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Landscape Restoration: Moving from Generalities to Methodologies

KAREN D. HOLL, ELIZABETH E. CRONE, AND CHERYL B. SCHULTZ

Large-scale, landscape-level restoration actions are widely implemented but receive little attention from academic ecologists. We review the methods used to assess the role of these processes in past studies, and suggest ways to use past and ongoing restoration activities to increase our understanding of large-scale processes and improve restoration projects. To make better use of past restoration, we recommend the use of a number of alternative analytical approaches that have become widely applied in conservation biology and wildlife management but have yet to be adopted in restoration ecology.

Keywords: Bayesian statistics, information-theoretic, large-scale, reclamation

Ecological restoration is among the most expensive and extensive conservation actions worldwide. For example, between 1986 and 1997, the US Army Corps of Engineers required that 17,500 hectares of wetlands be restored as compensatory mitigation for destroyed wetlands (NRC 2001). The price tags on some high-profile restoration projects, such as the Kissimmee River in Florida and the San Francisco Bay delta, range to billions of dollars. At the Golden Gate National Recreation Area (GGNRA) in San Francisco, more than 200,000 volunteer hours are spent annually on restoration (Theresa Kreidler, volunteer manager, GGNRA, personal communication, 2002), and smaller-scale volunteer restoration efforts are increasingly common worldwide.

Despite their vast spatial and economic extent, restoration efforts have typically focused narrowly on how to restore a given piece of land or waterway, and these efforts have not received much attention from academic ecologists. It is widely recognized that the long-term success of these efforts depends on the landscape matrix in which the projects are embedded (Hansson et al. 1995, Bell et al. 1997, Hobbs 2002). Nonetheless, this recognition has rarely translated into specific recommendations that are put to use on the ground. In part, this gap between general theory and application reflects the difficulty of investigating landscape-level patterns and processes, as landscape-level processes take place at spatial and temporal scales that are not amenable to traditional methodologies of experimental design and inferential statistics. Underutilization of large-scale restoration projects as experiments to inform ecological theory also results from other reasons, such as poor documentation of restoration protocols and lack of monitoring after restoration projects are in place.

We review ways in which large-scale, landscape-level patterns and processes have been incorporated and tested in past restoration studies, discussing the strengths and weaknesses of the different approaches. We suggest ways to use past and ongoing restoration activities to test hypotheses about the importance of landscape processes for ecosystem dynamics in general and restoration success in particular. To make better use of past restoration, we recommend the use of a number of alternative analytical approaches that have become widely applied in conservation biology and wildlife management but have yet to be adopted in restoration ecology.

What do we mean by landscape restoration?

As an initial step, we systematically reviewed the existing literature for landscape restoration studies. We documented methods that have been used to incorporate landscape processes in restoration planning, and we analyzed the results of past large-scale restoration when results were reported in the ecological literature (box 1). Over the past 20 years, the terms *landscape* and *restoration* have become increasingly common in the literature (figure 1) and have been defined in different ways. We use the inclusive definition of ecological restoration from the Society for Ecological Restoration

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Box 1. Survey of the existing literature

We searched the Biosis bibliographic search engine for journal articles in English citing landscape and restoration *(landscape** and *restor**, with * indicating a "wild card" search variable) between 1985 and 2000. Not surprisingly, the number of articles with these keywords increased dramatically in the late 1990s with the expansion of the fields of restoration ecology and landscape ecology (figure 1). During this time period the number of annual citations in Biosis remained nearly constant between 500,000 and 600,000, so increases in the number of citations in our survey are not an artifact of an increase in overall citations. We reviewed 301 articles, which we divided into five broad categories (figure 2), only the last of which attempted to link landscape-level processes with specific restoration projects.

Category 1: **Not landscape restoration.** We excluded 18% of the articles from further discussion because, although they included the terms *landscape* and *restoration,* these articles used the term *restore* in another context, such as restoring soil productivity in agriculture, or used *landscape* in the sense of landscaping for horticultural purposes.

Category 2: General reviews. The largest proportion (32%) of articles surveyed were review articles that highlighted the importance of restoring at large scales, either in general or with reference to a specific ecosystem type. Although these articles offered few details about specific methodologies used to evaluate or prioritize landscape processes, they provide a starting point from which to evaluate possibly important large-scale processes. Given the preponderance of literature reviewing large-scale processes, we refer readers to other recent reviews (e.g., Forman and Godron 1986, Bell et al. 1997, Turner et al. 2001).

Category 3: Ecology/conservation. A substantial percentage of the articles (17%) described basic studies in landscape ecology or the effects of human impacts on ecosystems. These articles usually briefly noted the need for restoration in the conclusions without offering specifics to guide these efforts. Common examples included studies of the effect of fragmentation on faunal groups (e.g., Knick and Rotenberry 1995, Sisk et al. 1997) and surveys of vegetation affected by different types of disturbance or abiotic gradients (e.g., Kirkman et al. 1998, Skartvedt 2000). These studies often provided background information for restoration efforts, but they did not specifically address how these processes could be incorporated in restoration planning or estimate the consequences of possible restoration strategies for populations, communities, or ecosystems of interest.

