Explanation, prediction, and maintenance of native species richness and composition in the central Great Basin

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INTRODUCTION

Explanation of the distribution of species long has been a focus of theoretical and applied ecology (Ricklefs and Schluter 1993; Rosenzweig 1995; Scott et al. 2002). Subdisciplines including biogeography, landscape ecology and conservation biology address where species occur, the mechanisms that help generate those patterns, and the extent to which humans may intentionally or inadvertently influence species distributions. Studies of past, present and future distributions of species in the Great Basin have yielded landmark contributions to all of these fields (e.g., McDonald and Brown 1992; Murphy and Weiss 1992; Lawlor 1998; Grayson 2000). The theory of insular biogeography, for example, drew heavily from research in the montane 'islands' of the Great Basin, isolated from the surrounding 'sea' of sagebrush as the regional climate became warmer and drier after the Pleistocene (e.g., Brown 1971; Lomolino 1996). The flora and fauna of the Great Basin also featured prominently in the earliest forecasts about the biological effects of rising concentrations of carbon dioxide and other greenhouse gases (e.g., McDonald and Brown 1992; Murphy and Weiss 1992). Increasing awareness of natural and anthropogenic changes in the environment of the Great Basin has intensified efforts to obtain information that may be relevant to understanding, maintaining and restoring native species and ecosystems.

This chapter provides an overview of four approaches to studying and managing faunal distributions in the Great Basin: documentation of historical changes; development of explanatory and predictive models; application of surrogate species, such as indicators or umbrellas, as planning tools and use of island biogeographic theory to anticipate ecological effects of climate change. These approaches are illustrated using case studies of native fishes, butterflies and birds. Both single-species and multiple-species approaches are considered, and

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the ability of each approach to provide improved guidance for management of ecosystem composition, structure and function is examined.

It is vital not only to draw strong ecological inferences from scientific investigations but also to conduct research that is transferable in space and time and has practical applicability. Therefore, most of the work highlighted in this chapter has focused on links between target species and aspects of the physical environment, such as elevation or topographic heterogeneity. Digital spatial data are increasingly accurate and cost-effective. Because similar physical variables often are related to both faunal and floral diversity patterns at multiple ecological levels of organization—from individual species to assemblages, and across a range of spatial scales— the focus of work presented here is particularly useful for synthetic research, management and restoration initiatives like the Great Basin Ecosystem Management Project.

HISTORICAL CHANGES

Ecological understanding of faunal distributions and the ability to apply that knowledge in a predictive context can be improved by elucidating how species distributions shift in response to natural and anthropogenic environmental change. One clear strategy for acquiring that knowledge is to document shifts in biodiversity patterns through time and correlate those shifts with known environmental perturbations. In many cases, however, the quantity and quality of historical data are limited. Another promising tactic is to explore abiotic and biotic variables that may help explain and predict species distributions.

Data on faunal distributions prior to the post-settlement period largely have been drawn from paleoecological evidence. Although fossil records are incomplete for most faunal groups, species distributions during the mid-late Holocene sometimes can be inferred from remains in

pack rat middens and from pollen deposits, which provide information on climate and the distribution of vegetation resources (Tausch et al., this volume).

Some knowledge of post-settlement faunal distributions has been drawn from historic (~1850 to 1950) and more recent field surveys. Unfortunately, issues related to access, survey methods and variation in species occurrence complicate efforts to assemble reliable databases on species distributions in the Great Basin. Historic presence records usually are credible, especially if the observer was a reputable naturalist, but lack of data rarely can be interpreted as a legitimate absence record. Much of the Great Basin is topographically complex and difficult to access by foot, let alone by vehicle. Consequently, historic survey efforts across the region were uneven, and records from museums and the archives of resource agencies may misrepresent species distributions across the entire Great Basin. Inaccessibility continues to plague contemporary surveys. Nonetheless, even basic presence data from faunal surveys throughout the twentieth century provided baseline information from which inferences can be drawn regarding historical changes in species distributions (e.g., Hubbs and Miller 1948; Brown 1971, 1978; Johnson 1978; Smith 1978; Dobkin and Wilcox 1986; Wilcox et al. 1986). Moreover, in the few cases in which historic photographs exist, repeat photography provides a novel and compelling way to 'see' changes in vegetation over many decades (Figure 1).

A substantial body of ecological literature is devoted to survey protocols, allocation of sampling effort in relation to area and species richness and species-specific detection probabilities. But, when present-day surveys are compared to historical records, poor documentation of methods and observations can inhibit detection of faunal change. Two problems are especially prevalent in older data sets: failure to record absences (i.e., locations where species were not encountered) and, to a lesser extent, failure to record common species.

For example, it appears that relatively ubiquitous species were not recorded during surveys of butterflies in the Toiyabe Range in the 1930s (Fleishman et al. 1997). Furthermore, it is possible that species with particular sensitivity to post-settlement human disturbance were lost from the Great Basin before any occurrence records were obtained.

Temporal variation in the distributions of many animals, especially those with short generation times, also hampers documentation of faunal changes. Most biological surveys are relatively short-term, involving a few years or even a single year. Moreover, the distribution of many species varies through time in response to changes in weather, resource availability and interspecific interactions; the average magnitude of that variation differs among taxa (Pollard 1988; Scott 1986; Fleishman et al. 1997). Thus, the point at which a 'snapshot' of occupancy is taken can affect both estimation of current species richness and occurrence, and appraisal of subsequent changes. Accordingly, more temporally extensive data generally are expected to yield more accurate assessments (Hanski et al. 1996; Hanski 1999; Moilanen 2000).

Unfortunately, management decisions rarely can be delayed until detailed species records are available. Ecologists and managers, therefore, seek tools to guide land-use planning in the absence of complete information. Within an ecosystem, relationships between species distributions and major physical gradients should remain relatively consistent over time—at least from a human perspective, if not from an evolutionary or geological perspective—regardless of whether species distributions actually may have shifted in response to environmental change. The process of developing and testing hypotheses about key environmental variables that affect species distributions allows one to infer how proposed management and restoration might be reflected by future species distributions (Fleishman and Mac Nally 2004). If convincing data exist on past changes in ecosystem structure and function, then, to a limited extent, it also may be

possible to estimate potential historic faunal patterns. Thus, predictive models of species

distributions and application of surrogate species are two of the most frequently touted short-cuts

for setting management objectives and developing effective strategies to achieve those targets.

PREDICTIVE MODELS OF SPECIES DISTRIBUTIONS

This section addresses methods to explain and predict two complementary aspects of

species distributions: species richness (the number of species in a specified location) and

occurrence (presence/absence) patterns of individual species. Species richness is an essential

component of biological diversity with broad relevance to management and restoration

(Stohlgren et al. 1995; Oliver and Beattie 1996; Longino and Colwell 1997; Ricketts et al. 1999).

Species richness also is an intuitive variable that is easily understood by diverse stakeholders.

Measures of species richness, however, do not directly address species composition (that is,

which species are present). Moreover, variables that influence species richness may have little

effect on the distributions of individual species. Rare or vulnerable species need not occur in the

locations with greatest species richness, and the distributions of species of special concern may

not overlap (Cody 1986; Thomas 1995; Fagan and Kareiva 1997; Freitag et al. 1997; Rubinoff

2001). It is, therefore, important to explain and predict both species richness and occurrence

(Margules and Pressey 2000).

Faunal distributions in the Great Basin, like many ecosystem-level phenomena in the

region (Chambers et al., this volume; Germanoski and Miller, this volume; Miller et al., this

volume), rarely have a stable or equilibrium state. Species that tend to occur in many small and

ephemeral local populations with dynamics that are linked by limited dispersal (i.e.,

metapopulations; Hanski and Gilpin 1997; Hanski 1999) may require special management

consideration because maintenance of suitable but temporarily unoccupied habitat is critical to their long-term persistence. The relevance of spatial and temporal scale to relationships among species richness, species occurrence and environmental parameters is increasingly apparent (Smith et al. 1998). Explanatory or predictive models, however, may be valid only at one spatial or temporal scale—or for one location or time period (Wiens 1989; Cooper et al. 1998). Testing the extent to which such models are transferable in space and time is essential.

