation in the number of species observed at a given area as a function of the grain and extent of the observations

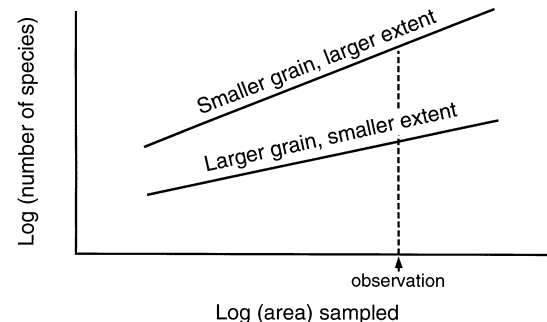


Figure 1. Grain and extent of sample observations affect the number of species observed at a fixed total area sampled (based on findings in Palmer & White (1994)). (A) Three grain sizes and three extents. (B) Expected effects of variation in grain and extent on the species–area relation.

rat sizes (0.01 to 1 ha) than later successional trees, as might be expected, since they reproduce only in scattered recent tree fall gaps. Structure (stand density and basal area) was less variable at smaller quadrat sizes (variance in these values was stable at 0.3 to 0.4 ha) than composition, which still had high variance at the largest (1 ha) grain size. Busing et al. (1993) concluded that previous studies in these old growth forests had overestimated biomass because relatively small plots had been placed subjectively around patches of large trees and had avoided gaps. Such subjective placement will bias estimates of tree mortality and growth rates as well. The strength of correlations between ecosystem attributes and the environment are also scale dependent. In a study of a 6.5 ha stand, the variables correlated with composition varied with the grain size of the quadrats (Reed et al. 1993).

Scale dependence is also important in conclusions about population structure and dynamics. Zedler & Goff (1973) showed that a shade-tolerant tree had a reverse-J, all-aged population structure at relatively small grain sizes, but a shade-intolerant tree attained this stable distribution only at grain sizes large enough to include many independent patches of different successional age. A number of rare plant species reproduce only at long intervals after disturbance to established adults or on patches spatially disjunct from adults (Menges & Gawler 1986; see discussion in White 1996). Reproduction in such populations will appear to be absent and age structures skewed if observed at small scales of time and space.

Species-area data are also strongly scale dependent on the scale of the observations (Fig. 1; Palmer & White 1994). As a result, species-area data are clearly interpretable only when the influence of sample grain and extent are known. Further, the scaling of species presence (as depicted by species-area curves) does not tell us about the scaling of the processes that are responsible for that presence. A species is counted as present when the first individual is encountered, but the presence of individuals may depend on phenomena at larger scales. In essence, species presence can be observed at a smaller scale than the area required for long-term population persistence. Different species will have different absolute probabilities of persistence for a given amount of area or population size. For example, Schoenwald-Cox (1983) examined the increase in population size of three groups of mammals with increasing preserve size. Using a population size of 1,000 individuals as a predictor of long-term persistence, she found that small herbivores required at least 10^3 ha, large herbivores required at least 10^5 ha, and large carnivores required at least 10^6 ha. Species were present on preserves that were smaller than these sizes, but presumably suffer higher risks of extinction as preserve sizes and population sizes de-

crease; indeed, preserve size is correlated with the number of extirpated mammal species in the western United States (Newmark 1987).

Conclusions about variation in ecosystems and the processes responsible for that variation will change with the temporal and spatial scale of observation. This is particularly a problem when events are temporally rare and episodic and spatially patchy, conditions that apply to causes of mortality and reproduction for a variety of species. A tendency to select the oldest patches as reference stands will bias results (leading to higher mean values and reduced variance for parameters like biomass); natural communities can be expected to show an internal patchiness related to the turnover of individuals and larger disturbance events. The ideal solution is to document scale dependence directly by sampling at a series of scales; failing this, we should acknowledge when conclusions are potentially limited by the scale of the observations.

Variation in Time. Temporal variation includes seasonal variation, interannual variation, and the dynamics produced by disturbance and succession (Fig. 2). Examples of seasonal changes include shifting dominance in herbaceous plant communities, migrations of animal populations, and variation in the rates of ecosystem processes such as productivity, nutrient transformations, and decomposition rates. Interannual variation includes random year-to-year variation, periodic or semi-periodic variation expressed over several to many years (the Southern Oscillation; Swetnam & Betancourt 1990), and short-to long-term directional change. Year-to-year variation may be an important mechanism by which biological variation is maintained, as the species finding optimum conditions for growth and reproduction vary from year to year (DeAngelis & White 1994; Tilman et al. 1996). Finally, the interplay of disturbance and succession is a well studied source of temporal variation in ecosystems. Reestablishing or simulating disturbance regimes is one of the most common goals in natural area restoration, particularly with regard to fire (Baker 1994) and river flow (Dahm et al. 1995).