Category 4: Historic landscapes. Twelve percent of the studies we reviewed documented historical landscapes and changes in land cover over time with the aim of characterizing a specific reference system for restoration efforts. In general, descriptions of reference systems help identify restoration goals with acceptable ranges of variability. Such well-defined goals are essential for effective design and evaluation of project success. Egan and Howell (2001) provide a detailed review of the techniques available for characterizing reference systems. Like basic ecological studies, however, these descriptions do not provide specific information about how to incorporate large-scale processes into ecological restoration.

Category 5: Landscape restoration. Twenty-two percent of the studies we reviewed addressed concrete questions about how to incorporate specific large-scale, landscape-level processes in ecological restoration or evaluated the importance of these processes in past restoration. These studies provide the basis for most of our review.

International: "assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER 2002). We define *landscape patterns* as the spatial relationships of ecosystem types (Forman and Godron 1986). We define *landscape-level processes* as the flow of genes, individuals, materials, and energy across large areas. Box 2 illustrates the wide range of large-scale processes that may influence recovery, using riparian forest native plant communities as an example.

In our systematic review, we defined landscape restoration studies first by compiling studies that included both words *(landscape* and *restoration)* in their abstracts or titles and then by screening those studies for examples that made concrete predictions or analyses of the importance of landscape-level patterns or processes for dynamics of restored populations, communities, or ecosystems (box 1). Most commonly, studies addressed restoration of fire (Baker 1994, Boerner et al. 2000), hydrology (Tockner et al. 1998, Curnutt et al. 2000), or dispersal of animals or plants (Harvey 2000, Singer et al. 2000). Less commonly studied processes and patterns included nutrient fluxes (Kronvang et al. 1999, Van der Peijl and Verhoeven 2000), erosion (Harden and Mathews 2000), and small-scale vegetation and nutrient distribution patterns (Ludwig and Tongway 1996). Interestingly, although a number of studies have discussed the importance of local adaptation and gene flow in restoration (Knapp and Rice 1996, Madsen et al. 1999, Montalvo and Ellstrand 2000a, 2000b), we did not find any genetic studies with the keywords *landscape* and *restore.* We suspect that this absence reflects a historic bias; although population geneticists have studied spatial patterns of adaptive evolution and drift for decades (Wright 1931), they have not adopted the term *landscape* to describe such studies.

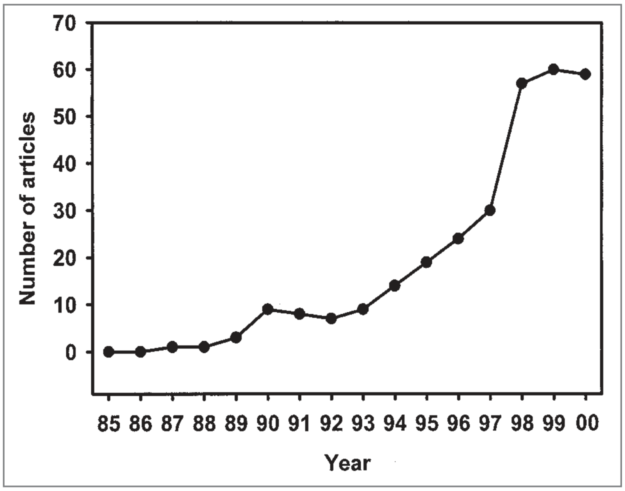

Figure 1. Number of articles in the Biosis bibliographic search engine between 1985 and 2000 citing the keywords **landscape*** *and* **restor***. *(* indicates "wild card" search variable.)*

A large number of the authors in our survey recognized the importance of a range of large-scale ecological patterns and processes in influencing ecosystem recovery and restoration; in fact, a third of the articles were review articles highlighting this point (figure 2). In contrast, only 22% of the articles reported on studies using specific restoration projects to predict or test the importance of landscape processes in restoration outcomes. In the remainder of this article, we discuss methods used in this subset of articles (figure 3). We recognize that any keyword search has inherent biases due to the selection of terms and that it is impossible to comprehensively survey the gray literature through keyword searches. Therefore, we draw on a few additional studies that illustrate useful methodologies for analyzing large-scale patterns and processes but did not come up in our systematic literature search (Koebel 1995, Liermann and Hilborn 1997, Schultz and Crone 1998, Montalvo and Ellstrand 2000a, 2000b, Armstrong and Ewen 2002, D'Antonio et al. 2002). Methods used to link landscape patterns and processes in restoration generally fell into three broad categories: (1) comparisons across sites, (2) large-scale manipulations, and (3) predictive models. We discuss each in turn, with emphasis on how restoration projects could be better designed and analyzed to inform future restoration efforts and ecological theory.

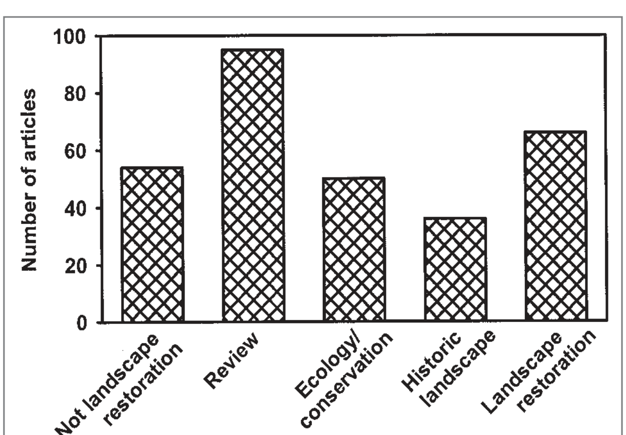

Figure 2. Categorization of articles citing the keywords **landscape*** *and* **restor***. *See box 1 for further discussion of categories.*

