

CHAPTER Multispecies Conservation Planning on U.S. Federal Lands

3

*Barry R. Noon, Kevin S. McKelvey,
and Brett G. Dickson*

Numerous laws directly, or indirectly, mandate the conservation of all species on public lands in the United States (Goble and Freyfogle 2002, Nagle and Ruhl 2002). Key laws relevant to the management of biodiversity on federal lands include the National Forest Management Act (NFMA; Noon et al. 2003) and the Federal Endangered Species Act (ESA; 1973). However, there are also many companion laws that govern the use of these same lands that are in conflict with a goal of maximizing the conservation of species and their habitats (e.g., Multiple Use Sustained Yield Act, 1960). Consequently, land managers must balance the trade-offs between the conservation of species and the exploitation of resources for short-term human use. It is commonplace for species and people to compete for the same set of limiting resources.

Most prominent among the laws protecting species and their habitats is the ESA, which stipulates that no federal action, or federally sanctioned action, on public or private lands shall jeopardize the continued existence of any species. Given the importance of maintaining biodiversity for both ethical and practical reasons—for example, to sustain environmental goods and services critical to human welfare (Hooper et al. 2005)—it is imperative that the scientific community provide land managers with the knowledge and tools needed to meet their conservation mandate.

Despite the importance of multispecies conservation planning from both a legal and practical perspective, we believe that current scientific understandings and methods provide only limited guidance to land managers. Studying multiple species and the range of spatial and temporal scales that they span has been identified as one of the key challenges in conservation biology (e.g., MacNally et al. 2002, Fischer et al. 2004a). However, as we discuss in the following text, progress is slow in part due to the complexity of the problem and to the lack of sufficient information on the abundance, distribution, life histories, and ecological relations of most species. In addition, much conservation science has been crisis driven, responding to the conservation needs of individual species experiencing threats to their persistence. A clear expression of the crisis-driven nature of conservation biology is that the vast majority of scientific

publications in this discipline focus on individual species at risk or small groups of imperiled species sharing similar life histories or habitats. The difficulties associated with directly evaluating multiple species coupled with this single-species emphasis in the primary literature has led to the adoption of surrogate measures; all studies that we are aware of that propose guidelines for multispecies conservation planning ultimately default to surrogate-based approaches. These surrogates tend to be based on small sets of species with presumed importance to general diversity and/or vegetation-based proxies. Both of these approaches, however, rely on largely untested premises.

In this chapter, we review past approaches and some noteworthy recent advances in multispecies conservation planning. We are encouraged by recent attempts to extend conservation planning from single to multiple species but find that even the most innovative new methods fall far short of addressing the hundreds to thousands of species found in most management areas. As discussed in the following sections, the challenges to multispecies conservation planning are great but not insurmountable if rigorous surrogate-based approaches are adopted.

THE CHALLENGE OF MULTISPECIES CONSERVATION PLANNING

In the following section we briefly review theories and general principles from ecology that suggest, at some level of resolution, that all species are fundamentally distinct. The purpose of this section is not to challenge these concepts but rather to evaluate whether they present insurmountable challenges to multispecies conservation planning on federal lands. Our discussion is mostly general and applies broadly to plant and animal species. However, the context of our discussion throughout this chapter is mostly on the conservation of vertebrate communities.

Niche Theory

We need look no further than ecological theory to understand why multispecies conservation planning is so difficult and why it seems impractical in most circumstances. Based on niche theory (e.g., Hutchinson 1957, Pulliam 2000), no two species can long occupy the same niche. Thus, all coexisting, sympatric species must differ along at least one critical niche dimension. Persistence for a species whose niche is included as a subset of another species is possible only until a critical, shared resource becomes limiting. Adjunct to this theory is the understanding that there must be some limit to the similarity of coexisting species (MacArthur 1967). The implication of niche theory to multispecies conservation planning is that it will be impossible to manage for all species unless all

relevant resources (i.e., niche axes) are sustained at sufficient levels to support viable populations.

Trophic Structure

Most species can be unambiguously positioned within a food web in terms of what they eat and who eats them. The foundational species for all food webs are the autotrophic species which fix carbon via the process of photosynthesis and create food for herbivorous species. Herbivores, in turn, support one or more trophic levels of predatory species. As a result, it is impossible to consider the conservation of any species without also considering its contribution to a community food web and its reliance on other species. In most ecological communities, many species occupy a given trophic level, and functional redundancies within any given food web are expected (Pimm 2002). However, due to niche-based differences, each species contributes in some unique way to food web dynamics and the stability of trophic hierarchies.

Allometric Scaling Relationships

The view of the niche as a static multidimensional resource space (Hutchinson 1957) does not explicitly incorporate concepts of time and space that are essential considerations for multispecies conservation planning. Scaling relationships are important topics in ecology—for example, in metapopulation biology (e.g., With 2004) and landscape ecology (e.g., Wiens 1989), where key areas of research focus on dispersal abilities and movement behaviors in heterogeneous landscapes. Many studies have demonstrated that species uniquely scale their spatial environment and that patterns of space-use (area requirements) are strongly correlated with differences in body mass (Cotgreave and Harvey 1992, Silva and Downing 1994). These allometric relations presumably reflect underlying differences among species in terms of their movement behaviors and food resource requirements. For example, space-use relationships differ predictably between birds and mammals and probably reflect the much greater movement ability provided by flight.

Differences in temporal scaling are also related to differences in body mass and taxonomy (McArdle et al. 1990). Such differences often lead to differences in demography. For example, age at first reproduction and life span have clear relationships to reproductive potential and survival rates, respectively. These aspects of life history, as well as growth potential, have long been recognized as being related to body mass (Peters 1983) and have led to a somewhat simplistic partitioning of species into r- or K-selected life histories. Even though allometric scaling relationships demonstrate important differences among species, they offer one possible way to group species according to similarities in space use and temporal scaling of the environment (Theobald and Hobbs 2002). We revisit this point below.