Data on climate variability can inform restoration decisions. The history of climate helps us interpret current conditions, anticipate future events, and evaluate processes responsible for ecosystem change. The probabilities of disturbances vary with climate (Swetnam & Betancourt 1990; Swetnam 1993). Ecosystems may also possess characteristics whose origins are explained by past, not current, environment, and may be on a trajectory of successional change that was determined by past events. It also will be important to evaluate whether future climatic variations have historic precedents.

At least in some cases, restoration must address multiple and interacting causes of temporal change. For ex-

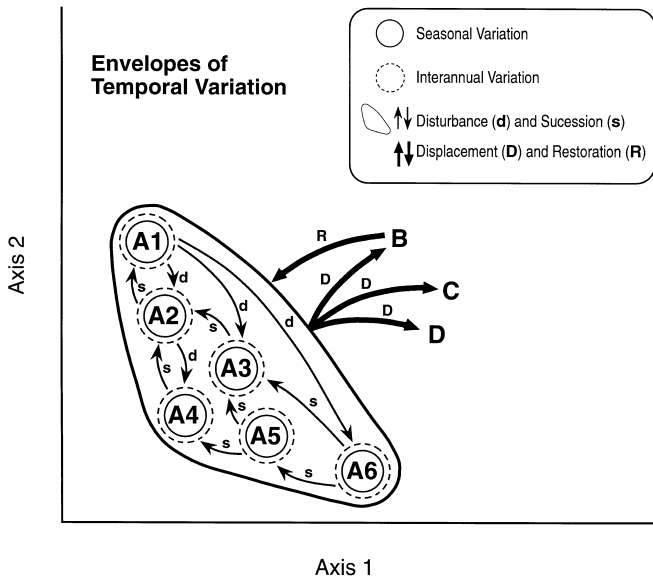


Figure 2. Temporal variation in a two-dimensional ordination or similarity space based on community structure and composition (after Walker & Boyer 1993). Temporal variation in ecosystems includes seasonal variation, interannual variation, and the dynamics caused by disturbance and succession. Human disturbance can displace systems within the bounds of the variation or outside these bounds—to points (B), (C), or (D). Disturbed states (B), (C), and (D) may have their own trajectories if left alone, and they may move toward the envelope or away from it. Restoration can then be defined as the attempt to move the composition, structure, or process back toward the envelope of natural variation (Walker & Boyer 1993). These envelopes of variation represent hypotheses, rather than facts demonstrated for any particular ecosystem. Even if real, the envelopes would likely change shape through time. Reference sites selected to represent locations (A1), (A2), and so on would also show variation due to sampling artifacts, differences in environment, history, and biotic interactions among reference sites, and stochastic factors.

ample, in the Everglades, local composition and structure reflect such factors as climate trends, sea level rise, seasonal precipitation, intense storms, human influence on water quality and flow, fires of various intensities, and successional processes (White 1994).

Variation in Space. Ecosystems vary in space because the physical environment varies along spatial gradients, human and natural disturbances create a mosaic of successional states, and ecological processes vary with the spatial context. The first two of these have relatively straightforward consequences for the selection and use of reference information. For example, similarity in environmental conditions is often used to match reference sites with the site to be restored. We consider spatial context in more detail.

Spatial context is the relationship of sites, be they reference sites or sites to be restored, to their surroundings. Spatial context includes the nature of the matrix surrounding sites, the nature of edges and boundaries, and the size, distribution, and isolation of the sites themselves. Spatial context can affect physical factors (e.g., edge effects on temperature and humidity) and disturbance regimes (e.g., increased rate of treefall along new forest edges). Further, spatial context can directly affect species composition and species-mediated functions, independent of the effects on environment and disturbance.

Changes to spatial context will often be a constraint in restoration. Many of the ecosystems we seek to restore will have altered spatial context—among other changes, they will often be smaller and more isolated than they were historically or in presettlement times. Changes in spatial context have consequences for ecosystem composition and process (Turner 1989; Harris & Silva-Lopez 1993; Pickett & Parker 1994; White 1996) and for the restoration potential of sites (Aronson & Le Floch 1996). Noss & Harris (1986) argue for restoration of site connectedness through protection of corridors.

A species may be absent from an isolated site not because it cannot compete on the site but because it has not yet dispersed to the site or, stated more generally, because its rate of dispersal to the site is less than its rate of extinction after it arrives on the site. Likewise, a species may be present on a site not because it is a good competitor or reproduces there, but because a high rate of dispersal to the site from nearby populations compensates for high mortality or low competitive ability. This is the mass effect or the source-sink dynamics of metapopulations (Shmida & Wilson 1985; Hanski & Gilpin 1991; White 1996).