Box 2. Ecological processes operating at large spatial scales that influence recovery and restoration of riparian forest native plant communities

Physical processes

- Water flow rate
- Water drawdown rate
- Flooding (frequency, timing, duration, magnitude)
- Scouring and erosion
- Sediment and nutrient deposition
- Chemical movement (fertilizers, pesticides)
- Fire

Population processes

- Dispersal and colonization of seeds
- Gene flow (seeds and pollen)

Community processes

- Movement of seed dispersers
- Movement of pollinators
- Movement of herbivores, seed predators, and parasites
- Movement of mutualists (e.g., mycorrhizal fungi)
- Dispersal and colonization of exotic plant species

Human alterations to processes

- Dams
- Levees
- Groundwater pumping
- Land-use changes (e.g., conversion of land uses, farming practices, exotics control)
- Precipitation (climate change)

Comparisons across sites

In 18 studies reviewed, investigators compared similar restoration techniques applied at numerous sites across a landscape to determine whether similar restoration methods led to consistent results: for example, revegetation after mining (Allen 1989, Holl and Cairns 1994), tropical reforestation (Haggar et al. 1997), and bottomland hardwood forest restoration (King and Keeland 1999). These studies provide a potentially powerful resource for testing relationships between the dynamics of restored communities and the characteristics of the surrounding landscape.

Importantly, although not surprisingly, restoration success often differed among sites compared in these studies (e.g., Allen 1989, Holl and Cairns 1994, Haggar et al. 1997). Authors often speculated about causes of these results, such as hydrology, soil patterns, or distance to source populations, but did not usually conduct analyses to separate out the importance of possible influences. For example, Allen (1989) studied the effect of mycorrhizal inoculum and seeding on vegetation establishment on reclaimed mines in arid shrub steppes in Wyoming. She hypothesized that substantial differences among the five sites studied resulted from soil differences and wind patterns, which are influenced by landscape patterns; she encouraged systematic analyses of these factors in future studies.

A limited number of studies that we reviewed compared the results of small-scale experiments or restoration efforts across the landscape as a function of landscape patterns or processes. Scowcroft and Jeffrey (1999) studied the effect of topographic position (ridge, side slope, or drainage bottom) on survival and growth of *Acacia koa* seedlings planted to restore high-elevation Hawaiian forest. Their results showed that *A. koa* survival was lowest on sites with prolonged freezing temperatures, which would make use of frost protection devices at these sites more cost effective. In a comparative study, Harvey (2000) determined that dispersal and proximity to seed sources were important to establishment of tropical forest seedlings in windbreaks in Costa Rica by measuring seedling establishment in previously planted windbreaks that were adjacent to or disconnected from primary forest. Similarly, King and Keeland (1999) surveyed a range of government agencies to synthesize information about bottomland hardwood forest restoration in the southeastern United States and concluded that the primary factor limiting success was lack of attention to hydrological restoration.

Although cross-site comparisons can be a valuable method for gaining insight into the effects of landscape processes on recovery, these comparisons are limited in that they generally do not directly manipulate the landscape process of interest; thus, it is impossible to test causality and there may be multiple potential explanations for observed patterns. In addition, we suspect that the greatest limiting factor for cross-site comparisons is the difficulty of retracing the details of restoration efforts, even when a single agency implements or coordinates similar restoration projects. We reiterate the common recommendation that managers should keep detailed documentation of restoration practices and use standardized monitoring protocols to facilitate such comparisons in the future (Holl and Cairns 2002). Nonetheless, lack of perfect documentation need not prevent analysis of past restoration efforts. Qualitative site histories (e.g., older versus newer restoration sites, or mixed-species versus mostly grass planting treatments) can often be created by interviewing managers and screening informal records.

Even when records are available, academic ecologists may be hesitant to compare restoration efforts across multiple sites, as these efforts encompass variation along numerous environmental gradients and management histories and do not serve as true replicates in the classical statistical sense. Traditional experimental approaches attempt to minimize differences among replicates in order to detect significant effects. To compare multiple restored sites, we encourage scientists to view site-to-site variability as an asset rather than a constraint. In comparing restored sites that have similar but not identical histories, researchers can ask whether, in practical terms, processes matter enough to substantially influence ecosystem dynamics, given real-world heterogeneity. For example, King and Keeland's (1999) survey of bottomland hardwood forest restoration concluded that hydrology most limited restoration success, but that species composition, planting method, and herbivory were also often important. Through quantitative cross-site analysis (which King and Keeland did not include in their paper), ecologists could partition the relative importance of these factors for restoration success.

To facilitate analysis of limited, noisy, and observational data, ecologists in wildlife biology and fisheries management increasingly use novel statistical approaches that have only rarely been applied in restoration ecology (box 3; Hilborn and Mangel 1997, Burnham and Anderson 1998). We encourage scientists interested in restoration to explore possibilities for using these methods for cross-site comparisons to strengthen the inferences drawn in spite of site-to-site heterogeneity. In particular, Bayesian methods estimate the plausible values of parameters or processes of interest (i.e., distributions versus means), emphasizing biological rather than statistical significance. Information-theoretic analyses test the relative support of multiple working hypotheses provided by observations or experiments. Both Bayesian and information-theoretic methods allow researchers to test which of a suite of different mechanistic models are most consistent with observational data, and both methods are more robust to small sample size and environmental "noise" than classical statistics.