Demography

At some level of resolution, all species differ in the fine points of their demography. For example, species differ in terms of their life history schedules—age- or stage-specific birth and survival rates—and in differences in sensitivity of population growth to changes in various vital rates (e.g., Wisdom et al. 2000). Such differences can lead to differential sensitivities to various environmental threats (e.g., habitat loss and fragmentation) and thus to different extinction likelihoods in the face of environmental change. In addition, some species persist as metapopulations, where persistence is determined not just by local population dynamics but by the relative extinction and colonization rates among local populations. These rates, in turn, are affected by distance among local populations, characteristics of the landscape matrix that separates these populations, and on the ability of individuals to move among local populations. The likelihood of successful movement among spatially disjunct populations will vary greatly by species due to both their mobility and fecundity (Noon and McKelvey 1996). Further, habitat requirements among species can be widely divergent, and the population-level effects associated with a particular landscape configuration will also vary between species. This variability, coupled with ongoing habitat loss and fragmentation, suggests that each species may have unique conservation requirements expressed as the amount and spatial arrangement of its habitat on the landscape.

Movement and Landscape Connectivity

Animal movement is motivated by a complex suite of environmental cues and ecological processes, including the location of conspecifics, prey, and competitors in time and space. However, the movement patterns of species cannot be separated from the habitat and landscape features that connect individuals or populations. Taylor et al. (2006:29) characterize landscape connectivity as a dynamic emergent property resulting from “the interaction between a behavioral process (movement) and the physical structure of the landscape.” For multiple species on a heterogeneous landscape, connectedness depends on the organisms under investigation and how relevant landscape attributes are distributed. Due to differences in life and ecological histories (e.g., body size, mobility, migration rates), co-occurring species can simultaneously perceive a landscape as both connected and disconnected (Pearson et al. 1996, With et al. 1997, Taylor et al. 2006). Thus, the methods used to quantify connectivity require careful consideration of how organisms differentially interact with the landscape during movement events (Tischendorf and Fahrig 2000) and how these events are influenced by management or land-use activities. With increasing levels of habitat loss and fragmentation, for example, dispersal events can be disrupted (King and With 2002), forcing species to navigate novel environments with features that may threaten their distribution or persistence (Gardner and Gustafson 2004, Aurambout et al. 2005).

BROAD STRATEGIES FOR MULTISPECIES CONSERVATION PLANNING

Given the preceding discussion, it is clear that all species are fundamentally distinct from one another in at least one significant dimension. Taken at face value, this recognition makes the challenge of managing for the conservation of all or most species appear insurmountable. The task seems all the more daunting in the context of an ongoing and accelerating human-caused transformation of the landscape. However, the necessity of striving to conserve as much biodiversity as possible remains a scientific, legal, and ethical imperative. As a result, the challenge of multispecies conservation planning becomes redefined in terms of identifying and implementing management strategies that will achieve some constrained maximal conservation outcome. The solution will be unavoidably constrained for at least three reasons. First, only some fraction of the available landscape will be devoted to a primary objective of species conservation. Second, beyond the land itself, the amount of resources allocated to conservation will compete with other societal objectives. Third, the earth's resources are finite, and all users are participants in a zero-sum game; resources exploited for direct human uses are generally not available to support the rest of the natural world (Vitousek et al. 1997).

Most comprehensive conservation strategies are similar in that they invoke a set of key conservation planning principles. For example, the selection of reserve sites is based on characteristics such as their representation, resilience, and redundancy (Shaffer and Stein 2000) or complementarity, irreplaceability, and vulnerability (Sarkar et al. 2006). A conservation strategy has representation and complementarity if it provides for habitat for each species at one or more locations on the landscape. Resilience means that reserve areas are sufficiently large so as to incorporate normal disturbance regimes without compromising the persistence of any species. Redundancy implies that the spatial distribution of species and their habitats is sufficiently broad that the dynamics of local populations of a species are spatially decoupled. Irreplaceability puts an emphasis on sites that support unique species found nowhere else, and vulnerability ranks sites by their degree of threat. Collectively, these characteristics act as constraints on site selection.

The design of most comprehensive multispecies conservation planning efforts invoke some form of a “coarse filter” and/or “fine filter” approach (e.g., Hunter et al. 1988, Hunter 1991, Noss and Cooperrider 1994, Noss 1996, Haufler et al. 1996, Cushman et al. 2008). The coarse filter is usually considered to function at broad spatial scales (100s to 1000s of km²) and to reflect underlying ecological processes that are operative over long temporal scales (decades to centuries). The fine filter is most often used in reference to individual species or groups of functionally related species (e.g., species guilds, Block et al. 1987). In general, coarse filters are composed of fairly broad ecological, often vegetative, classifications and do not utilize direct measurements of vertebrate species.

Some authors have referred to a collection of surrogate species as a coarse filter of sorts (e.g., Tognelli 2005). However, in our discussion, we consider all direct measures of species to represent a fine filter approach.

Filtering approaches are not necessarily confined to this coarse/fine dichotomy. Decisions concerning reserve design and location can also be cast in terms of biotic and abiotic “filters” that account for both coarse- and fine-scale processes important to biodiversity. The multiple filter analogy invokes hierarchical levels of biological organizational levels, which are strongly correlated with hierarchies of spatial scales (e.g., Poff 1997; Probst and Gustafson, this volume).