The size, isolation, and surroundings of sites can have both deterministic and stochastic influences on species presence (Bell et al. 1997; Ehrenfeld & Toth 1997). Deterministic variation results from differences among species in extinction and dispersal rates. If some species are area-sensitive (prone to extinction on small sites because they occur in sparse populations or have low reproductive outputs), their loss will be predictable from the size of the site. If some species have poor dispersal, they will be absent from isolated sites; their presence will be predictable from site isolation. The result of such variation in extinction and dispersal rates will be that species lists will be hierarchically nested. That is, the species lists of small and isolated areas will be predictable subsets of the species list of larger and less isolated areas. The loss of area-sensitive species after habitat fragmentation is an example of this deterministic effect. The importance of site area and isolation in restoration will be greatest for animals dependent on large home ranges and seasonal migrations. The most obvious example is the loss of area-sensitive predators, with resulting increases in her-

bivores and grazing impacts to plant communities. However, spatial context can also influence species with other important ecosystem roles, such as pollinators, seed dispersers, mycorrhizal fungi, pathogens, and herbivores.

Variation in species presence can also be stochastic, leading to non-nested species lists. For example, the simplest form of the theory of island biogeography predicts that species richness will be correlated with island size and isolation, but that species composition will show continuous turnover (MacArthur & Wilson 1967). Composition at any one time will be an unpredictable subset of the species pool. Small and isolated areas will have a subset of the species pool, but the subset present will differ among sites at any particular time of observation. Non-nested species lists can be caused by mechanisms other than those proposed by island biogeography. For example, if a habitat becomes fragmented, random extinctions in each fragment would produce non-nested species lists.

The nestedness of species lists is critical to how restoration provides for overall species richness (Patterson 1987). If species lists among a series of restored sites are nested, the largest area contains the species of all other sites. A sufficiently large restored area may contain all possible species. On the other hand, if species lists are not nested, only a collection of separate sites will contain the full species pool. Managers can potentially control the overlap of species lists and the movement of species among sites to support the species richness of a collection of small restored areas.

A Paradigm for Regional Spatial Variation: the Distance Decay of Similarity. Geographic variation results from climatic gradients, disturbance history, the biogeography of species, and spatial context. This spatial correlation among biotic, environmental, and historical factors produces a general expectation termed the “distance decay” of similarity or the “first law of geography” (Tobler 1970), the proposition that the similarity between any two places will decrease or decay with the distance between them. This means that, at some level, nature is everywhere unique and that the value of reference sites varies directly with distance to the restored area. Regional variation suggests that no one reference site is ever a perfect match for a site to be restored; rather, our conceptual model should be one of interpolation among multiple sites and sources of information. Pickett and Parker (1994) make an analogous claim for temporal variation: ecosystems are likely to have unique histories, so that no one reference site observed at an arbitrary time should be used to determine goals for a restoration project. The distance decay of similarity among intact natural areas is likely to be more rapid for compositional similarity than for structural similarity, and more

rapid for infrequent and rare species than for common and dominant ones.

Relations between Temporal and Spatial Variation. Variation in space and time is not independent, as our discussion has already implied. For example, the seasonal movement of animals implies a place to move to and return from and a matrix that permits this movement (see Gardner et al. 1989 for a quantitative treatment of this problem). Interannual variation that causes shifts of populations along gradients implies that an adequate amount of gradient space is available to accommodate these shifts (e.g., the shifting prairie mosaic of Cottam 1987; Fig. 3). Mass effects on local composition and the dynamics of metapopulations also imply a dependence of temporal dynamics on spatial variation. Disturbance may create a shifting mosaic of successional states—and thus a situation in which a temporal source of variation creates a dynamic spatial pattern. In turn, the spatial pattern provides conditions for both early and late successional species and, hence, influences temporal dynamics (Pickett & Thompson 1978). The role of spatial variation in providing for response to temporal change suggests that some ecosystem functions are dependent on large spatial scales. Spatial extent and connectedness are sometimes the explicit focus of conservation and restoration (Noss & Harris 1986).

The interaction of spatial and temporal variation has been addressed in studies of disturbance at landscape scales. Disturbance can produce a dynamic equilibrium or shifting mosaic of patch states. Factors that increase the likelihood of achieving equilibrium are small patch size relative to landscape size, disturbance return times longer than recovery times, probabilities of disturbance being independent in space, and a feedback between patch state and the probability of disturbance (Shugart 1984; White & Pickett 1985).