There is no single or ideal way to model species richness or occurrence. Instead, there are numerous complementary alternatives. Species richness or occurrence potentially can be explained as a function of variables related to the resource requirements of the assemblage or species of interest, such as food sources or percent cover of woody vegetation (Braithwaite et al. 1989; Austin et al. 1990; Lindenmayer et al. 1990; Scott et al. 2002). Obtaining such data, however, can be time-consuming and expensive, particularly throughout extensive areas.

A second approach employs variables that can be quantified easily, at fine resolution and over large areas, using remote sensing data or geographic information systems (GIS) (Busby 1991; Caicco et al. 1995; Neave and Norton 1998; Fleishman et al. 2001b). Data sets and methods for deriving these variables are increasingly available and affordable, and obtaining values for many variables does not require field visits (Austin et al. 1990; Guisan and Zimmerman 2000; Jackson et al. 2000). These are important practical advantages in the Great Basin. Species occurrence models built using remote sensing and GIS data are well-suited to restoration efforts because they easily can be linked with GIS-based models of alternative revegetated landscapes (Lambeck 1997; Bennett 1999; Huxel and Hastings 1999). Connecting occurrence models with revegetation models allows one to estimate the quantity and distribution of suitable habitat for each species that would be available under alternative scenarios. Thus, one

can gauge the overall potential of each alternative to achieve specified ecological objectives (e.g., Rieman et al. 2000).

A third popular alternative for explaining species richness—rarely tested empirically—is to employ 'indicator' species, the presence of which is correlated with the richness of their taxonomic group (Kremen 1994; Pearson 1994; Prendergast 1997; Carroll and Pearson 1998). Reliable indicators of species richness, if they can be found (Niemi et al. 1997; Scott 1998), offer several practical benefits. For example, if the indicators are easier to detect—especially by inexperienced observers—than related species, it may be considerably faster and cheaper to monitor the indicators than to conduct comprehensive surveys (Gustafsson 2000).

Case studies

Species richness: butterflies.—Predictive models of species richness of butterflies in the central Great Basin have been developed as a function of (1) topographic and climatic variables derived from GIS and (2) the occurrence of certain 'indicator' species (see page 16). From 1996–1999, standard methods were used to conduct comprehensive inventories of resident butterflies in 49 locations in 10 canyons in the Toquima Range (Fleishman et al. 1998, 2000) . The Toquima Range data, which included 56 species of butterflies, were used to build the species richness models.

For each inventory location, GIS was used to derive 14 predictor environmental variables that reasonably might be expected to affect, thus to predict, butterfly distributions, including geographic coordinates, elevation, slope and aspect, area, precipitation, solar insolation, topographic exposure and heterogeneity and distance to the nearest source of permanent water (for a complete description see Fleishman et al. 2001b; Mac Nally et al. 2003). Squares of the

environmental variables also were used to accomodate potential non-linear responses (e.g. declines in species richness at extremes of a variable).

Ordinary multiple linear regression is not ideal for modeling richness data because the error distribution of richness data is expected to be Poisson rather than Gaussian (normal) (Cameron and Trivedi 1998). Species richness (the dependent variable) was fitted by using Poisson regression. With many independent variables, Schwarz's information criterion (SIC, Schwarz 1978) is an effective and statistically robust method to identify the most efficient model (Mac Nally 2000). Every possible permutation of predictor variables is calculated and SIC for each is computed—the minimum SIC is sought. SIC is an 'optimal' statistic, a compromise between model fit (ability to explain observed variation or deviance in the dependent variable) and model complexity (number of predictor variables). In addition, hierarchical partitioning was used to identify the most likely causes of variation in species richness (Chevan and Sutherland 1991; Mac Nally, 2000). Hierarchical partitioning jointly considers all possible models and is designed to alleviate problems of multicollinearity among predictor variables. The increase in model fit associated with each predictor variable is estimated by averaging its additional explanatory power in all models in which that variable appears.

The model that was obtained suggested that species richness of butterflies in the central Great Basin can be predicted using just three variables that are easy to quantify across virtually any landscape: elevation, the square of elevation and a measure of local topographic heterogeneity. These variables were included in the minimum-SIC model and also had substantial independent explanatory power. The model explained 57% of the total deviance (the Poisson-regression equivalent of variance) of observed species richness of butterflies (Mac Nally et al. 2003; Figure 2).

It is possible to infer why these particular variables were correlated with species richness. For example, species richness tended to increase as elevation increased, although a negative coefficient associated with the square of elevation indicated a flattening of the curve at lowest and highest elevations. Overall, the relationship between species richness and elevation probably reflects a gradient in climatic severity (Fleishman et al. 2000). In the Toquima Range, low elevations are dry, with few larval hostplants and adult nectar sources. Climate also may constrain species richness at higher elevations in the Toquima Range. Temperature, precipitation and wind conditions at high elevations often limit butterfly flight time and reproduction (Kingsolver 1983, 1989; Springer and Boggs 1986; Dennis and Shreeve 1989; Dennis 1993; Boggs and Murphy 1997). Nonetheless, because much of the Toquima Range is relatively low (below 3000 m), higher elevations are not extremely harsh for butterflies. Species richness of butterflies also increased with increasing topographic heterogeneity. Varied topography may support correspondingly diverse plant communities, may offer numerous locations for seeking mates and may provide shelter from extreme weather events (Scott 1986).

From 2000–2002, the same field methods were used to conduct inventories of butterflies in a total of 39 locations in eight canyons in the nearby Shoshone Mountains and to derive environmental variables for those locations. The Shoshone Mountains data will be used to test the predictions of the species richness model developed using data from the Toquima Range.

Species occurrence: butterflies.—The same inventory data and topographic and climatic variables described in the species richness case study above were used to predict occurrence (presence or absence) of individual species of butterflies in the central Great Basin. Meaningful models were obtained for 36 of the 56 resident species of butterflies recorded from the Toquima

Range (Fleishman et al. 2001b). The models explained 8-72% of the deviance in occurrence of those species (mean = 34%, SD = 18%).

Validation data collected from the Shoshone Mountains in 2000–2001 were used to assess the success of the occurrence predictions. Predictions were relatively successful overall (73%), with success rates for predicted absences uniformly higher than for predicted presences. Increasing the temporal extent of data from one to two years elevated success rates for predicted presences, but decreased success rates for predicted absences, leaving overall success rates essentially the same. The latter result is not surprising because species composition in almost every ecological system is temporally variable to some extent. On one hand, it is possible that a species will be present at a study location in some years but absent in others, perhaps because weather conditions are unfavorable; thus, over time, the success of presence predictions should increase. On the other hand, many species eventually will appear as 'accidentals' in locations that are outside their typical distributional range. Thus, the success of absence predictions is likely to decrease somewhat over time.

Although species occurrence rates (proportion of locations in which each species was found) were correlated between the modeling and validation data sets (Spearman's $r_s = 0.56$, $P < 0.001$), occurrence rates for many species increased or decreased substantially, and erroneous predictions were more likely for those taxa (Figure 3). Model fit (measured by the proportion of explained deviance in the explanatory model) was an indicator of the probable success rate of predicted presences ($r_s = 0.59$, $P \approx 0.005$), but not of predicted absences or overall success rates. The difference in occurrence may be a temporal effect (different sets of years), a geographic effect (Toquima Range vs. Shoshone Mountains) or both. Ongoing work will allow for

discrimination among these effects, improving both ecological understanding and predictive

capacity.

Species occurrence: fishes.—Native fishes in the Great Basin fall into two general categories

with respect to their patterns of distribution: isolated endemics, and widespread species that may

be locally rare (Minckley and Deacon 1991). For isolated endemic species, the conservation

strategy is relatively simple in concept—maintain or restore existing habitat, and consider

translocations to provide insurance against local extirpations. For widespread species, developing

an appropriate conservation strategy can be far more difficult, because managers must contend

with a large number of local populations and potentially suitable patches of habitat. Time and

money always are limited, and typically can be allocated only to a small proportion of

populations or habitat patches.

Much recent work in the Great Basin has focused on Lahontan cutthroat trout

(*Oncorhynchus clarki henshawi*), a widespread taxon listed as threatened under the U.S.