Filter-based approaches to multispecies conservation generally seek to characterize ecological systems in terms of indicators of function, structure, and composition (Lindenmayer et al. 2000). Noss (1990), for example, proposed an exhaustive set of candidate indicators based on four scales of ecological organization—landscape, community-ecosystem, population-species, and genetic—and three primary attributes of biological diversity—function, structure, and composition. Function-based indicators include direct measures of processes and their rates. Examples include primary productivity, rates of nutrient cycling, and water flows. Structure-based indicators, measured at local and landscape scales, include elements such as vegetation structural complexity, among-patch vegetation heterogeneity, landscape connectivity, and landscape pattern (i.e., the distribution and abundance of different patch types). While these metrics are often assumed to constitute a “coarse filter” because of their ability to predict broad-scale patterns of biological diversity (Hunter 1991; Haufler et al. 1996, 1999), both function- and structure-based indicators can be measured at multiple spatial scales ranging from local to regional. In addition, there are composition-based indicators that entail direct measurement at the species level and include information on each species’ distribution, life history, demography, or behavior. These are often referred to as “fine filter” assessments because they evaluate the effects of management practices on individual species (Haufler et al. 1996).

Coarse Filter Approaches

Coarse filter approaches are often based on broad-scale criteria such as climate, soils, geology, and vegetation cover types (Kintsch and Urban 2002). For example, the conservation planning framework of The Nature Conservancy uses ecoregional classifications (e.g., Bailey 1995) as an initial way of partitioning the landscape into a set of conservation areas that span the native species and ecosystems of a region (Groves et al. 2002). Ecosystems are often proposed as the appropriate level for conservation planning at broad spatial scales (Noss 1996). However, ecosystems can seldom be portrayed as discrete geographical units because they do not have tangible boundaries that allow them to be mapped (Pickett and Cadenasso 2002). Often, the boundaries established for

ecosystems are artificial and vary according to one's goals. Thus, the spatial and temporal dimensions of an ecosystem are usually user-defined, rendering them a dimensional conceptual unit (Fauth 1997). Moreover, the communities and habitat features that define ecosystems are not always neatly contained within a single jurisdictional boundary. As a result, ecosystems have limited utility as a map-based unit for conservation planning. For the purposes of conservation planning at broad spatial scales, ecosystems are often referred to as a target conservation unit, but in practice, ecosystems are usually equated with dominant vegetation communities or physical landscape features.

For example, on public lands in the Pacific Northwest, reference is made to managing the late-seral Douglas-fir ecosystem to sustain native biodiversity (Forest Ecosystem Management Assessment Team 1993). In the southeastern United States, management may be targeted to sustain key processes characteristic of bottomland hardwood forest communities. In the Rocky Mountains, we might be interested in sustaining the species and processes characteristic of alpine lake ecosystems. In order to define ecosystems and their boundaries in this way, it is common practice to partition the landscape into patch types. The default coarse filter for most public land management decisions defines patches on the basis of dominant vegetation communities and their successional stages.

If coarse filter attributes are defined as the characteristics of a vegetative patch mosaic, the relationship between these metrics and the dynamics of any animal species or group of species is at least two steps removed from reality. The first assumption is that vegetation composition and structure per se can be used as a surrogate for a species' habitat. The second is that various successional stages or structural configurations of vegetation types can be related to habitat quality and thus species abundance or probability of occurrence. Given the ubiquity of both of these assumptions, it is surprising how few formal tests have been conducted. Most of the widely used habitat relationship models, for example, are heuristic rather than quantitative (Schulte et al. 2006). The relationships between these heuristic understandings and broad landscape characteristics are often based in expert opinion (Marcot et al. 2001, Raphael et al. 2001). In many cases, consistency in expert opinion is equated to expected model performance, a tenuous assumption at best. As such, the efficacy of these approaches is entirely unknown.

Statistical explorations of multiscale habitat relationships suggest that evaluations based on broadly defined cover-types may not provide robust surrogates for multispecies distribution or abundance patterns (MacNally et al. 2002). For example, Cushman and McGarigal (2004) tested the correlations between multiscale vegetative characteristics and breeding bird abundance in three watersheds in Oregon. Data included detailed plot level information, stand type and seral stage, and compositional characteristics of the surrounding landscape. For all species, total variance explained was about 60%, with the plot variables having the greatest explanatory power. Landscape composition variables only

explained 4% of the variance in each of the three drainages. Patch characteristics alone explained 5–6% of variance in bird abundance (also see Cushman et al. 2008).

While limited in area and only pertaining to breeding birds, Cushman and McGarigal's (2004) results suggest that the efficacy of coarse filter approaches should not be assumed. It is, in fact, unlikely that proxy-on-proxy relationships will have high explanatory power, since power declines multiplicatively with each proxy step. Thus, it is unlikely that coarse filter approaches alone will be sufficient for effective multispecies conservation.

Mesofilter Approaches

Hunter (2005) recently proposed the concept of the mesofilter to bridge the gap between more traditional coarse and fine filter approaches. The mesofilter concentrates on habitat elements that are too small to be the focus of reserve design strategies, but that often may be limiting the populations of some species. Sample elements retained by the mesofilter include large logs and snags, riparian zones, seeps and springs, and rock outcrops (Schulte et al. 2006). For many species, these fine-grained habitat features may be more important than vegetation community type; however, collection of these data is limited to ground-based plots. As such, spatial mapping of these attributes and extrapolation to unsampled areas must be accomplished through statistical imputation methods (Ohmann and Gregory 2002) and the precision of model estimates will vary greatly between habitat elements.