Turner et al. (1993) examined equilibrium, stability, and variance as functions of two ratios: the ratio between the area disturbed in a disturbance event and landscape extent, and the ratio between disturbance interval and recovery time (Fig. 4). Equilibrium is defined as a constant proportion of the landscape in various successional states, although the location of patches of various successional age shifts through time (Fig. 5). Stability is defined as the continued presence of all successional states, although the proportion of each may fluctuate greatly (high variance landscapes) or hardly at all (low variance landscapes). Turner et al. (1993) suggest that managing high variance landscapes and disequilibrium landscapes will be difficult; this argument also applies to the restoration of natural disturbance regimes in such landscapes.

Reference information has been used to define temporal and spatial variation as a basis for ecosystem

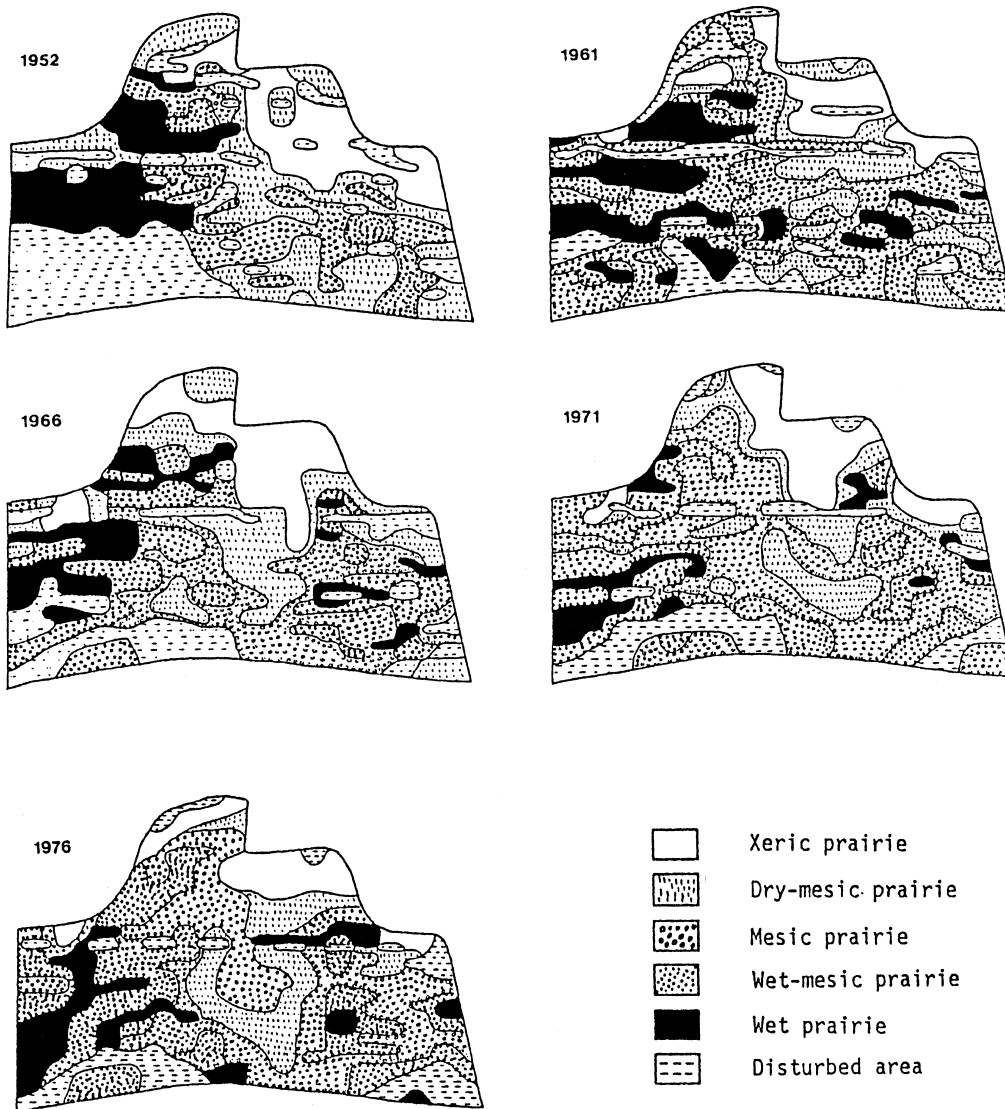


Figure 3. Prairie community shifts on the University of Wisconsin Arboretum's restored prairies. Much of the change was attributed to climate variation (Cottam 1987).