Endangered Species Act. The distribution of Lahontan cutthroat trout in the western Great Basin

is related to both local and regional environmental gradients. Cutthroat trout in this region occur

almost exclusively in small streams, ranging from less than one meter to six meters in width

during summer low flows. Within occupied streams, the downstream distribution limit of

cutthroat trout is related to three factors: perennial surface flow, maximum water temperature

during the summer and the presence of non-native trout (Dunham et al. 1999, 2000, unpublished

ms). Among streams, the elevation of the downstream distribution limits of cutthroat trout can be

predicted by summer air temperature gradients. At the within-stream scale, however, summer air

temperatures do not vary enough to be useful for predicting fish distributions.

Although thermal gradients have predictable effects on the distribution of cutthroat trout, the effect of non-native trout on cutthroat trout appears to be less predictable. In some localities, cutthroat trout co-occur with non-native trout, but in other localities the distribution of cutthroat trout is dramatically decreased when non-natives are present. Non-native trout are believed to be a major cause of declines of cutthroat trout, but no single mechanism to explain their impact has been identified (Young 1995).

Watersheds that provide thermal conditions suitable for cutthroat trout exist throughout the western Great Basin, but local populations are most likely to occur in relatively large, interconnected stream reach (patch) complexes (Dunham et al. 1997, 2002). Most stream reaches with suitable thermal conditions are quite small or isolated, and do not currently support local populations. If the goal is to facilitate recovery of Lahontan cutthroat trout, then restoration of stream flows, restoration of suitable thermal conditions and eradication of non-native trout is especially important in smaller streams. Research on cutthroat trout demonstrates that the type and magnitude of threats to the persistence of native species can vary among localities. Information on these threats may be useful for spatially explicit prioritization of management actions (e.g., Rieman et al. 2000).

SURROGATE SPECIES

Efforts to predict species richness and occurrence suggest that relatively simple models can be used effectively to understand and predict contemporary faunal distribution patterns. Data used to build and validate the models described above were collected using rigorous, standardized protocols implemented over many locations and years. Unfortunately, with limited time and money, it will be difficult to conduct efforts of similar magnitude for the full diversity

of faunal assemblages present in the Great Basin. Even relatively well-known taxonomic groups have not yet been surveyed comprehensively across the region. For example, since the early 1990s, researchers have detected many populations that earlier workers did not observe, including mammals in select mountain ranges (Grayson and Livingston 1993; Lawlor 1998; Grayson 2000; Grayson and Madson 2000) and native fishes in isolated stream systems (Hepworth et al. 1997). For lesser-known faunal groups, many species are still being described (Weaver and Myers 1998; Hershler 1998, 1999; Kulkoyluoglu 2000; Christopher and Fugate 2001). It is unlikely that exhaustive inventory data will be available for most taxonomic groups in the Great Basin within the foreseeable future. A popular suggestion for addressing this dilemma is to use surrogate species.

In theory, some species can serve as reliable and cost-effective measures of other variables that are difficult and expensive to measure directly, including total species richness; ecosystem functions, such as primary productivity, rates of nutrient cycling, and water flows; or ecosystem 'integrity' (e.g., Franklin 1988; Noss 1990; Angermeier and Karr 1994; Lindenmayer et al. 2000). This reasoning has led to a variety of 'surrogate species' concepts (Caro and O'Doherty 1999), including umbrellas (Andelman and Fagan 2000; Fleishman et al. 2000), indicators (Landres et al. 1988; Noss 1990; Landres 1992; Lindenmayer 2000), ecosystem engineers (Jones et al. 1994, 1997; Coleman and Williams 2002; Reichman and Seabloom 2002), keystone species (Mills et al. 1993; Fauth 1999), flagship species (Leader-Williams and Dublin 2000) and focal species (Lambeck 1997; Zacharias and Roff 2001) (Table 1).

Experimental evidence to validate the utility of surrogate species is sparse. This is not surprising because the lack of resources for inventories, monitoring and research is a primary motivation for using surrogate species. Furthermore, guidance on how to select effective

surrogate species is lacking, and there have been few efforts to identify specific management

scenarios in which surrogate species are most likely to be useful. As the following case studies

from the Great Basin illustrate, workers have begun to address these issues by developing

objective methods for selection of umbrella and indicator species.

Case studies

Umbrella species.—The concept of umbrella species—species whose conservation might confer

a protective 'umbrella' to numerous other species—is straightforward and appealing. It is often

faster and cheaper to sample a few species than to inventory an entire assemblage. Therefore,

umbrella species should reduce the time and money that must be invested in collecting data to

prioritize land use alternatives.

Selection of umbrella species ought to be prospective; in practice, it almost always has

been retrospective. Species typically have been suggested as umbrellas not on the basis of their

geographic distribution or life history, but because they are legally protected. As a result,

conservation biologists and land managers have been restricted to asking—after the fact—

whether additional species will benefit from the conservation of listed species.

Lahontan cutthroat trout, for example, are listed as threatened under the U.S. Endangered

Species Act and are an element of aquatic ecosystems throughout much of the Great Basin.

However, conservation of this species is not likely to be an effective mechanism for conserving

many additional aquatic or amphibian species. Other native fishes in the Great Basin frequently

have resource requirements or geographic ranges different from those of cutthroat trout.

Moreover, many aquatic invertebrates (e.g., spring snails, ostracods, caddisflies) are poorly

known, and often inhabit streams and springs that do not support fishes of any kind. In the face

of limited information on species' ecology and distributions, the best strategy for conserving the diversity of aquatic species native to the Great Basin may be to identify and protect representatives of a wide range of aquatic cover types (Palik et al. 2000) and to maintain known hydrological connections and distinct hydrological units whenever possible (Angermeier and Winston 1999).

On a more positive note, recent work on butterflies and birds suggests that effective umbrella species can be selected using objective ecological criteria (Fleishman et al. 2000, 2001c). Ecologists have identified three key aspects of a species' distribution and biology—co-occurrence of species, occurrence rate and sensitivity to human disturbance—that should be considered when selecting umbrella species. These three factors then were used to develop a numerical index that measures the potential of each species to serve as an umbrella for other members of its regional taxonomic group (Fleishman et al. 2000).

Perhaps the most important criterion for selecting umbrella species is co-occurrence—the proportion of species in the same group of animals or plants that is present where a potential umbrella species occurs. For example, an average of 78% of the butterfly species recorded from canyons in the Toiyabe Range occurred in the canyons in which the Apache silverspot butterfly (*Speyeria nokomis apacheana*) was present. Co-occurrence rarely has been considered explicitly in attempts to identify umbrella species. Instead, it often has been assumed that protecting species with large home ranges will conserve resources for species that have smaller home ranges. But species with large home ranges often are habitat generalists, and it may be impossible, and unnecessary, to protect all locations where they occur. Also, because species richness tends to vary considerably over small distances, conservation of only a portion of the area occupied by a species with a large home range may miss locations with the greatest species

richness. Therefore, selection of umbrella species should focus not on how many places a species occurs, but rather on how species-rich those places are. To illustrate, the Apache silverspot butterfly was present in just seven of the canyons that were surveyed. However, those seven canyons had greater average species richness of butterflies than did the 18 canyons occupied by the swallowtail butterfly *Papilio rutulus*.

Spatial distribution is the second criterion for selecting umbrella species. An ideal umbrella species is neither ubiquitous nor extremely rare, but instead falls between those two extremes. Ubiquitous species are unlikely to serve as effective umbrellas because they inevitably occur in many locations with relatively low species richness, and it is not feasible to protect all areas in which they are present. Rare species, too, are unlikely to serve as effective umbrellas because they occur in so few locations.

The third consideration for selecting umbrella species is sensitivity to disturbance. It is most useful to characterize sensitivity to human land-use, as opposed to sensitivity to natural phenomena, such as weather extremes, and it is presumed that sensitive species will provide a protective umbrella for other species that are equally or less sensitive to human activities. Different species may respond quite differently to similar disturbances, and even the same species may respond differently to different disturbances. Therefore, the index of sensitivity can be tailored to any taxonomic group or ecosystem (Fleishman et al. 2001c). For example, urbanization has considerable adverse influence on native birds in broadleaf forests in the eastern United States. Parameters such as nest height and territory size can be used to assess the sensitivity of birds to urbanization (Brown 1985; Ehrlich et al. 1988; Hansen and Urban 1992). By contrast, one of the primary human disturbances affecting butterflies in broadleaf forests is forest fragmentation. Sensitivity of butterflies to forest fragmentation can be assessed using

parameters such as larval host plant specificity and home range size (Garth and Tilden 1986; Scott 1986; Iftner et al. 1992; Loder et al. 1998).