Fine Filter Approaches

Fine filter approaches involve the direct measurement of species' spatial distribution patterns (presence/absence or abundance) rather than application of a surrogate or index metrics. However, the number of species that constitute an ecosystem is enormous. It is impossible to track them all and, even if possible, the relationships between multiple population trajectories and ecosystem function remains obscure. For these reasons, fine filter approaches address some subset of species that may go unprotected by the coarse filter or, alternatively, act as presumed surrogates for other species or the ecosystem as a whole.

Threatened, at-risk, and rare species.— A logical approach to conservation planning is to focus on those species most at risk of local or global extinction. This is the approach taken for conservation of North American bird species under The Partners in Flight program (Panjabi et al. 2005). This has also been the approach adopted for recovery planning for species listed under the ESA. For obvious reasons, the vast majority of recovery efforts for listed species have focused on single, and not multiple, species. An exception to single species planning for imperiled species has been the application of multispecies Habitat Conservation Plans to private lands affected by the ESA (Noss et al. 1997).

Perhaps the highest profile example of the imperiled species approach is the forest planning exercise that led to large changes in federal land management in the Pacific Northwest (Forest Ecology Management Assessment Team 2003). The Forest Ecology Management Assessment Team started with a reserve structure carefully designed to provide for a well-distributed population of northern spotted owls (*Strix occidentalis*; Thomas et al. 1990). This plan was then examined for adequacy in protecting a suite of additional species representing a wide variety of animals, plants, and fungi (Raphael and Molina 2007). Because of the necessary niche separation between species, the spatial extent of the reserve design expanded greatly in this process, and protections were added to areas between reserves.

Focal Species.— In the 2000 NFMA regulations applicable to Forest Service lands, focal species were defined as surrogate measures used in the evaluation of ecological sustainability, including species and ecosystem diversity (Noon and Dale 2003). The key characteristic of a focal species is that its status and trend provide insights to the integrity of the larger ecological system to which it belongs. Focal species serve an umbrella function in terms of encompassing habitats needed for many other species, play a key role in maintaining community structure or processes, are sensitive to changes likely to occur in the area, or otherwise serve as an indicator of ecological sustainability (Committee of Scientists 1999:38–39). The focal species concept described in the 2000 regulations differed subtly, but significantly, from the previous “management indicator species” concept used by the Forest Service. Rather than acting as an indicator of the outcome of a specific management prescription, the status and trend of focal species are to allow induction upward to the conservation status of entire suites of species. As such, the concept is inclusive of the variety of surrogate species concepts such as keystone, umbrella, indicator, and engineering species.

Potential Focal Species Categories.— The following is a list of species “types” that may serve as conservation targets, or surrogates for unmeasured species, for the purpose of multispecies conservation planning (see Lambeck 1997, Caro and O’Doherty 1999, Favreau et al. 2006). The unifying principle across all these categories is that the status and trend of these species types should provide information beyond their own measurement.

1. *Indicator species:* “An organism whose characteristics (presence or absence, population density, dispersion, reproductive success) are used as an index of attributes too difficult, inconvenient, or expensive to measure for other species or environmental conditions of interest” (Landres et al. 1988:317, Landres 1992). In addition, Patton (1987) described an indicator as an organism so intimately associated with particular environmental conditions that its presence indicates the existence of those conditions. Indicator species can be further broken down into three categories (Caro and O’Doherty 1999):

- *Early warning indicator*: Provides an early warning of a stressor acting on a key ecosystem process (traditional interpretation of an indicator species from ecotoxicology). For example, changes in lichen communities in forest ecosystems may act as indicators of stress arising from atmospheric pollution.
 - *Population surrogate indicator*: Species whose status and trend are indicative of the status and trends of other species. This species type is related to the guild indicator concept of Block et al. (1987).
 - *Biodiversity indicator*: A species, or more commonly a taxonomic group, that acts as a surrogate for a number of poorly known taxonomic groups.
2. *Umbrella species*: A species that needs such large areas of habitat that managing for its viability addresses the viability concerns of numerous other species with similar habitat but smaller area requirements (after Wilcox 1984). The principal requirement of an umbrella species is that its range is large compared to sympatric species. Many large-bodied, wide-ranging animals are candidate umbrella species—for example, bison in prairie ecosystems and carnivores in forested ecosystems. Additional discussions of the umbrella species concept are found in Lambeck (1997), Andelman and Fagan (2000), Fleishman et al. (2000, 2001), and Roberge and Angelstam (2004).
 3. *Keystone species*: Species which significantly affect one or more key ecological processes or elements to an extent that greatly exceeds what would be predicted from their abundance or biomass (Mills et al. 1993, Power et al. 1996). For example, sea otters prey strongly on the herbivores that consume kelp forests. Diverse kelp forests, in turn, support diverse communities of vertebrates and invertebrates.
 4. *Strong interactors*: A species whose dynamics are affected by, or greatly affect, the dynamics of other species in the community (Christianou and Ebenman 2005). Energy-maximizing predators in freshwater aquatic ecosystems often exert strong top-down control on the structure and composition of their prey communities.
 5. *Link species*: A species that occupies a key position in a food web and efficiently transfers energy and matter between trophic levels. For example, prairie dogs in grassland ecosystems efficiently convert primary plant productivity into animal biomass. Prairie dog biomass, in turn, supports a diverse predator community (Smith and Lomolino 2004). These are similar to the bottom-up members of food webs discussed by Jordán et al. (1999).

6. *Ecological engineers*: Species that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials (Jones et al. 1994, 1997). For example, beavers alter and restructure riparian habitats and greatly increase the diversity of both plant and animal communities as a consequence.