In a restoration-related example, Liermann and Hilborn (1997) used a Bayesian analysis to compare the ability of fish stocks to recover from low population sizes caused by overfishing. An earlier, classical analysis of the same data (Myers et al. 1995) reported that there was no conclusive evidence that fish stocks could not recover from low densities. Liermann and Hilborn (1997) concluded there was a nearly 50% probability that stocks could not recover and, therefore, recovery should be a management concern. The contrasting conclusions of these studies depended critically on how the researchers interpreted results of stocks with few data at low densities, a common occurrence. Myers and colleagues (1995) based their conclusions primarily on the stocks with sufficient data to test the hypothesis of no recovery with high statistical power, using only approximately 20% of the stocks for which data were available. Liermann and Hilborn (1997) included all stocks, which resulted in a

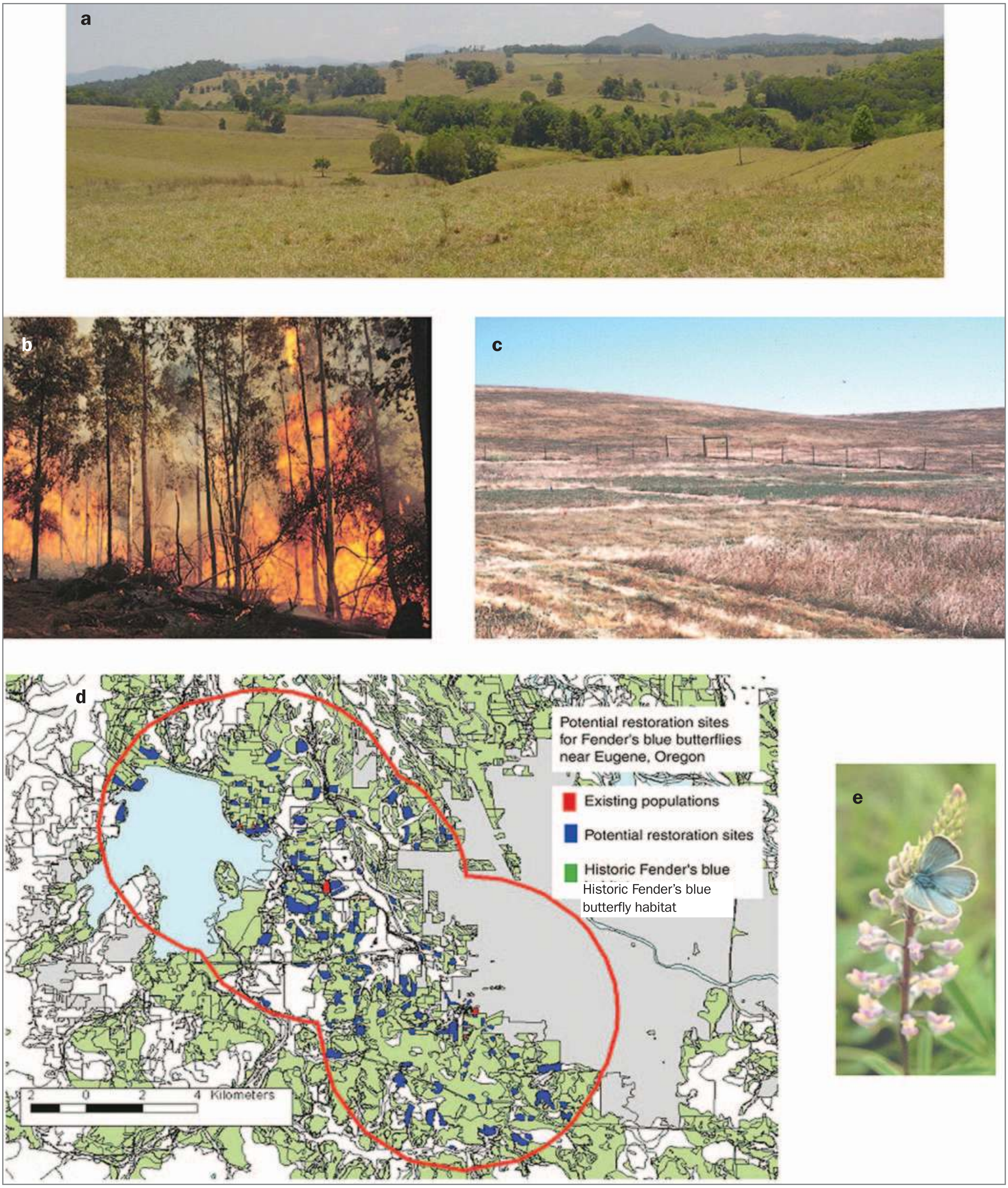

Figure 3. Examples of approaches to landscape restoration. (a) Restoration of a rain forest corridor in Queensland, Australia, to promote animal movement and seed dispersal among remnant patches. (b) Controlled burn in restored jarrah forest near Perth, Western Australia. (c) Small-scale experiment to inform grazing regimes in coastal prairie in northern California. (d) Geographic information system mapping and population modeling exercise to prioritize prairie sites to restore for Fender's blue butterfly near Eugene, Oregon. (e) Fender's blue butterfly. Photographs: Karen Holl (a), Carl Grant (b), Grey Hayes (c), and Cheryl Schultz (e).