Research suggests that umbrella species chosen with co-occurrence of species, occurrence rate and sensitivity to human disturbance in mind may be an efficient way to help achieve a target level of species protection (Fleishman et al. 2001c). Data on bird and butterfly species from three different ecosystems—chaparral, broadleaf forest and sagebrush steppe— were used to test whether objectively selected 'umbrella species' were more effective as umbrellas than randomly selected species. Results suggested that umbrella species could be used to identify a smaller subset of locations for conservation, while still protecting the same proportion of species. In other words, umbrella species can help choose where to locate competing land uses when the amount of land dedicated to conservation is limited.

Using an umbrella species drawn from one taxonomic group is not likely to help protect a large proportion of the species in other taxonomic groups. For instance, it may be possible to identify several species of birds whose conservation is likely to confer a protective umbrella to numerous co-occurring species of birds, but birds are unlikely to function as effective umbrellas for other taxonomic groups (also see Andelman and Fagan 2000; Rubinoff 2001). For butterflies and birds, umbrella species identified using objective methods were no more effective than randomly selected species for cross-taxonomic applications (Fleishman et al. 2001c, Figure 4).

Indicator species.—'Indicators' of species richness have distributions that are correlated with species richness of their taxonomic group (Kremen 1994; Pearson 1994; Prendergast 1997; Carroll and Pearson 1998). For butterflies in the Great Basin, it seemed that widespread species would not be useful for modeling variation in species richness (and so, would have little potential

to serve as indicator species), while restricted species, which occur at relatively few sites, often have highly specific ecological requirements that are not shared with many other species. Therefore, of the 56 resident species of butterflies recorded from the Toquima Range (see page 7), only the 22 species occurring in ≥ 30% and ≤ 70% of our 49 study locations were considered as potential indicator species. Thus, species richness at each location, including the potential indicator species, was modeled as a function of the incidence of a set of indicator species drawn from those 22 species.

The modeling process identified a set of five indicator species whose incidences accounted for 88% of the deviance in butterfly species richness in the Toquima Range (Mac Nally and Fleishman 2002): *Ochlodes sylvanoides*, *Everes amyntula*, *Euphilotes ancilla*, *Speyeria zerene* and *Coenonympha tullia*. These five indicator species encapsulate a diversity of life-history characteristics found among the resident butterfly fauna of the biogeographic region. This may explain why this particular suite of species was so strongly associated with variation in species richness. For example, the phenologies of flight activity of the species span the field season. In addition, the group of indicator species includes taxa with varied larval hostplants. Two species feed on different genera in the family Poaceae and one each feeds on Polygonaceae, Fabaceae and Violaceae.

Predictions from the model based on these five indicator species were strongly correlated with observed values of butterfly species richness in 29 sites in the Shoshone Mountains (Pearson rank-correlation 0.799, Figure 5). More than 90% of the observed species richness values fell within the 95% credible intervals of the predictions. Although the number of indicator species contributed to overall species richness in the validation locations (maximum difference of four), this explained little of the difference between locations with the fewest and the most

species (32 species). The average absolute deviation was 3.6 species, but four sites contributed disproportionately to this deviation. The latter sites had from 7 to 14 fewer species than predicted, possibly because a drought cycle during the inventory period eliminated otherwise reliable sources of running or standing water in those sites. The average absolute deviation for the other 25 sites was just 2.7 species. A demonstrably effective model of species richness as a function of indicator species is one of several tools that may help to produce increasingly well-informed strategies for addressing diverse management objectives. On a cautionary note, however, identification of appropriate and effective surrogate species frequently requires considerable research and validation.

ANTICIPATING FUTURE DISTRIBUTIONS OF SPECIES

Desert ecosystems are thought to be highly responsive to environmental changes, including shifts in temperature and precipitation, invasion by nonnative plants, and altered disturbance regimes (Sala et al. 2000; Smith et al. 2000). For example, declines in species richness and changes in species composition of native plants and animals in the Great Basin are anticipated if recent climate change predictions—2–3˚ C increases in temperature, a 10% decrease in summer precipitation and a 15–40% increase in precipitation during other seasons (US EPA 1999)—prove accurate (McDonald and Brown 1992; Murphy and Weiss 1992; Grayson 2000; Fleishman et al. 2001a). Active partnerships among interdisciplinary teams of researchers and land mangers help to develop understanding of the effects of land-use and climate change in the Great Basin, and, in turn, to develop practical alternatives for maintaining and restoring sustainable ecosystems.

Island biogeography frequently has been invoked to explain faunal distributions in montane ecosystems, in which many species have been isolated by elevation (Wilcox 1980; Myers 1986; Meffe and Carroll 1994; Guisan et al. 1995). In the Great Basin, island biogeography may help explain the composition of montane faunas and predict how those faunas will respond to climate change (MacArthur and Wilson 1967; Diamond 1975; Shafer 1990; McDonald and Brown 1992; Murphy and Weiss 1992; Boggs and Murphy 1997). Because mean air temperature decreases 0.6˚C with every 100 m increase in elevation, a 3˚C rise in average temperature might require a species to shift its distribution upward 500 m in order to track a specific thermal environment (Schneider et al. 1992). Forecasts about the effects of climate change in the Great Basin usually have assumed that (1) regional temperature will warm by roughly 3˚C, (2) vegetation zones will shift upward by 500 m, thereby decreasing in area, and (3) animals that are closely associated with particular vegetation zones likewise will move upward by 500 m (McDonald and Brown 1992; Murphy and Weiss 1992; Fleishman et al. 1998). Murphy and Weiss (1992), for example, estimated the number of butterfly species that would be extirpated by climate change on the basis of the species' associations with vegetation zones (e.g., piñon-juniper, alpine). Similarly, McDonald and Brown (1992) predicted that a 3˚C rise in temperature would lead to the extirpation of 9-62% of the montane mammals in various Great Basin mountain ranges and 21% of the mammals in the Great Basin as a whole.

Clearly, the vegetation-based scenario above simplifies both climatic changes and biological responses to those changes. To some extent, oversimplification of climate change scenarios is necessary to accommodate scientific uncertainty and model tractability (Sala et al. 2000). Nonetheless, several caveats are worth noting. First, although resources for some animals are associated with a particular thermal zone, others have a comparatively opportunistic

distribution. The occurrence of a particular plant species, for instance, may be driven more by availability of water or certain soils than by elevation or temperature per se. Second, plant species have individual responses to climate change: a vegetational community does not move en masse (Gleason 1926; Huntley 1991; Tausch et al. 1993; Guisan et al. 1995; Risser 1995; Kupfer and Cairns 1996). As a result, it may not be possible to predict how resource distributions for various animals will change on the basis of predicted shifts in vegetation zones. Third, animals often require resources in addition to plants.

Relatively recent data from several taxonomic groups suggest that it may be appropriate to revise or expand earlier paradigms of Great Basin biogeography. For example, using an expanded set of data on mammals in the Great Basin, Lawlor (1998) found that present-day assemblages are considerably more dynamic than previously understood. Similarly, Fleishman et al. (2001a) found that while most species of butterflies in the Great Basin may persist at the regional level, the number of butterfly extirpations at the mountain range level may vary considerably among ranges. In ranges with an average crest elevation below ~3000 m, the magnitude of losses may depend on whether butterflies can exploit isolated, high-elevation peaks.

During the Middle Holocene, approximately 8000-5000 years ago, temperatures in the Great Basin were several degrees warmer than today (Van Devender et al. 1987). Thus, it might be expected that most of the montane species that currently inhabit the Great Basin would be able to tolerate the magnitude of climatic warming forecast over the next several centuries; species that were extremely sensitive to the effects of increased temperatures may already have been extirpated. However, it is not clear whether the Middle Holocene warming, which was caused by changes in solar insolation and accompanied by increases in summer precipitation,

will be comparable to projected patterns of climate change (Grayson 2000). In addition, faunal responses to climate change may depend in part upon the speed at which those changes occur and the extent to which not only the mean but also the variance in climate parameters increases (McLaughlin et al. 2002).