As mentioned previously, fine filter refers to the direct measurement of individual species or guilds. While fine filter measurements, being direct, would seem to be free from the proxy-on-proxy issues that plague the coarse filter, this is not the case. For the measured species, presence/absence or relative abundance measures are, in fact, proxy statistics for density or population size. They have the advantage that they are mechanistically linked to the desired measurements, but the inevitable loss of explanatory power associated with working through an index of population size rather than size itself should not be ignored. Far more critical for the purpose of multispecies monitoring, however, is the issue associated with using population trend data for one species as a proxy for the trends of many other species. The potential problems with this approach were elucidated by Landres et al. (1988) and Landres (1992) but, to our knowledge, there have been too few tests of the surrogate species approaches to fully evaluate its efficacy (Favreau et al. 2006).

Mixing Coarse and Fine Filter Approaches

Root et al. (2003) developed a multispecies conservation algorithm that assessed habitat importance for 40 species in California based on an integration of vegetation maps (the coarse filter) and wildlife habitat relationships models (the surrogate fine filter). They used data from the California GAP Analysis Project to create a vegetation polygon map where each polygon on the map was designated a habitat suitability score separately for each species. A composite map, based on the individual species maps, combined information across all species into a single value for each polygon based on the sum of the habitat suitability scores. In addition, Root et al. (2003) developed a weighted multispecies conservation score for each polygon using a weighting factor based on a formal population viability assessment or different indices of threat faced by each of the 40 species. The final map, at the scale of the entire state of California, provided a multispecies conservation score for each vegetation polygon that reflected both occurrence and degree of threat. Use of this approach requires information on the habitat relationships for each species expressed relative to the vegetation classes in the GAP database, and knowledge of how suitability varies by class. This information is available for many species from habitat relationships models but suitability ratings are based on assumed abundance relationships, which are generally unknown.

Comprehensive conservation planning is not restricted to coarse and fine filter approaches; other conceptual tools are often used to complement the filter

approach. For example, Schulte et al. (2006) reviewed conceptual tools used for multispecies conservation planning in large-scale forest management plans. They found that the concept of filters (coarse, meso, and fine) are most widely used but that other principles drawn from landscape ecology including reserve design principles, matrix management, and connectivity via networks or corridors are used to refine the filter-based approaches. However, they point out that currently there is too little empirical support at the temporal and spatial scales required for comprehensive conservation planning to support the use of any of these conceptual tools without close monitoring of the desired outcomes.

RECENT ADVANCES IN MULTISPECIES CONSERVATION PLANNING

Because multispecies conservation planning is now recognized as one of the major challenges to biodiversity conservation, there has been a significant increase in the number of researchers addressing this problem. Also, with advances in spatial modeling techniques (e.g., Guisan and Zimmerman 2000) and the increased availability of spatial data, moving from single to multiple species evaluations is increasingly possible. Because of data limitations and computing requirements, these approaches are currently limited in the number of species that can be simultaneously evaluated. However, we believe the new methods discussed in this chapter are significant for having made the important first step of moving from single to multiple species conservation planning while largely avoiding the use of surrogate-based filters.

To facilitate discussion of recent advances in multispecies conservation planning, we have partitioned the topic into various categories. These categories, however, are not distinct, but rather they overlap somewhat in data requirements, methods, and objectives. For example, habitat suitability models (e.g., Root et al. 2003, Zielinski et al. 2006a), probability of occurrence models (Moilanen et al. 2005), and population viability models (Haight et al. 2002, Carroll et al. 2003) can all serve as input to reserve selection algorithms.

Probability Surfaces for Species Occurrences

A wide variety of methods exist for predicting the occurrence of species at local to broad spatial scales (see Guisan and Zimmermann 2000, Scott et al. 2002, Elith et al. 2006). The recent coupling of statistical techniques with geographic information systems (GIS) has increased capabilities for modeling and visualizing the occurrence of individual species in time and space, typically as raster-based probabilistic surfaces. In addition, a useful conceptual model to map the spatial distribution of multiple species at several spatial scales has recently been developed (Fischer et al. 2004b, Fischer and Lindenmayer 2006). However, we are aware of very few empirical examples of models developed to

simultaneously predict the probability of occurrence for multiple species. Logistic regression is perhaps the most common statistical approach to modeling the probability of species occurrence. In these models, binary information on the presence-absence of a single species (dependent variable) is used to estimate a conditional probability of occurrence as a linear function of multiple independent predictor variables (e.g., Pereira and Itami 1991, Carroll et al. 1999, Klute et al. 2002; see Hosmer and Lemeshow 2000). Often, values for the predictor variables are extracted directly from digital data layers in a GIS (e.g., landcover type and elevation). Once the relevant parameters have been estimated, these models can be implemented within a GIS to produce a probabilistic, cartographic surface encompassing the inferential or spatial extent of the independent variables (Niemuth et al., this volume). Numerous tools, including cross-validation techniques and receiver operating characteristic curves, for example, can be used to evaluate model performance and prediction errors (see Fielding and Bell 1997; Shifley et al., this volume).

One common extension of multiple logistic regression is the probabilistic predictions of habitat selection by individual species (e.g., resource selection functions; Manly et al. 2002). Similarly, new methods for estimating probability of site occupancy by a species use multiple logistic regression as their statistical foundation, and permit the adjustment of estimates using models of detection probability (see MacKenzie et al. 2006). Other methods for predicting probability of occurrence that are easily implemented in a GIS include Mahalanobis distance (Clark et al. 1993, Knick and Dyer 1997), Bayesian weights-of-evidence (Bonham-Carter et al. 1989), and kernel density estimation (Worton 1989, Bailey and Gatrell 1995). Segurado and Araújo (2004) and Elith et al. (2006) provide a current and comprehensive review of other methods used to predict the occurrence and distribution of species and that can be used to generate probabilistic surfaces.