Box 3. Alternative statistical approaches

During the past decade, a number of statistical approaches have become widely applied in conservation biology and wildlife management. These approaches have the potential to inform analysis of restoration efforts. We provide a brief description of each statistical approach and refer readers to more detailed references.

Classical methods include all analyses taught in most introductory biostatistics classes (e.g., Sokal and Rohlf 1995, Zar 1999). They focus primarily on testing whether data differ significantly from a null hypothesis, and therefore they are most applicable to yes-or-no questions about whether a process or pattern is detectable. Because the yes-or-no answer depends on the magnitude of tested effects, on the sample size, and on the background variability, these methods are likely to be adversely affected by small sample sizes and high environmental variation, which makes them poorly matched to most restoration studies. They are, however, the methods with which people are most familiar and for which software packages are most readily available.

Likelihood methods find parameters that best fit the observed data for a given model and error distribution. The emphasis is on the values of the best fit parameters, although null hypothesis testing and confidence limits are straightforward to calculate. The advantage of these methods is that they are extremely flexible and allow any kind of linear or nonlinear model to be potentially fit to data, with a wide variety of parametric likelihood functions, including functions appropriate for strongly skewed and nonnormal data. The primary disadvantages are that likelihood functions are therefore more complicated to specify, and fewer software packages are able to fit such models to data. Likelihood methods most naturally match cases in which researchers are interested in testing hypotheses but data do not meet the assumptions of classical statistics, and cases in which the estimated magnitude of a process is of most interest, such as estimating parameters for input into models. Likelihood methods provide the basis for Bayesian and information-theoretic analyses (see Edwards 1972, Hilborn and Mangel 1997).

Information-theoretic approaches compare suites of models that are fit to data using likelihood methods; they assess which models best extract the "signal" in the data without fitting the "noise." These methods are particularly well matched to many questions in restoration ecology, because they group hypotheses into three categories: (1) a single best model, (2) models that are clearly worse than the best model and can be rejected, and (3) models that do not fit the data as well as the best model but cannot be rejected on the basis of existing data. Given limited data and multiple working hypotheses about how ecosystems function, we find these categories more informative than a single decision to accept or reject a null hypothesis. Commonly reported statistics from information-theoretic approaches include Akaike's information criterion, or AIC, which ranks the ability of a suite of models to fit the data by penalizing models for their number of parameters, and Akaike weights, which estimate the relative proportions of the total information captured from each model within a set of models. Not only are information-theoretic analyses more complicated to design than classical analyses, there are no commonly reported absolute statistics of model fit (e.g., analogs of r^2 in linear regression) associated with information-theoretic approaches. Akaike weights, for example, always sum to one across a set of models and can be highly sensitive to the set of models being compared. Information-theoretic methods have been widely adopted to analyze mark–recapture wildlife studies and are only beginning to be applied in other ecological contexts (see Burnham and Anderson 1998).

Bayesian statistics estimate the probability that a hypothesis is true, given prior knowledge and current data. In this context, a hypothesis typically refers to a specific value of a model parameter, as opposed to different sets of factors compared in information-theoretic approaches. In other words, Bayesian analyses produce a probability distribution for parameters of interest, such as the relative difference in abundance or species diversity between sites with different restoration histories. Because Bayesian statistics emphasize parameter distributions rather than point estimates, Bayesian methods are particularly well suited to stochastic simulation models in which values are sampled from the estimated distributions. In addition, Bayesian methods are designed to incorporate information from multiple sources, because they explicitly use results of past studies as well as current experiments or observations to reach conclusions. This is particularly applicable to situations in restoration, which include many unreplicated observations and manipulations. Like information-theoretic methods, Bayesian analyses are more complicated to set up than classical analyses. However, the most controversial aspect of Bayesian analysis is the need to explicitly specify prior knowledge about a system to formulate a hypothesis. If prior knowledge reflects prior beliefs rather than prior data collection, this can bias results toward supporting prior beliefs. This problem is easy to overcome by testing the consequences of making different prior assumptions or by using only quantitative data to construct prior distributions. Moreover, regardless of the statistical analysis used, scientists and managers make prior assumptions about the functioning of a system in choosing experimental questions or management actions; the Bayesian approach simply incorporates these assumptions explicitly in analysis (see Gelman et al. 1995, Dixon and Ellison 1996).

much broader distribution of the probability that stocks could not recover from low density. The risk of using the classical hypothesis-testing approach for management decisions such as restoration is that a possible outcome may be ignored because it is not statistically significant using available data, although it is sufficiently probable to be a biological concern to managers.

Large-scale manipulations

Direct manipulations of large-scale processes clearly overcome many of the limitations of cross-site comparisons. A few studies in our survey drew on field data from large-scale replicated restoration manipulations. Boerner and colleagues (2000) analyzed the effect of spatial patterns of moisture, soil pH, and biomass on nutrient cycling following fires in two 75- to 90-hectare watersheds. They found that soil carbon and nitrogen dynamics were strongly influenced by the intensity of the fire and by the moisture index of the site where the sampling plot was located; as a result, fire increased the heterogeneity in soil properties across the landscape. Singer and colleagues (2000) used data from 31 translocations of bighorn sheep *(Ovis canadensis)* in the western United States to analyze whether successful colonization of new patches from translocated populations was a function of a number of factors, such as population size, habitat patch size, proximity of nearby patches, and barriers to movement. They found that the presence of large rivers, continuous conifer forest, and flat terrain between existing populations and potential habitat reduced colonization rates more than the absolute distance between sites. Populations translocated into larger suitable habitat patches were also more likely to colonize nearby patches.