MANAGEMENT AND RESTORATION IMPLICATIONS

The Great Basin is not a simple or generalizable system. Instead, as demonstrated throughout this volume, ongoing studies across diverse scales are revealing numerous complexities and exceptions that defy easy classification or management. Work on the fauna of the Great Basin strongly indicates that it is possible to increase the effectiveness of maintenance and restoration efforts—whether aimed at native species or ecosystem condition more broadly— by evaluating both species-level attributes and ecosystem-scale system attributes. In many cases, as demonstrated in this chapter, exploring species responses to physical environmental variables is a powerful, practical method for explaining why faunal distributions may have shifted in the past—and for predicting how those distributions may be affected by future ecological changes, whether natural or anthropogenic. Meeting the wide range of management goals in the Great Basin, as in any ecosystem, requires adoption of an interdisciplinary approach that considers species diversity patterns in concert with ecological processes.

Synthesis of historic and contemporary data on faunal distributions, vegetation, and hydrology may contribute meaningfully to development of holistic management and conservation strategies. For example, there is considerable debate about the extent to which species diversity per se affects ecosystem processes such as primary productivity and nutrient cycling (Pimm 1991; Loreau 2000; Tilman 1999; Waide et al. 1999; Mittelbach et al. 2001).

Some authors have proposed that many species are functionally redundant—that they serve the same purpose with respect to ecosystem processes (Walker 1992). If so, species richness may provide evolutionary 'insurance' in the event of long-term environmental change (Yachi and Loreau 1999; Tilman 2000; Loreau et al. 2001). In the short term, however, the number of species may be less critical than the functional ecological role that each species performs (Tilman et al. 2001).

Investigation of the functional role of species may prove particularly relevant to comprehensive restoration efforts. In many situations, revegetation and management of water flows largely will be sufficient to restore major ecological processes. Occasionally, however, a particular species affects key ecological processes to an extent that greatly exceeds what would be predicted from its abundance or biomass (Mills et al. 1993; Fauth 1999). Maintenance of such 'keystone' species (see Table 1) may be critical to achieving restoration success.

Because large-scale disturbance regimes also help to maintain ecological processes, reinstating those perturbations often is considered to be a major restoration goal in its own right. Maintaining viable populations of some native species also may require reestablishment of natural cycles of fire (Covington et al. 1997; Fulé and Covington 1999) and flooding (Lake 1995; Smith 1998; Meretsky et al. 2000; Richter and Richter 2000). Clearly, manipulation of disturbance cycles, let alone restoration of historic patterns, can be prohibitively expensive and politically contentious. Although actions taken to return disturbance processes to an ecosystem may have variable success with respect to the status of target species (Sher et al. 2000; Walters et al. 2000; Swengel 2001; Gabbe et al. 2002), those actions have considerable ecological benefits at other levels. Efforts to understand interactions between the composition, structure and function

of ecosystems not only inform ecological theory, but are central to the development of effective management frameworks and strategies for ecosystem maintenance and restoration.

ACKNOWLEDGMENTS

LITERATURE CITED

Andelman, S. J., and W. F. Fagan. 2000. Umbrellas and flagships: efficient conservation

surrogates, or expensive mistakes? Proceedings of the National Academy of Sciences

97:5954–5959.

Angermeier, P. L., and J. R. Karr.1994. Biological integrity versus biological diversity as policy

directives. Bioscience **44**:690–697.

Austin, M. P., A. O. Nicholls, and C. R. Margules. 1990. Measurement of the realized qualitative

niche: Environmental niches of five *Eucalyptus* species. Ecological Monographs **60**:161–

177.

Bennett, A.F. 1999. Linkages in the landscape. The roles of corridors and connectivity in wildlife

conservation. International Union for the Conservation of Nature, Gland, Switzerland.

Boggs, C. L., and D. D. Murphy. 1997. Community composition in mountain ecosystems:

climatic determinants of montane butterfly distributions. Global Ecology and

Biogeography Letters **6**:39–48.

Braithwaite, L. W., M. P. Austin, M. Clayton, J. Turner, and A. O. Nichols. 1989. On predicting

the presence of birds in *Eucalyptus* forest types. Biological Conservation **50**:33–50.

Brown, E. R., technical editor. 1985. Management of fish and wildlife habitats in forests of

western Oregon and Washington. USDA Forest Service R6-F&WL-192-1985. Portland,

Oregon, USA.

Brown, J. H. 1971. Mammals on mountaintops: non-equilibrium insular biogeography. American

Naturalist **105**:467–478.

_____. 1978. The theory of insular biogeography and the distribution of boreal mammals and

birds. Great Basin Naturalist Memoirs **2**:209–228.

Busby, J. R. 1991. BIOCLIM—a bioclimatic analysis and predictive system. Pages 64–68 *in* C. R. Margules and M. P. Austin, editors. Nature conservation: cost-effective biological surveys and data analysis. CSIRO, Canberra, Australia.

Caicco, S. L., J. M. Scott, B. Butterfield, and B. Csuti. 1995. A gap analysis of the management status of the vegetation of Idaho (U.S.A.). Conservation Biology **9**:498-511.

Cameron, A. C., and P. K. Trivedi. 1998. Regression analysis of count data. Cambridge University Press, Cambridge, United Kingdom.

Caro, T. M., and G. O'Doherty. 1999. On the use of surrogate species in conservation biology. Conservation Biology **13**:805–814.

Carroll, S. S., and D. L. Pearson. 1998. Spatial modeling of butterfly species richness using tiger beetles (Cicindelidae) as a bioindicator taxon. Ecological Applications **8**:531–543.

Chevan, A., and M. Sutherland. 1991. Hierarchical partitioning. The American Statistician **45**:90–96.

Christopher, R. D., and M. Fugate. 2001. *Branchinecta hiberna*, a new species of fairy shrimp (Crustacea: Anostraca) from western North America. Western North American Naturalist **61**:11–18.

Cody, M. L. 1986. Diversity, rarity, and conservation in Mediterranean-climate regions. Pages 122–152 *in* M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts, USA.

Coleman, F. C., and S. L. Williams. 2002. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends in Ecology and Evolution **17**:40–44.

Cooper, S. D., S. Diehl, K. Kratz, and O. Sarnelle. 1998. Implications of scale for patterns and processes in stream ecology. Australian Journal of Ecology **23**:27-40.

Covington, W. W., P. Z. Fulé, M. M. Moore, S. C. Hart, T. E. Kolb, J. N. Mast, S. S. Sackett, and M. R. Wagner. 1997. Restoring ecosystem health in ponderosa pine forests of the southwest. Journal of Forestry **95**:23–29.

Dennis, R. L. H. 1993. Butterflies and climate change. Manchester University Press, Manchester, UK.

_____, and T. G. Shreeve. 1989. Butterfly wing morphology variation in the British Isles: the influence of climate, behavioural posture and the hostplant-habitat. Biological Journal of the Linnaean Society **38**:323–348.

Diamond, J. 1975. The island dilemma: lessons of modern biogeographic studies for the design of nature reserves. Biological Conservation **7**:129–146.

Dobkin, D. S., and B. A. Wilcox. 1986. Analysis of natural forest fragements: riparian birds in the Toiyabe Mountains, Nevada. Pages 293–299 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, USA.

Dunham, J. B., G. L. Vinyard, and B. E. Rieman. 1997. Habitat fragmentation and extinction risk of Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*). North American Journal of Fisheries Management **17**:910–917.

_____, M. M. Peacock, B. E. Rieman, R. E. Schroeter, and G. L. Vinyard. 1999. Local and geographic variability in the distribution of stream-living Lahontan cutthroat trout. Transactions of the American Fisheries Society **128**:875–889.

_____, B. E. Rieman, and J. T. Peterson. 2002. Patch-based models of species occurrence: lessons from salmonid fishes in streams. Pages 327–334 *in* J. M. Scott, P. J. Heglund, M.

L. Morrison, M. Raphael, J. Haufler, and B. Wall, editors. Predicting species occurrences: issues of scale and accuracy. Island Press, Covelo, California, USA.

_____, R. E. Schroeter, and B. E. Rieman. In review. Predicting the distribution of Lahontan cutthroat trout in relation to maximum stream temperatures. North American Journal of Fisheries Management.

Ehrlich, P. R., D. S. Dobkin, and D. Whey. 1988. The birder's handbook. Simon and Schuster, New York, New York, USA.