management (Landres 1992; Swetnam 1993; Morgan et al. 1994; Wright et al. 1995; Stephenson 1996). One series of approaches seeks to describe the extremes and bounds of ecological variation. The "natural range of variation" in its purest form is the range of variation in the absence of human influence. The "historical range of variation" is a phrase that avoids the connotations of "natural," given the important but often undocumented influence of Native Americans on some sites. The historical range of variation is the range of variation over a period of record, ideally encompassing multiple generations of dominant plants, a time span that would also encompass much of the relevant variation in animal populations and physical factors. "Ecological variation" explicitly encompasses both spatial and temporal variation. Finally, "reference variation" is the variation defined through reference sites and other sources of reference information. Aronson et al. (1995) term reference

variation the "ecosystem of reference"; this "ecosystem" is an abstraction and generalization of information from multiple sources. Aronson and co-workers have presented operational definitions for vital ecosystem attributes (Aronson et al. 1993) and vital landscape attributes (Aronson & Le Floch 1996) that they propose as key variables to assess with reference information at these two scales.

Defining bounded variation recognizes that ecosystems are neither static nor spatially homogeneous. It allows us to ask whether particular ecosystem states have a precedent and whether current trajectories and restoration methods are leading the ecosystems toward the range of historical variation. However, it cannot be assumed that ecosystems had well-defined bounds of variation, nor that such bounds are stable through time. In the best cases, variation would have recognizable bounds on time scales of decades or centuries to several

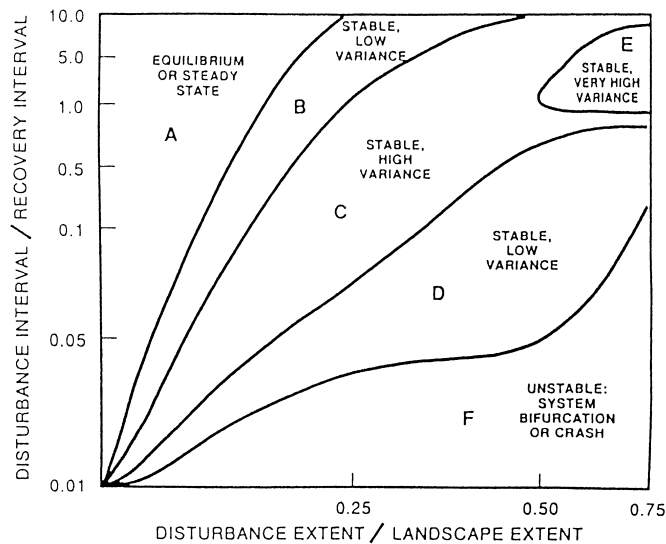


Figure 4. Landscape equilibrium and stability as a function of two ratios, disturbed area/landscape area and disturbance interval/recovery time (Turner et al. 1993). Equilibrium landscapes are stable and have constant proportions of the landscape in various successional states (they have no variance). Stable landscapes can range from low to high variance (all successional states persist, but the proportion of the landscape each occupies varies through time).

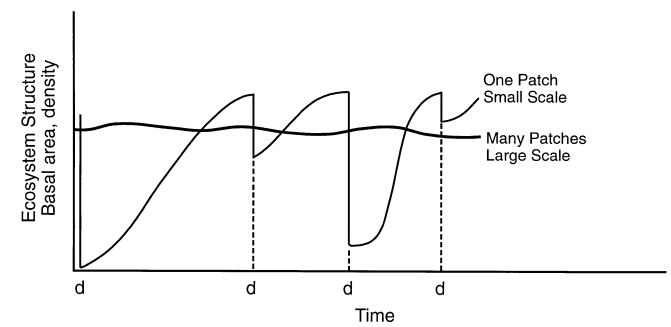
millennia and on spatial scales of hundreds to thousands of hectares. In the worst cases, no such bounds of variation are recognizable: the bounds of variation simply increase continuously as we expand the temporal or spatial scale of observation (Fig. 5).

Discussion: Approximating Ecological Variation

The Values and Limitations of the Sources of Reference Information. The place- and time-based nature of reference information allows us to classify reference information based on closeness in space and time to the site to be restored (Table 2). These categories can be used to describe four broad kinds of reference information: contemporary information from the site to be restored (same place, same time), historical information from the site to be restored (same place, different time), contemporary information from reference sites (different place, same time), and historical information from reference sites (different place, different time).