When reliable information on the spatial location of multiple species is available, and when a suite of meaningful covariates can be specified, probabilistic models of the occurrence of single species can be used to inform multispecies conservation planning efforts. It is possible to combine multiple probabilistic surfaces derived from one of the statistical models described earlier to create a single, synthetic surface predicting the occurrence of >1 species of interest. For example, Moilanen et al. (2005) described an approach to quantifying priority areas for multispecies conservation planning using a connectivity algorithm and probability of occurrence surfaces developed for seven indicator species in eastern Australia (after Wintle et al. 2005). Using the computer program ZONATION (Moilanen et al. 2005), they hierarchically aggregated, or “zoned,” priority areas based on concentrations of high probability values, which were then assumed to simultaneously support high connectivity and persistence for multiple species. Recently, the ZONATION algorithm has been used to identify a reserve design for 23 species of butterflies in the United Kingdom (Early and Thomas 2007).

Significant advances have been made recently in the integration of environmental data with presence-only location data (e.g., Tsoar et al. 2007). For example, program MAXENT (Phillips et al. 2006) creates a probability of occurrence grid for multiple species based on the spatial intersection of environmental and species presence data via a GIS interface. Predicted probabilities of habitat suitability can then be thresholded to identify candidate reserve boundaries.

Improved and reliable models of species occurrence will be necessary to assess the impacts of management and environmental changes on the collective properties of biodiversity (Guisan et al. 2006). Probabilistic surfaces and associated visualization techniques (Millsaugh et al., this volume), derived from any number of statistical models, can convey complex information that is relatively easy to interpret and communicate. However, because no single best model can be applied to all species in all environments, emphasis should be placed on identifying the model that best matches the ecology of the species, community, or system under investigation (Barry and Elith 2006), and on the data, assumptions, and goals of the analysis (Segurado and Araújo 2004).

Generation of empirically based probability surfaces, whether for single or multiple species, requires sampling animal occurrence with sufficient intensity to assign probabilities of detection to covariate GIS elements. Further, it requires that GIS variables provide high explanatory power. These data requirements currently make these approaches most useful when applied to a small group of focal species that collectively act as comprehensive biodiversity surrogates.

Addressing Landscape Connectivity for Multiple Species

For all but rare endemic species, conservation objectives will not be achieved with a single reserve or a single population. Rather, local populations widely scattered across the landscape, but connected by movement, will be necessary. Few of these populations will be large enough to avoid problems faced by small populations, such as extirpation due to stochastic factors and inbreeding depression. Connectivity maintenance is therefore one of the most critical aspects of multispecies conservation. Connectivity, however, is notoriously difficult to directly measure. Not only are observed dispersal events rare, but the results of observed dispersals are seldom known. The probability of locating an organism in a distant location is low, and the probability of subsequently tracking an individual to determine mating behavior and reproductive success is very small. Past dispersal events that did affect the population through breeding do, however, leave characteristic genetic patterns. Areas of high mixing are relatively genetically similar, and isolated populations are more divergent. Historically, genetic samples were collected from populations on either side of a putative barrier, and the null hypothesis that both samples came from the same population is tested. When rejected, the putative barrier was assumed to be real.

While not without merit, this approach assumes *a priori* that we can identify important barriers, an assumption that is significantly weakened if population substructure exists on either side of the barrier. Recently, a growing number of techniques seek to characterize a surface of genetic differences based on evaluation of individuals, and relate these surfaces to mapped landscape characteristics such as topography. Dubbed “landscape genetics” (Manel et al. 2003), this approach is new, and its possibilities largely unexplored. Cushman et al. (2006) used landscape genetic methods to correlate 108 different landscape resistance patterns to patterns of genetic differences in black bears (*Ursus americana*). Bear genetic patterns best correlated with low resistance movement through mid-elevation forests and avoidance of both high and low elevation zones and open areas. Cushman et al.’s (2006) methods are broadly applicable to other species—requiring a spatially distributed genetic sample of individuals from a species of interest and mapped landscape attributes to define a plausible suite of potential resistance surfaces.

The reserve design algorithm ZONATION directly addresses connectivity by creating a grid-based connectivity surface (Moilanen et al. 2005). For each species considered, the likelihood of successful dispersal from location *i* to location *j* is estimated from Hanski’s incidence function equation (Hanski 1994) based on the occupancy status of cells and their distance apart. Every cell with a connectivity value above a threshold is selected to produce clusters of cells and incipient reserves.

McRae (2006) used concepts from electronic circuit theory to predict gene flow and genetic structuring in heterogeneous landscapes. Briefly, the isolation-by-resistance (IBR) model uses circuits as models of population or landscape networks. The model represents populations or raster habitat cells connected by dispersal as nodes connected by resistors. Effective conductance calculated among nodes can be used to predict gene flow, whereas effective resistance is used to predict genetic differentiation. Greater connectivity among populations or habitat patches is predicted when more connected pathways are available. The IBR model can accommodate a broad range of available habitat data, from simple range maps to quantitative habitat models. The model could easily be extended to predictions for multiple species by assigning conductance values to cells that characterize the minimum habitat requisites of a set of species of interest, or by combining output values from individual IBR analyses into a single conservation solution.

Reserve Selection Algorithms

In the Northwest Forest Plan (Forest Ecosystem Management Assessment Team 1993), areas were added to the northern spotted owl reserve structure based on expert opinion. Because so many species were evaluated, and each species added conservation requirements to the plan, reserves were large, and between-reserve constraints were significant. The result for public lands in the

Cascades and Coast Ranges of Washington, Oregon, and northern California was that timber harvest was reduced to 5% of preplan levels. While this approach favors species conservation, in many areas large reductions in resource extraction are not socially acceptable. This understanding has led to the idea of developing more efficient reserve systems by either seeking maximal coverage (greatest number of species protected) for a fixed area or expenditure, or a minimum reserve set (smallest expenditure) for a target set of species using the tools of linear and nonlinear optimization (e.g., Pressey et al. 1993, Bevers et al. 1995, Possingham et al. 2000, Cabeza and Moilanen 2003).