Fagan, W. F., and P. M. Kareiva. 1997. Using compiled species lists to make biodiversity comparisons among regions: a test case using Oregon butterflies. Biological Conservation **80**:249–259.

Fauth, J. E. 1999. Identifying potential keystone species from field data—an example from temporary ponds. Ecology Letters **2**:36–43.

Fleishman, E., G. T. Austin, and D. D. Murphy. 1997. Natural history and biogeography of the butterflies of the Toiyabe Range, Nevada (Lepidoptera: Papilionoidea). Holarctic Lepidoptera **4**:1–18.

_____, G. T. Austin, and A. D. Weiss. 1998. An empirical test of Rapoport's rule: elevational gradients in montane butterfly communities. Ecology **79**:2482–2493.

_____, D. D. Murphy, and P. F. Brussard. 2000. A new method for selection of umbrella species for conservation planning. Ecological Applications **10**:569–579.

_____, G. T. Austin, and D. D. Murphy. 2001a. Biogeography of Great Basin butterflies: revisiting patterns, paradigms, and climate change scenarios. Biological Journal of the Linnean Society **74**:501–515.

_____, R. Mac Nally, J. P. Fay, and D. D. Murphy. 2001b. Modeling and predicting species occurrence using broad-scale environmental variables: an example with butterflies of the Great Basin. Conservation Biology **15**:1674–1685.

_____, R. B. Blair, and D. D. Murphy. 2001c. Empirical validation of a method for umbrella species selection. Ecological Applications **11**:1489–1501.

_____, and R. Mac Nally. 2004. Linking models of species occurrence and landscape reconstruction. Transactions of the Western Section of the Wildlife Society: in press.

Franklin, J. F. 1988. Structural and functional diversity in temperate forests. Pages 166–175 *in* E. O. Wilson, editor. Biodiversity. National Academy Press, Washington, D.C., USA.

Freitag, S., A. S. van Jaarsveld, and H. C. Biggs. 1997. Ranking priority biodiversity areas: an iterative conservation value-based approach. Biological Conservation **82**:263–272.

Fulé, P. Z., and W. W. Covington. 1999. Fire regime changes in La Michilía Biosphere Reserve, Durango, Mexico. Conservation Biology **13**:640–652.

Gabbe, A. P., S. K. Robinson, and J. D. Brawn. 2002. Tree-species preferences of foraging insectivorous birds: implications for floodplain restoration. Conservation Biology **16**:462–470.

Garth, J. S., and J. W. Tilden. 1986. California butterflies. University of California Press, Berkeley, California, USA.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club **53**:7–26.

Grayson, D. K. 1993. The desert's past: a natural prehistory of the Great Basin. Smithsonian Institution Press, Washington, D.C., USA.

_____, and S. D. Livingston. 1993. Missing mammals on Great Basin mountains: Holocene extinctions and inadequate knowledge. Conservation Biology **7**:527–532.

_____, and D. B. Madson. 2000. Biogeographic implications of recent low-elevation recolonization by *Neotoma cinerea* in the Great Basin. Journal of Mammalogy **81**:1100–1105.

_____. 2000. Mammalian responses to Middle Holocene climatic change in the Great Basin of the western United States. Journal of Biogeography **27**:181–192.

Guisan, A., J. I. Holten, R. Spichiger, and L. Tessier, editors. 1995. Potential ecological impacts of climate change in the Alps and Fennoscandian mountains. Conservatory and Botanical Garden of Geneva, Geneva, Switzerland.

_____, and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling **135**:147–186.

Gustafsson, L. 2000. Red-listed species and indicators: vascular plants in woodland key habitats and surrounding production forests in Sweden. Biological Conservation **92**:35–43.

Hall, E. R. 1946. Mammals of Nevada. University of California Press, Berkeley, California, USA.

Hansen, A. J., and D. L. Urban. 1992. Avian response to landscape pattern: the role of species' life histories. Landscape Ecology **7**:163–180.

Hanski, I., and M. E. Gilpin, editors. 1997. Metapopulation biology. Academic Press, San Diego, California, USA.

_____, A. Moilanen, T. Pakkala, and M. Kuussaari. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. Conservation Biology **10**:578–590.

Hepworth, D. K., M. J. Ottenbacher, and L. N. Berg. 1997. Distribution and abundance of native Bonneville cutthroat trout (*Oncorhynchus clarki utah*) in southwestern Utah. Great Basin Naturalist **57**:11–20.

Hershler, R. 1998. A systematic review of the hydrobiid snails (Gastropoda: Rissooidea) of the Great Basin, western United States. Part I. Genus *Pyrgulopsis*. Veliger **41**:1–132.

_____. 1999. A systematic review of the hydrobiid snails (Gastropoda: Rissooidea) of the Great Basin, western United States. Part II. Genera *Colligyrus*, *Eremopyrgus*, *Fluminicola*, *Pristinicola*, and *Tryonia*. Veliger **42**:306–337.

Hubbs, C. L., and R. R. Miller. 1948. The zoological evidence: correlation between fish distribution and hydrographic history in the desert basins of western United States. Pages 17–166 *in* The Great Basin with emphasis on glacial and postglacial times. Bulletin of University of Utah **30**.

Huntley, B. 1991. How plants respond to climate change: migration rates, individuals and the consequences for plant communities. Annals of Botany **67**:15–22.

Huxel, G. R., and A. Hastings. 1999. Habitat loss, fragmentation, and restoration. Restoration Ecology **7**:309–315.

Iftner, D. C., J. A. Shuey, and J. V. Calhoun. 1992. Butterflies and skippers of Ohio. Ohio Biological Survey Bulletin New Series **9**(1).

Jackson, L. J., A. S. Trebitz, and K. L. Cottingham. 2000. An introduction to the practice of ecological modelling. BioScience **50**:694-706.

Johnson, N. K. 1978. Patterns of avian geography and speciation in the Intermountain Region. Great Basin Naturalist Memoirs **2**:137-159.

Jones, C. G., J. H. Lawton, and M. Shacak. 1994. Organisms as ecosystem engineers. Oikos **69**:373–386.

_____. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology **78**:1946–1957.

Kingsolver, J. G. 1983. Thermoregulation and flight in *Colias* butterflies: elevational patterns and mechanistic limitations. Ecology **64**:534–545.

_____. 1989. Weather and the population dynamics of insects: integrating physiological and population ecology. Physiological Zoology **62**:314–334.

Kremen, C. 1994. Biological inventory using target taxa: a case study of the butterflies of Madagascar. Ecological Applications **4**:407–422.

Kulkoyluoglu, O. 2000. Distribution and ecology of freshwater Ostracoda (Crustacea) collected from springs of Nevada, Idaho, and Oregon: a preliminary study. Western North American Naturalist **60**:291–303.

Kupfer, J. A., and D. M. Cairns. 1996. The suitability of montane ecotones as indicators of global climatic change. Progress in Physical Geography **20**: 253–272.

Lake, P. S. 1995. Of floods and droughts: river and stream ecosystems of Australia. Pages 659–690 *in* C. E. Cushing, K. W. Cummins, and G. W. Minshall, editors. River and Stream Ecosystems 22. Elsevier, Amsterdam, Netherlands.

Lambeck, R. J. 1997. Focal species: a multi-species umbrella for nature conservation. Conservation Biology **11**:849–856.

Landres, P. B. 1992. Ecological indicvators: panacea or liability? Pages 1295-1318 *in* D. H. McKenzie, D. E. Hyatt, and V. J. McDonald, editors. Ecological indicators, Volume 2. Elsevier Applied Science, New York, New York, USA.

_____, J. Verner, and J. W. Thomas. 1988. Critique of vertebrate indicator species. Conservation Biology **2**:316–328.

Lawlor, T. E. 1998. Biogeography of Great Basin mammals: paradigm lost? Journal of Mammalogy **79**:1111–1130.

Leader-Williams, N., and H.T. Dublin. 2000. Charismatic megafauna as 'flagship species.' Pages 53–80 *in* A. Entwistle and N. Dunstone, editors. Priorities for the conservation of mammalian diversity: has the panda had its day? Cambridge University Press, Cambridge, UK.

Lindenmayer, D. B., C. R. Margules, and D. B. Botkin. 2000. Indicators of biodiversity for ecological sustainable management. Conservation Biology **14**:941–950.