A common problem in learning from ongoing restoration efforts is that when restoration explicitly includes manipulation of large-scale processes through pilot projects or management actions, such as controlled release from dams or controlled burns (e.g., Nolan and Guthrie 1998, Tockner et al. 1998, Hardy et al. 1999), there is no meaningful way to replicate these actions in space. Obviously, it is impossible to replicate a specific flooding regime along the Danube or Rhine Rivers. Nonetheless, such actions can be extremely informative, particularly when combined with adaptive management *(sensu* Walters 1997), that is, with specific plans to use detailed monitoring of ongoing actions to inform future decisions. For example, channel meandering was restored along a 20-kilometer stretch of the Kissimmee River in Florida and was followed by extensive monitoring of water quality, fish, invertebrates, and birds. This information was combined with hydraulic and hydrologic modeling to select among the restoration alternatives for the entire river (Koebel 1995). Similarly, a large pilot project with monitoring is under way on the Danube River to test the effects of restoring river-floodplain connectivity and water quality on aquatic flora and fauna (figure 4; Tockner et al. 1998). Unfortunately, although "adaptive management" is a widely

Figure 4. Pilot project to restore channel movement along a side channel of the Danube River, Austria. (a) Site before restoration. (b) Same location 1 year after restoration. Photographs: Christian Baumgartner.

used buzzword in restoration, examples in which monitoring results inform future management plans are exceptions among large-scale restoration projects. Plans rarely incorporate adequate monitoring and analysis of data to inform future decisions (Walters 1997).

A number of statistical approaches are more robust than classical hypothesis testing to assess unreplicated manipulations. Information-theoretic analyses, which compare the ability of multiple mechanisms to explain patterns, provide stronger causal evidence than classical analyses. In these analyses, researchers compare the quantitative match between multiple models and observations, a more stringent test than simple acceptance or rejection of a null hypothesis (box 3). In a recent study, Armstrong and Ewen (2002) assessed the success of reintroductions of New Zealand robins to an island composed of remnant and regenerating restored forest patches. They used an information-theoretic analysis to test factors influencing colonization of restored patches, including patch size, isolation, and number of resident robins in each year. They found that colonization of remnant forest patches was most affected by patch size and by the number of resident robins (competition), but that isolation of patches could plausibly reduce colonization probability. The magnitude of the distance effect, however, was so small that it was not ecologically significant (8% reduction in colonization probability of the most isolated patches relative to the most connected), even if statistically detectable.

Single large-scale manipulations at different sites lend themselves particularly well to meta-analysis, that is, to statistical comparison of results from different studies (e.g., Arnqvist and Wooster 1995, Osenberg et al. 1999). Like most kinds of analyses, meta-analyses can be conducted using classical, Bayesian, or information-theoretic methods (box 3). Such analyses are particularly powerful if applied to experimental manipulations rather than to observational data or cross-site and cross-population comparisons. Meta-analyses are increasingly being used to compare results of basic ecological and global change experiments (Arnqvist and Wooster 1995) but have rarely been used in restoration. In a recent report, D'Antonio and colleagues (2002) used meta-analysis to synthesize the effects of many seemingly contradictory studies on the use of fire to restore native species in California grasslands. In contrast to most individual studies, this comparison showed that fire did not have a straightforward positive or negative effect on the relative amounts of native and exotic species. Rather, fire benefited both native and exotic forbs, had minimal long-term effects on native and exotic grasses, and interacted strongly with grazing and precipitation in influencing plant community composition. We encourage further use of meta-analysis because of its potential to make more powerful predictions by drawing on the common use of similar restoration methodologies at multiple sites.

Finally, methods have been developed in limnology to detect alteration after unreplicated manipulations (Stewart-Oaten and Murdoch 1986, Carpenter et al. 1989, Cottingham and Carpenter 1998). In general, these methods focus on testing whether single, treated lakes differ from multiple, untreated lakes, or whether single, treated lakes (or small groups of treated lakes) changed more after manipulation than did unmanipulated control lakes. Such analyses provide stronger inferences about the likely effects of unreplicated manipulations and could be used to estimate the effects of a variety of large-scale restoration actions, such as restoring river channel geomorphology or reintroducing fire.

Predictive models

In many cases, neither cross-site comparisons nor large-scale manipulations are feasible. Cross-site comparisons are limited by the availability and distribution of past restoration efforts. Manipulations are limited because restorationists often can only implement one management option, so the question arises as to how to decide which option to select. To this end, many studies in our literature survey used models to prioritize sites to restore across the landscape or to predict the effects of landscape patterns or processes on recovery.