There is an extensive literature on methods to optimally select areas for inclusion into a biodiversity reserve design (e.g., Williams et al. 2005, Sarkar et al. 2006). Many methods focus on selecting the smallest possible number (area) of reserves that will achieve the objective of including all species in at least one reserve (Pressey et al. 1993, Possingham et al. 2000 [program SITES]). This has been called the minimum representation problem (Possingham et al. 2000). There are many variants on these methods, but most cast the problem as an optimization exercise where the goal is to minimize social and economic costs constrained by biodiversity objectives (McDonnell et al. 2002). The optimization algorithms are generally based on the principle of comprehensive species representation at minimal economic cost, a goal achieved by optimally selecting some minimal set of complementary reserve sites. Data requirements for these methods include information on the presence-absence of each species on each candidate reserve site. Since the number of possible solutions is equal to 2^n , where n is the number of candidate sites, finding optimal solutions often requires nonlinear optimization software, and the methods can be very computer intensive.

Other objectives for reserve selection can be addressed in the optimization problem. Most common are a site's irreplaceability and its vulnerability (Lawler et al. 2003). Irreplaceable sites contain species that are found nowhere else among the candidate sites and thus must be included in any solution in order to obtain complete representation (Pressey et al. 1994). To sustain the objective of full representation requires identification of sites that are vulnerable to loss and contain species that are poorly represented elsewhere among candidate sites (Wilson et al. 2005). Sites can also be prioritized for inclusion if they contain species that are threatened with extinction or generally at risk because of their rarity (e.g., Pressey et al. 2003).

Most reserve selection algorithms are based on presence-absence distribution data and cannot directly address issues of persistence. However, a key assumption of reserve selection algorithms is that the selected sites and their configuration allow for species persistence across the reserve system. Even though this goal is an obvious one, it is much more difficult to implement because it requires far more information. To design reserve systems with persistence explicitly evaluated as a conservation objective requires additional information on each species' ecology and life history, including information

on dispersal abilities and how persistence likelihood scales with local population size (Carroll et al. 2003, Nicholson and Possingham 2006, Nicholson et al. 2006). Multispecies optimization approaches that include persistence objectives as design criteria are currently limited to a relatively small number of well-studied species (e.g., Zielinski et al. 2006a).

Maximizing the Persistence Likelihood of Multiple Species

Most reserve selection algorithms do not directly address the persistence likelihoods of species within the reserved areas. Rather, the algorithms represent a static spatial analysis of biodiversity patterns and do not generally include information on demographic processes. To incorporate population dynamics, for example, reserve algorithms can include objective functions that minimize the extinction risk of a set of focal or umbrella species (reviewed in Nicholson and Possingham 2006). These algorithms are similar to those used in static reserve selection in that they invoke realistic constraints such as available area or level of funding that can be dedicated for conservation. Recent research in this area has built on and extended earlier work aimed at optimizing the spatial pattern of multispecies wildlife habitat in the Pacific Northwest (e.g., Hof and Raphael 1993, Bevers et al. 1995).

Nicholson et al. (2006) used a spatially realistic metapopulation model to estimate extinction risk for a set of 10 well-studied species. Their optimization objective was to maximize persistence likelihood simultaneously across the 10 species, and their model incorporated spatially explicit information on the location, quality, and configuration of habitat, as well as detailed information on the ecology and demography of the focal species. Their model invoked a patch-based view of the landscape, where patches were allowed to vary in quality by species, but matrix properties were not explicitly incorporated. In addition to distributional data for each species, their models required difficult-to-acquire life history data including home range size, number of female dispersers per home range, mean dispersal distance, how extinction risk scales with patch area, and habitat quality values for the different patch types. The authors found that optimizing an objective function that minimized extinction risk outperformed other objective functions based on maximizing the area of habitat given a financial constraint.

Holzkämper et al. (2006) also used a spatial optimization approach to simultaneously address the conservation of three bird species. The species chosen had differing habitat requirements, and this introduced the important reality that multispecies conservation planning involves inescapable trade-offs among the habitat requirements of the species considered. Their model does not view the landscape in terms of a competing set of reserve patches as in Nicholson et al. (2006), but rather as composed of contiguous polygons (patches) of adjacent land use types. Given information on the species habitat requirements and

assuming similar area requirements for each species, their optimization model aims to maximize habitat suitability for the three species by identifying the optimal configuration and composition of the landscape. This model also has strict data requirements for parameterization, including knowledge of the species distributions, territory sizes, and habitat suitability values in terms of a set of environmental covariates and landscape metrics.

Use of spatial optimization methods for multispecies planning, in the future, is likely to be an important advance. However, these methods are unlikely to be widely available for conservation planning in the near term, particularly for land managers whose responsibilities often include oversight for diverse taxa and hundreds of species. The requirements for information on distribution, habitat relationships, and, for the extinction models, demographic information may preclude their practical use for most large-scale conservation planning efforts. The exception may be the case where viability-based algorithms focus on a small number of well-studied species that collectively span a range of life histories, habitat, and area requirements that they serve as comprehensive surrogates for the unmeasured species (e.g., Carroll 2003).