_____, R. B. Cunningham, M. T. Tanton, A. P. Smith, and H. A. Nix. 1990. Habitat requirements of the mountain brushtail possum and the greater glider in the montane ash-type eucalypt forests of the central highlands of Victoria (Australia). Australian Wildlife Research **17**:467–478.

Loder, N., K. J. Gaston, and H. R. Arnold. 1998. Body size and feeding specificity: macrolepidoptera in Britain. Biological Journal of the Linnean Society **63**:121–139.

Lomolino, M. V. 1996. Investigating causality of nestedness of insular communities: selective immigrations or extinctions? Journal of Biogeography **23**:699–703.

Longino, J. T., and R. K. Colwell. 1997. Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. Ecological Applications **7**:1263–1277.

Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos **91**:3–17.

_____, S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science **294**:804–808.

Mac Nally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between—and reconciliation of—'predictive' and 'explanatory' models. Biodiversity and Conservation **9**:655–671.

_____, A. F. Bennett, G. W. Brown, L. F. Lumsden, A. Yen, S. Hinkley, P. Lillywhite, and D. Ward. 2002. How well do ecosystem-based planning units represent different components of biodiversity? Ecological Applications **12**:900–912.

_____, and E. Fleishman. 2002. Using 'indicator' species to model species richness: model development and predictions. Ecological Applications **12**:79–92.

_____, _____, J.P. Fay, and D.D. Murphy. 2003. Modeling butterfly species richness using mesoscale environmental variables: model construction and validation. Biological Conservation **110**:21–31.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, New Jersey, USA.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature **405**:243–253.

McDonald, K. A., and J. H. Brown. 1992. Using montane mammals to model extinctions due to climate change. Conservation Biology **6**:409–415.

McLaughlin, J. F., J. J. Hellmann, C. L. Boggs, and P. R. Ehrlich. 2002. Climate change hastens population extinctions. Proceedings of the National Academy of Sciences (USA) **99**:6070–6074.

Meffe, G. K., and C. R. Carroll. 1994. Principles of conservation biology. Sinauer, Sunderland, Massachusetts, USA.

Meretsky, V. J., D. L. Wegner, and L. E. Stevens. 2000. Balancing endangered species and ecosystems: a case study of adaptive management in Grand Canyon. Environmental Management **25**:579–586.

Miller, J. R., and P. Cale. 2000. Behavioral mechanisms and habitat use by birds in a fragmented agricultural landscape. Ecological Applications **10**:1732–1748.

Mills, L. S., M. E. Soule, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. Bioscience **43**:219–224.

Minckley, W. L., and J. E. Deacon. 1991. Western fishes and the real world: the enigma of endangered species revisited. Pages 405–414 *in* W. L. Minckley and J. E. Deacon, editors. Battle against extinction: native fish management in the American West. University of Arizona Press, Tucson, USA.

Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson,and L. Gough. 2001. What is the observed relationship between species richness and productivity? Ecology **82**:2381–2396.

Moilanen, A. 2000. The equilibrium assumption in estimating the parameters of metapopulation models. Journal of Animal Ecology **69**:143–153.

Murphy, D. D., and S. B. Weiss. 1992. Effects of climate change on biological diversity in western North America: species losses and mechanisms. Pages 355–268 *in* R. L. Peters and T. E. Lovejoy, editors. Global warming and biological diversity. Yale University Press, New Haven, Connecticut, USA.

Myers, N. 1986. Tropical deforestation and a mega-extinction spasm. Pages 394–409 *in* M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts, USA.

Neave, H. M., and T. W. Norton. 1998. Biological inventory for conservation evaluation IV: composition, distribution and spatial prediction of vegetation assemblages in southern Australia. Forest Ecology and Management **106**:259–281.

Niemi, G. J., J. M. Hanowski, A. R. Lima, T. Nicholls, and N. Weiland. 1997. A critical analysis on the use of indicator species in management. Journal of Wildlife Management **61**:1240–1252.

Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchial approach. Conservation Biology **4**:355–364.

_____, M. A. O'Connel, and D. D. Murphy. 1997. The science of conservation planning. Island Press, Washington, D.C., USA.

Oliver, I., and A. J. Beattie. 1996. Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. Ecological Applications **6**:594–607.

Palik, B. J., P. C. Goebel, L. K. Kirkman, and L. West. 2000. Using landscape hierarchies to guide restoration of disturbed ecosystems. Ecological Applications **10**:189–202.

Pearson, D. L. 1994. Selecting indicator taxa for the quantitative assessment of biodiversity. Philosophical Transactions of the Royal Society of London—Series B: Biological Sciences **345**:75–79.

Pimm, S. L. 1991. The balance of nature? University of Chicago Press, Chicago, USA.

Pollard, E. 1988. Temperature, rainfall and butterfly numbers. Journal of Applied Ecology **25**:819–828.

Prendergast, J. R. 1997. Species richness covariance in higher taxa—empirical tests of the biodiversity indicator concept. Ecography **20**:210–216.

Rieman, B. E., P. F. Hessburg, D. C. Lee, R. F. Thurow, and J. R. Sedell. 2000. Toward an integrated classification of ecosystems: defining opportunities for managing fish and forest health. Environmental Management **25**:425–444.

Reichman, O. J., and E. W. Seabloom. 2002. The role of pocket gophers as subterranean ecosystem engineers. Trends in Ecology and Evolution **17**:44–49.

Richter, B. D., and H. E. Richte. 2000. Prescribing flood regimes to sustain riparian ecosystems along meandering rivers. Conservation Biology **14**:1467–1478.

Ricketts, T. H., E. Dinerstein, D. M. Olson, and C. Loucks. 1999. Who's where in North America? BioScience **49**:369–381.

Ricklefs, R., and D. Schluter. 1993. Species diversity in ecological communities. University of Chicago Press, Chicago, Illinois, USA.

Risser, P. G. 1995. The status of the science examining ecotones. Bioscience **45**: 318–325.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.

Rubinoff, D. 2001. Evaluating the California gnatcatcher as an umbrella species for conservation of southern California coastal sage scrub. Conservation Biology **15**:1374–1383.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science **287**:1770–1774.

Scheider, S. H., L. Mearns, and P. H. Gleick. 1992. Climate-change scenarios for impact assessment. Pages 38–55 *in* R. L. Peters and T. E. Lovejoy, editors. Global warming and biological diversity. Yale University Press, New Haven, Connecticut, USA.

Schwarz, G. 1978. Estimating the dimension of a model. Annals of Statistics **6**:461–464.

Scott, C. T. 1998. Sampling methods for estimating change in forest resources. Ecological Applications **8**:228–233.

Scott, J. A. 1986. The butterflies of North America. Stanford University Press, Stanford, California, USA.

Scott, J. M., P. J. Heglund, M. Morrison, M. Raphael, J. Haufler, and B. Wall, editors. 2002. Predicting species occurrences: issues of scale and accuracy. Island Press, Covello, California, USA.

Shafer, C. L. 1990. Nature reserves, island theory and conservation practice. Smithsonian Institution Press, Washington, D.C., USA.

Sher, A. A., D. L. Marshall, and S. A. Gilbert. 2000. Competition between native *Populus deltoides* and invasive *Tamarix ramosissima* and the implications for reestablishing flooding disturbance. Conservation Biology 14:1744–1754.

Smith, G. R. 1978. Biogeography of intermountain fishes. Great Basin Naturalist Memoirs **2**:17–42.

Smith, D. I. 1998. Water in Australia. Resources and management. Oxford University Press, Oxford, UK.

Smith, S. D., T. E. Huxman, S. F. Zitzer, T. N. Charlet, D. C. Housman, J. S. Coleman, L. K. Fenstermaker, J. R. Seemann, and R. S. Nowak. 2000. Elevated CO_2 increases productivity and invasive species success in an arid ecosystem. Nature **408**:79–82.

Springer, P., and C. L. Boggs. 1986. Resource allocation to oocytes: heritable variation with
altitude in *Colias philodice eriphyle* (Lepidoptera). American Naturalist **127**:252–256.

Stohlgren, T. J., J. F. Quinn, M. Ruggiero, and G. S. Waggoner. 1995. Status of biotic
inventories in US national parks. Biological Conservation **71**:97–106.

Swengel, A. B. 2001 A literature review of insect responses to fire, compared to other
conservation managements of open habitat. Biodiversity and Conservation **10**:1141–
1169.