The most common application of models to landscape restoration in the papers we reviewed was to construct fairly straightforward rule-making models to prioritize sites to restore. These studies usually overlaid geographic information system (GIS) layers, readily available for site and landscape features, and developed ranking systems for sites based on these features. These approaches commonly incorporated a range of criteria into ranking systems, such as soil type, vegetation type, presence of endangered species, connectivity with intact habitats, rarity of ecosystem, potential for restoration, land ownership, and property value (Smallwood et al. 1998, Clark and Slusher 2000, Palik et al. 2000). The GIS models, which combine large amounts of information in a systematic manner, are useful in coordinating and prioritizing restoration efforts. Developing the coverages and rules for prioritizing sites often includes a stage of bringing together various individuals involved in restoration to agree on rankings. This stage offers a systematic way to incorporate expert opinion and forces groups to state their values explicitly. Clark and Slusher (2000) describe a reserve design protocol for the heavily degraded Kankakee watershed in Indiana. The process started with an expert workshop in which various government and nonprofit agencies outlined their conservation goals and delimited geographic areas that met these goals. These focal areas were overlain with maps showing vegetation type, transportation routes, soil moisture, land ownership, and location of sensitive species. The researchers used reserve design software to prioritize areas for acquisition and restoration that maximized specific conservation goals. This allowed comparison of maps produced using different conservation priorities.

In addition to site-prioritization models, a number of studies we reviewed used ecosystem models to simulate different restoration options and predict the effects of landscape patterns or processes on recovery. Such modeling techniques include linking hydrologic and population dynamic models to predict the effects of different hydrologic manipulations on bird and fish populations (DeAngelis et al. 1998, Gaff et al. 2000), using GIS-based state transition models to predict the effect of reinstating a fire regime on the vegetation mosaic and landscape patterns (Baker 1994), and combining deterministic hydrological and biogeochemical models to predict the effects of floodplain reconnection on nutrient cycling (Van der Peijl and Verhoeven 2000). Modeling approaches allow researchers to predict the effects of various management actions over spatial and temporal scales that are impossible to manipulate in the field. For example, DeAngelis and colleagues (1998, Gaff et al. 2000) considered the effects of different hydrologic management regimes on various faunal species in the Everglades up to 50 years in the future. It would be impossible to test all such regimes in the field, and managers cannot wait 50 years to decide which management decision to select. Such models allow comparison of alternative management regimes. Also, the construction of such models often serves the important role of highlighting data gaps and helping to prioritize future data collection.

Several challenges, however, limit the predictive ability of ecosystem models. Such models usually require detailed data that are not often available. Although researchers often assume that more detailed models make more accurate predictions, more detailed models are usually less well supported by field data, leading to unspecified differences in accuracy (Walters 1997). Predictive models rarely include confidence limits of parameter estimates or calculations of the extent to which model predictions change as a parameter is moved to its upper and lower confidence limits (see Ruckelshaus et al. 1997). Perhaps most importantly, all predictive models are based on particular assumptions about how landscapes and ecosystems function. Constructing a model entails so many assumptions that it is nearly impossible to state all of them explicitly. Like uncertainty in parameter estimates, unstated assumptions about ecosystem function make model predictions appear more certain than they actually are. This uncertainty is more difficult to quantify than parameter confidence limits and error propagation, because there are numerous possible alternative assumptions at each stage of the modeling process.

In a clear example of unstated model assumptions, DeAngelis and colleagues (1998) argue that deer are important interactors in Everglades ecosystems because they are both the primary herbivores and the primary prey for endangered panthers. They base their analyses on a model that does not include effects of deer herbivory on plant communities, implicitly assuming that deer only have positive effects on panthers (i.e., increased food supply). At a minimum, their verbal description of the system suggests that alternative models for ecological relationships could include ones in which deer herbivory plays a significant role in limiting tree seedlings, resulting in reduced hunting cover for panthers. Had the researchers considered this option, the range of plausible predictions would almost certainly be much larger, as deer could have positive or negative effects depending on their abundance relative to tree seedlings.

Although not all examples of unstated assumptions we found in our survey were as striking, in our opinion the problem is widespread throughout the spectrum of models used in restoration planning. In GIS models, mapped features such as water tables, soils, or plant communities potentially relate to differences in habitat quality, but quantifying these relationships accurately would take years (and possibly decades) of careful study. Furthermore, little is known about how genes, individuals, or disturbances such as fires and floods move across heterogeneous landscapes. Thus, to evaluate possible differences in disturbance, connectivity, or habitat quality, researchers typically guess or rely on expert opinion about how the available GIS coverages or data for model parameterization relate to these differences. Admittedly, it is not practical to quantify all relevant relationships when restoration planning occurs at a large scale and is aimed to maximize the abundance of multiple species. In these cases, we encourage restorationists to compare the predictions of multiple models, representing a broad suite of assumptions about how communities, landscapes, or ecosystems function. Because they explicitly link mechanistic models with statistical confidence, Bayesian and information-theoretic methods are more naturally suited to model selection and parameter estimation uncertainty than are classical statistics.

In our review, only a small number of predictive models appeared to be parameterized with data collected at the scale and scope of the restoration question. These studies tended to focus on restoration designed for a particular species or process, in cases where researchers only needed to evaluate a limited number of options. In an effort to prioritize actions to restore grizzly bear *(Ursus arctos)* populations in western Montana, Mace and colleagues (1999) developed a GIS model with roads, human activity, elevation, and vegetation and collected 7 years of radio telemetry data on grizzly bear locations in the region. They used logistic regression to identify which habitat variables best explained male and female grizzly bear presence or absence during different seasons. They found that bears use different habitats at different times of the year, a finding that allowed them to make specific recommendations about when and where closing roads and restricting human access would most benefit these populations. We feel that parameterizing models with data collected at an appropriate scale and including the variance in these parameters is critical to making predictions that accurately portray the level of confidence that should be placed in model outcomes.