Contemporary information from the site to be restored (same place, same time). The value of contemporary on-site information is that the problem of reference site match is moot and we can collect direct evidence on trends (succession, population age, and size structure), change in process (relict fire dependent species, absence of repro-

A. Spatial Scale



B. Temporal Scale

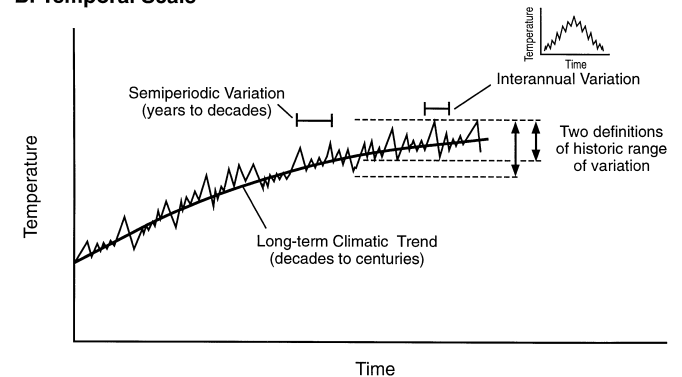


Figure 5. The range of variation in ecosystem parameters as a function of spatial and temporal scale. (A) The structure of a community varies widely at the patch scale, as a function of disturbance and succession. If many independent patches are averaged across a landscape, structural attributes have a stable mean. (B) Variation in temperature at several temporal scales. The historic range of variation depends on the time scale of the observations.

duction), change in components (absent species, exotic species invasions), and process legacies (meander bends in channelized rivers). Contemporary data give us a direct picture of current conditions, like the physical and chemical properties of soils, hydrology, topography, microbial populations, species composition, and successional status, thereby suggesting methods for restoration, as well as allowing us to conjecture about past and future states. The limitation of contemporary on-site information is that snapshot views of ecosystem process can be misleading; we need long-term data to give context to the "invisible present" (Magnuson et al. 1991). Ecosystem processes have nonstationary rates, and responses often are nonlinear, involve time lags, or are indirect (the response of some species is mediated by the response of others). Also, human impacts may have obscured the very variables that require restoration—there is a danger of using a site to be restored as the only reference for its own restoration. We often lack models to extrapolate current conditions backward or forward in time.

Table 2. A short synopsis of the values and limitations of reference information for four sources of data defined by closeness in space and time to the site to be restored.

Closeness in Time	Closeness in Space	
	Same Place	Different Place
Same Time	Climate equivalency moot Unknown historical effects Indirect evidence for past states	
	Site equivalency moot	Site not equivalent; all sites unique environmentally or historically
Different Time	Unknown past climates and historic effects Direct evidence of past states	
	Site equivalency moot	Site not equivalent; all sites unique environmentally or historically

Historical data from the site to be restored (same place, different time). The value of historical data from the site to be restored is, again, that the question of site match is moot and we can discover direct evidence for changes that mandate restoration. The limitations of historical data include a record of insufficient length or resolution, poor spatial resolution, biases in the historical record (e.g., the differential production and preservation of pollen), unmeasured but correlated changes in the environment, and complex responses to past environmental change. Understanding the causes of temporal variation can be difficult because of spurious correlations, inertia, time lags, and non-linear responses. Between the period of historical record and the present, environmental conditions may have changed in unknown ways; our conclusions may not apply to current conditions. Different species (e.g., trees versus herbaceous plants) may respond at different rates to the same physical change (e.g., climate change or disturbance). Historical phenomena can depend in unknown ways on spatial context. For example, historical fire frequency may reflect fires that ignited in areas adjacent to the study area, rather than fires originating within it.

Historical data are often ambiguous on a key point: our ability to directly associate physical environmental factors and disturbance regimes with ecosystem structure and function. The farther back in time we go, the more problematic this ambiguity becomes. Understanding the "rules" by which the past state becomes the present state would allow us to extrapolate trends from past to predicted current state. In this sense, historical data can represent important reference points, even though they cannot be accepted as descriptions of restoration goals for contemporary environments (Falk 1990).

Contemporary information from reference sites (different place, same time). The value of contemporary reference

sites is that they provide direct evidence of how measured processes affect composition, structure, and dynamics under current environmental conditions—we do not have to worry about unknown environmental conditions. Further, if the natural areas selected for reference sites are extant, we can continue to collect information, test new hypotheses, and use the sites for controlled experiments. Potential limitations of reference sites derive from all aspects of spatial variation in ecosystems (Table 3). Reference sites may represent remnants of natural habitat and thus may be small in size. Thus, the reference site may represent only a sample of the original spatial and temporal variation present. A fragmentary reference site may already have been compromised by species loss or edge effects. Reference sites may be set in an altered spatial context so that some of the ecosystem characteristics reflect either altered processes or are a relict of previous conditions (e.g., populations of herbivores increase because of surrounding land use). Conversely, reference sites with an intact spatial context may have conditions that will never be achievable for a site whose context cannot be restored as part of the project. Reference sites may be at a large spatial distance from the site to be restored, may be different in environmental conditions (surviving sites may be less productive or accessible than sites to be restored), and may reflect ecosystem inertia (i.e., ecosystem characteristics do not reflect the current environmental conditions). Current ecosystem conditions may reflect historic but undocumented rare events.