Tausch, R. J., P. E. Wigand, and B. Burkhardt. 1993. Viewpoint: plant community thresholds,
multiple steady states, and multiple successional pathways: legacy of the Quarternary.
Journal of Range Management **46**:439–447.

Thomas, J. A. 1995. The conservation of declining butterfly populations in Britain and Europe:
priorities, problems and successes. Biological Journal of the Linnean Society
56(Supplement):55–72.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general
principles. Ecology **80**:1455–1474.

_____. 2000. Causes, consequences and ethics of biodiversity. Nature **405**:208–211.

_____, P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and
productivity in a long-term grassland experiment. Science **294**:843–845.

United States Environmental Protection Agency (US EPA). 1999. Climate change and Nevada.
Publication EPA 236-F-98-007o.
http://www.epa.gov/globalwarming/impacts/stateimp/nevada/index.html.

Van Devender, T. R., R. S. Thompson, and J. L. Betancourt. 1987. Vegetation history of the
deserts of southwestern North America: the nature and timing of the Late Wisconsin—

Holocene transition. Pages 323–352 *in* W. F. Ruddiman and H. E. Wright, Jr., editors. North America and adjacent oceans during the last deglaciation. Geological Society of North America, Boulder, Colorado, USA.

Waide, R. B., M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday, and R. Parmenter. 1999. The relationship between productivity and species richness. Annual Review of Ecology and Systematics **30**:257–300.

Walker, B. 1992. Biodiversity and ecological redundancy. Conservation Biology **6**:18–23.

Walters, C., J. Korman, L. E. Stevens, and B. Gold. 2000. Ecosystem modeling for evaluation of adaptive management policies in the Grand Canyon. Conservation Ecology **4(2)** online (http://www.consecol.org/Journal/).

Weaver, J. S., and M. J. Myers. Two new species of Caddisflies of the genus *Lepidostoma* Rambur (Trichoptera: Lepidostomatidae) from the Great Basin. Aquatic Insects 20: 189–195.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology **3**:385–397.

Wilcox, B. A. 1980. Insular ecology and conservation. Pages 95–117 *in* M. E. Soulé and B. A. Wilcox, editors. Conservation Biology: an evolutionary—ecological perspective. Sinauer, Sunderland, Massachusetts, USA.

_____, D. D. Murphy, P. R. Ehrlich, and G. T. Austin. 1986. Insular biogeography of the montane butterfly fauna in the Great Basin: comparison with birds and mammals. Oecologia **69**:188–194.

Yachi, S., and M. Loreau. 1991. Biodiversity and ecosystem productivity in a fluctutating environment: the insurance hypothesis. Proceedings of the National Academy of Sciences (USA) **96**:1463–1468.

Young, M. K., editor. 1995. Conservation assessment for inland cutthroat trout. U.S. Forest

Service General Technical Report RM-256. Rocky Mountain Research Station, Fort

Collins, Colorado, USA.

Zacharias, M. A., and J. C. Roff. 2001. Use of focal species in marine conservation and

management: a review and critique. Aquatic Conservation: Marine and Freshwater

Ecosystems **11**:59–76.

Table 1. Definitions of different categories of surrogate species.

Category	Definition
umbrella	Species whose conservation confers a protective umbrella to numerous co-occurring species.
indicator	Species whose distribution, abundance, or population dynamics can serve as substitute measures of the status of other species or environmental attributes.
keystone	Species that significantly affects one or more key ecological processes or elements to an extent that greatly exceeds what would be predicted from its abundance or biomass.
ecosystem engineer	Species that, via morphology or behavior, modifies, maintains, and creates habitat for itself and other organisms.
flagship	Charismatic species that serves as a symbol to generate conservation awareness and action.
focal species	Species used, for any reason, to help understand, manage, or conserve ecosystem composition, structure, or function.

FIGURE LEGENDS

Figure 1. Birch Canyon as photographed by members of the Linsdale expedition in the 1930s, and as photographed by Peter Goin in 2001.

Figure 2. Fitted species richness versus observed species richness of butterflies in the Toquima Range. Fitted values are based on a model of species richness as a function of elevation, the square of elevation, and a measure of local topographic heterogeneity.

Figure 3. Species occurrence rates (proportion of inventory locations in which each species was found) in the modeling-building (Toquima Range) versus validation (Shoshone Mountains) data sets (Spearman's $r_s = 0.56$, $P < 0.001$).

Figure 4. Proportion of species in a given taxonomic group and ecosystem that would be protected using umbrella species from a different taxonomic group (open bars) versus species drawn at random from the same taxonomic group (black bars). Bfs, butterflies; shrub, coastal chaparral shrubland in California; forest, broadleaf forest in Ohio.

Figure 5. Mean predicted species richness versus observed species richness values for all model validation sites in the Shoshone Mountains. Predictions were obtained using a model of species richness as a function of five 'indicator' species.

FIGURE 1. Photograph of Birch Canyon (Toiyabe Range, Lander Co., NV) as taken by the

Linsdale expedition in 1930, and rephotgraph of the same location by Peter Goin in 2001.

Permission to use these images has been obtained from the Museum of Comparative

Zoology, University of California, Berkeley and from Peter Goin.

FIGURE 2
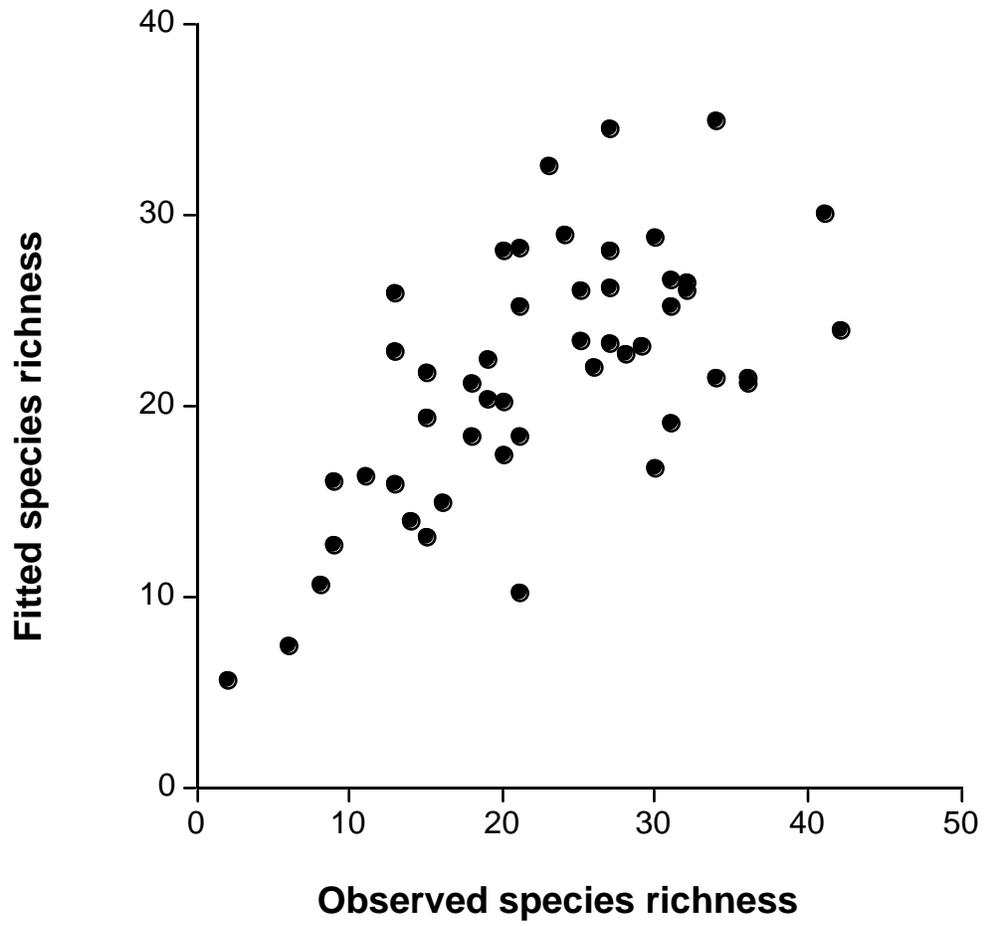
FIGURE 3

FIGURE 4

FIGURE 5