Combining multiple methods

Many of the limitations of the previous approaches can be overcome by using a combination of methods (De Mars and Wassen 1993, Schultz and Crone 1998, Kronvang et al. 1999). The practical constraints of conducting large-scale replicated experiments necessitate creatively combining data from different sources. Current restoration projects often rely on single methods of inference, using only experiments, modeling, or field monitoring. By combining data from different sources, it is possible to increase predictive power. De Mars and Wassen (1993) used regional hydrological models combined with more localized field studies of vegetation, water depth, and water quality to make recommendations to restore hydrology in wetland nature reserves in the Laegieskamp area of the Netherlands. They note the importance of the larger-scale models to coordinate the various government agencies with jurisdiction over different portions of the land.

Small-scale experiments can be particularly powerful in combination with population or ecosystem models, though care must be taken in extrapolating from smaller to larger scales. Schultz and Crone (1998) used field data of butterfly demography and small-scale experiments on different prairie-burning frequencies to parameterize models that tested different burn strategies to restore habitat for the endangered Fender's blue butterfly *(Icaricia icarioides fenderi)* in Oregon. Multiple burn strategies could not have been tested at large scales because of the risk to this endangered species. This study also illustrates the important issue of quantifying uncertainty when combining data across scales. To provide an estimate of the uncertainty in their outcome, Schultz and Crone (1998) bounded model parameter estimates with confidence limits in the field data. Not surprisingly, these confidence limits were large, but the model still provided information about the relative outcomes of a range of management options. Most importantly, small-scale experiments or planned large-scale manipulations can be used to test key aspects of uncertainty about how ecosystems function and to develop appropriate ecosystem models.

Combining small-scale experiments with other sources of data allows testing of a wider range of hypotheses. Walters and colleagues (1992) note that, even with little quantitative information about a particular system, researchers typically hold qualitative beliefs about how the system works, which point to a particular method of restoration as most likely to succeed. Comparing restoration methods experimentally at landscape scales means investing time and money to use methods that researchers believe are not the best, as well as those most likely to succeed. In some cases, risky strategies can be tested using small-scale experiments. For example, restoration provides an excellent opportunity to test the relative importance of local adaptation versus inbreeding depression in plants by comparing establishment and success of sites planted from local versus nonlocal seed sources (Montalvo and Ellstrand 2000b). Large-scale restoration with nonlocal genotypes, however, could lead to maladaptive genotypes spreading into wild populations. Montalvo and Ellstrand (2000a, 2000b) tested this question for the southern California subshrub *Lotus scoparius* using a combination of genetic analyses, greenhouse studies, field plantings, and large-scale soil and climate data. Their results demonstrated clear reduction in fitness caused by outbreeding of local with nonlocal plants, indicating that restricted gene flow should be maintained in *L. scoparius.*

Conclusions

An increasing amount of money and volunteer labor is being spent on restoration efforts worldwide. A common conclusion of many of these restoration efforts is that success varies substantially among sites. At least in part, this varying success results from differences in hydrology, microclimate, and movement of plants, animals, and disturbance regimes. Much of the potential information from past and ongoing restoration studies remains untapped. We see promising opportunities for continuing to test the importance of these processes in determining the dynamics of restored communities, particularly because the vast majority of restoration projects have not been analyzed or interpreted in a broader ecological context.

We advocate increased collaboration between managers and researchers to conduct large-scale, replicated, manipulative projects, as they can be powerful experiments (e.g., Boerner et al. 2000, Singer et al. 2000). Although replicated experimental manipulation is often not feasible because of social, economic, and ecological constraints, this does not preclude learning about landscape processes from restoration efforts. Some of the best studies we have seen are not necessarily the most logistically or computationally extensive. Rather, the creative use of past research and the combination of multiple methods may increase understanding of processes at large scales in space and time. We encourage comparison of the predictions of multiple models, representing a suite of possible mechanisms about important factors, followed by subsequent empirical testing of the hypotheses generated from the modeling exercises. Moreover, many statistical techniques are widely used in other branches of ecology and ecosystem management to address the common issue of lack of replication in individual studies; these techniques could also be employed in restoration.

Ecologists are increasingly asked to predict the effects of human intervention at large scales in space and time. Because they involve manipulation or re-creation of entire ecosystems, ecological restoration efforts provide potentially powerful tests of the current understanding of large-scale processes. Past lack of attention to restoration by ecologists must be corrected; we encourage academic ecologists to explore opportunities for working with past and ongoing restoration to test large-scale processes in natural systems. One way to encourage such collaborations is by targeting research funding to scientific studies that are coupled with management actions. Many government management agencies and nonprofit organizations fund implementation of restoration projects with a minimal research budget, while governmental science funding agencies often support research on ecological principles that could be applied to restoration but are unlikely to provide sufficient funding to conduct manipulations at the scale at which many restoration projects are implemented.

In conclusion, we reiterate the call to managers to take steps to make their efforts more useful to furthering ecological understanding, such as collecting long-term monitoring data using standardized methods and keeping detailed records of restoration protocols. We also encourage them to consult with scientists in the early stages of restoration planning, as even minor modifications to projects (e.g., selecting monitoring protocols, setting aside a small area of the site to be restored for manipulative plots) can vastly increase the ability to learn from restoration efforts. Capitalizing on existing restoration efforts and expanding collaborations between academic researchers and management personnel offers enormous potential to improve understanding of the importance of landscape processes for ecosystem dynamics in general and restoration success in particular.

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