A related use of reference sites is space-for-time substitution, in which chronosequences of stands are assembled to infer historical variation and long-term ecosystem dynamics (Pickett 1989). While this has value and may be the only means to infer temporal dynamics,

Table 3. Typical limitations of reference information from reference sites.

Limitations of Reference Sites
Small size, unknown scale dependence, partial sample of spatial and temporal variation
Changed spatial context
Spatial distance from the site to be restored
Bias of remnant natural areas to less productive or accessible sites
Environmental distance from the site to be restored
Ecosystem inertia: lack of correspondence of composition and structure with current environmental conditions
Undocumented environmental factors
Undocumented rare events
The asymmetry of information:
Presences tell us that a species can tolerate the conditions but not how well it is doing
Absences don't distinguish between a failure to disperse to the site and an inability to tolerate the site

it does suffer from the limitation that currently observed rates and processes may differ from the unobservable ones of the past. Further, this application has the same problem we have just discussed: non-equivalency of the sites in the chronosequence.

Historical data from reference sites (different time, different place). The value of historical data from reference sites is that they provide a direct picture of past states, variability, and human impacts. The limitations are potentially more severe than those for historical data from the site to be restored, since both temporal and spatial uncertainties apply.

Interpolating and Extrapolating Nature's Variation. The selection of reference information often begins with the search for sites and periods of time that are a close match with the conditions we seek to restore. We might, for example, seek reference information from sites that are in all ways identical to the site to be restored, except for the elements or processes that require restoration. The reference information would tell us about both what the ecosystem should be like and what should be restored. This matching (to establish comparability) and subtraction (to establish the factors that require restoration) is perhaps the most obvious approach to selecting and using reference information.

The value of reference sites used in this way will vary directly with the closeness of the match and the completeness of our understanding of the factors that cause variation. Ideally, reference sites would be close in environmental conditions and geographical position and have documented disturbance history, known and minimal, of human influence, and known and minimal fragmentation effects. The problem of understanding historical environments suggests that the closer in time reference data are to the present and the more recently that a site diverged (for whatever reason) from reference conditions, the more apt we are to be able to interpret the implications of reference site data.

While this "match and subtraction" approach for using reference information is attractive, it has limits. All reference sites may differ in some significant ways from the site to be restored, all reference sites may have been altered, or historical data may be absent. Further, the site to be restored could represent unique or novel conditions; the potential reference sites may have never existed. Some reference conditions, while they give us insight into ideal conditions, cannot be directly applied in restoration (e.g., the pristine reference area is large enough to support area-sensitive species and natural patch dynamics, but the area to be restored is small). Finally, at least at some scales, nature is made up of unique places with unique histories (Pickett & Parker 1994), so that no one reference site should be expected to be an ideal

match with a site to be restored. In sum, spatial data have the problem of uncertainty about site match, and historical data have the problem of uncertainty about temporally correlated change in unmeasured variables.

The problem of identifying matching, undisturbed sites reinforces the need for an alternative approach: the use of multiple sources of information from sites and times that have both similarities and differences with the site to be restored. Multiple sources of reference information can be used to produce a description of ecological variation. This is a broader and more important goal than selecting a single reference site as a restoration target, since it will give a spatial and temporal context to the restoration project and allow us to determine what part of that variation is to be restored. Achieving the ideal condition of high similarity between reference and restoration sites is a special case of the more general problem, the analysis of all similarities and differences.

Recognizing the multivariate nature of selecting and using reference information expands the potential information sources. Reference information need not be from identical sites; its use can be interpreted as a function of similarity to the site to be restored. In general, few sites will represent an ideal match to the site to be restored, and many more than stand at some distance from that site. The value of such sites is a function of their spatial, historical, and environmental distance from the site to be restored: the lower the distance and the more we can understand this distance, the more valuable the information will be.

Restoring nature suggests an image of restoring a tapestry that has developed holes and worn spots. The existence of the holes is what compels us to do restoration, but the same holes make our task difficult. The surviving parts of the tapestry may represent a biased subset of the original pattern (e.g., old growth forests may survive only on the least productive sites in a landscape), some of the functional attributes of the tapestry may have been provided by the unbroken nature of the cloth, and to some degree each spot on the tapestry may have been unique rather than an element repeated elsewhere in the design. Of course, nature, unlike a tapestry, also continues to evolve through time: even without human-imposed changes, nature does not remain static. This image and our discussion of the values and limitations of reference information suggest that the process of using reference information is one of interpolation and extrapolation using multiple sources of information. Our challenge is to combine insights from data sets that are individually incomplete and to form hypotheses about how ecosystems can be restored. Restoration can, in fact, help us achieve a better understanding of ecosystems because it is inherently experimental (Diamond 1987).

Summary: Research Questions for the Selection and Use of Reference Information

The selection and use of reference information is a challenging, but fundamental, task in restoration ecology. Only research and additional practical experience will help us meet this challenge. In this section, we outline five research areas that will advance the practice of restoration: ecological variation at multiple scales; models and tests for integrating diverse sources of reference information; sensitivity of restoration to variation in reference information; feasible, site-specific restoration goals; and ecological variation, diversity, and resilience.

Ecological Variation and Multiple Scales. Using reference information requires that we address the patterns and causes of ecological variation at multiple scales (Michener 1997). Long-term data give context to present observations (Magnuson et al. 1991). We need additional work on climate variation, including ties between climate and disturbance regimes. We need to examine the nature of historic variation and the usefulness of the range of variation approach to determining restoration goals. We need to further document the influence of Native American populations. We need to further assess the influence of spatial context on species with important ecological functions and be able to assess when an altered spatial context limits restoration.

Models and Tests for Integrating Diverse Sources of Information. The use of multiple sources of reference information involves building a model, at least conceptual and sometimes quantitative, of temporal and spatial variation. Yates & Hobbs (1997) provide an example of a quantitative model defining a series of ecosystem states and rates of transitions between these states (degradative in one direction and restorative in the other). We need continued development and tests of such models. Because this is usually done informally, we need to learn to more carefully document how we determine restoration goals from multiple sources of information. We need to learn how to link historical information and current conditions, determining the rules by which the past became the present and the present will lead to a range of possible future states.

Sensitivity of Restoration to Variation in Reference Information. Given variation in nature, we can ask: how precise does a restoration prescription have to be? When can we determine that a site is in fact restored because it either fits within a range of ecological variation or is on a trajectory that will allow it to develop toward that range of variation? What are the most meaningful kinds of data and ecosystem attributes and processes that make the most difference in successful restoration?

How does the cost of restoration alternatives affect benefits—the degree of approach to restoration goals?

Some ecosystem characteristics are likely to be relatively easy to predict with reference information, while others are more difficult. Among the former are dominant species, species presences (versus abundances), and successional pathways (versus the amount and spatial distribution of patches). Among the most difficult will be rare species, rare and extreme events, stochastic events and processes, interannual variation, and fragmentation effects. We may have to be very precise when we want natural disturbance regimes to prevail unassisted by management and when we manage rare species, species with sporadic or episodic reproduction, and species with narrow ecological tolerance. On the other hand, patterns of dominants and persistence at regional scales may not require as much precision.

Feasible, Site-Specific Restoration Goals. Reference information can be used to determine the potential of a site for various restoration goals. For example, an altered spatial context can be a constraint in restoration. On small and isolated sites of an ecosystem type that was once continuous and extensive, only a subset of restoration goals is feasible. How do we establish feasible, site-specific restoration goals, when restoration of natural processes or restoration to an original ecosystem is impossible? For example, restoration goals can be nested: a small patch of remnant prairie can be restored and managed for wildflower diversity even though natural fire and buffalo are absent. At the other extreme, large expanses of prairie could be restored in such a way that these factors were given free reign.

Feasible restoration goals also can include getting an ecosystem into a condition from which it will develop toward a longer-term goal (versus putting it in that condition through immediate restoration). Feasible goals can include getting a site off a human-induced trajectory (i.e., preventing further loss), rather than restoration toward an original condition.

Ecological Variation, Diversity, and Resilience. Because restoration often seeks to undo the last several centuries of human influence, restoration ecologists often focus on the past. However, this focus obscures a goal that is more important than simply recreating past conditions: the restoration of ecosystems that will be self-sustaining and resilient (Pavlik 1996). Resilience can be defined as the persistence of species and community variation despite fluctuation in abundance and shifts in location (DeAngelis & White 1994). Self-sustaining describes a state in which natural processes, without the aid of human management, maintain the desired dynamic state.

Nature's resilience may be a function of its spatial and temporal variation (Tilman et al. 1996). We need to

know what the roles of short-term temporal variation and small-scale spatial variation are in maintaining diversity and whether diversity, in turn, generally supports resilience. We need to know how much variation is enough, given likely environmental change, and how close we have to be—that is, how quantitatively (versus qualitatively) we have to characterize and restore this variation. These questions are central to restoration and to our understanding of nature itself.

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