Genetic Monitoring

Recently, abundance estimation for many species has undergone a transformation from live trapping and tagging to noninvasive sampling and the use of DNA “tags” for Capture/Mark/Recapture (CMR) or other analyses. Even poor quality DNA can be used reliably to determine species presence-absence and distribution patterns (Zielinski et al. 2007), information that is fundamental to all conservation strategies. These methods, while transformative for many species, underutilize genetic data—genetic differences between individuals devolve into counts. While most widely applied in aquatic systems, genetic data can be directly used to monitor population performance (Schwartz et al. 2007). The advantages of this approach lie in the wealth of information associated with each genetic sample. For example, estimation of population connectivity and effective population size are much more sensitive to the number of loci and alleles per locus than they are sample size. At sample sizes >100 , power is insensitive to sample size and is entirely dependent on the genes analyzed. Additionally, because genes integrate across a local population, rigorously representative sampling is much less important. Because it is possible to make strong inferences from samples from a small proportion of the population and from imperfectly collected data, genetic monitoring provides promising and cost-effective approaches for population analyses for multiple species at large spatial scales.

Given that few species have any history of data collection to evaluate trends, genetic methods, being less sensitive to data quality, offer the possibility of retrospective studies, where samples from the past such as museum specimens can be genetically compared to current samples to infer trend

(Schwartz et al. 2007). In an excellent example of a retrospective study, Østergaard et al. (2003) analyzed genetic heterozygosity in brown trout (*Salmo trutta*) in Demark from 1944 to 1997. Older samples were obtained from scale collections. Østergaard et al. (2003) concluded that the population was stable, but maintenance of genetic diversity was dependent on gene flow between small local populations.

A SAMPLE STRATEGY FOR MULTISPECIES CONSERVATION

The Nature Conservancy (TNC) has been a leader in the development of broad-scale conservation strategies that have multispecies conservation as a priority objective. For example, Poiani et al. (2000) proposed that biodiversity conservation on TNC lands focus on ecosystem- and landscape-level concepts. Specifically, they proposed a strategy based on three types of functional conservation areas—sites, landscapes, and networks—defined by ecosystems and species targeted for conservation. Sites aim to conserve species or ecosystems that exist at local scales (meters to thousands of hectares); landscapes seek to conserve many ecosystems and multiple species at scales ranging up to millions of hectares; and networks are integrated sites or landscapes that provide for movement and connectivity. A distinguishing aspect of the Poiani et al. (2000) approach is the consideration of ecological processes (e.g., fire, flood, hydrology) as part of their evaluation of functionality.

Four spatial scales of assessment are used in their conservation framework—local, intermediate, coarse, and regional (Poiani et al. 2000). Each of these scales can be associated with plant or animal species or ecosystems. Ecosystems are broadly defined to include plant and animal communities and ecological process but, in practice, often default to boundaries defined by vegetation community types similar to traditional coarse filter approaches. Ecosystem scale can thus vary as a function of the degree of resolution applied to the plant community data. Animal species with diverse ecologies are also used as surrogates to represent a range of scales based on differences in the species' mobilities, home range sizes, and migration patterns.

Though not explicitly cast in terms of a coarse filter-fine filter framework, the four scales of analysis used by Poiani et al. (2000) have elements that can be aligned with traditional coarse and fine filter approaches. A distinguishing characteristic of their approach, however, is that species are used as coarse as well as fine filter elements for conservation planning. For example, similar to the umbrella species concept (Fleishman et al. 2000), wide-ranging animals such as migrating ungulates and top-level predators are specified as conservation targets for regional scale assessments.

Currently, TNC uses a comprehensive conservation planning process that extends the Poiani et al. (2000) approach and draws on elements of both coarse

and fine filter strategies (Groves et al. 2002). Five criteria are used to identify priority conservation areas on the landscape: degree of existing protection, conservation value, threat, feasibility, and leverage (Groves et al. 2000). The process of identifying conservation value begins by identifying conservation targets that may be defined on the basis of spatial scale and biological organization. Levels in these two hierarchies include broad-scale physical features of the landscape (e.g., soils, geology, topography, and climate), ecoregions (combinations of physical features and dominant vegetation community types [Bailey 1995]), biological communities, and individual species. A key objective of the TNC approach is to conserve ecosystems, but the reality is that ecosystems are usually defined on the basis of dominant vegetation types (the coarse filter).

In the TNC biological hierarchy, the finest scale includes information on the genetic diversity of target species to address viability concerns of small, isolated populations. Second, the population abundance of individual species—particularly rare, keystone, or umbrella species—is evaluated. Third, representative biological communities for a given planning area provide a coarse filter target, whereby maintenance of community dominant species indicates whether critical interactions and processes are also being maintained. Fourth, ecosystems, when they can be delineated on the basis of disturbance regimes or geological or topographic features, are included as conservation targets. Finally, portions of entire landscapes including multiple ecosystems are evaluated for inclusion in the final conservation strategy. Full implementation of the TNC conservation planning algorithm is data intensive, requiring information on local population sizes, genetic diversity, and spatial distribution patterns. In practice, however, surrogate measures are used for many of these data elements, and recourse is made to the coarse filter components as needed.

More recently, practical approaches to land use and management planning have begun to emerge that link comprehensive biodiversity mapping efforts with science-based public processes. The Forest Ecosystem Restoration Analysis (ForestERA) Project (Sisk et al. 2006) is an interdisciplinary approach to landscape-scale (e.g., 10^4 – 10^6 ha) resource management and planning that integrates spatially explicit data and models within a collaborative decision-making framework. Using GIS-based tools, the ForestERA process couples fine and coarse filter information to map and prioritize large areas for restoration and conservation on lands that are typically under the jurisdiction of the Forest Service. For example, empirically derived models of indicator species occurrence and demographic rates of focal species are commonly selected and combined to represent “high value” landscape or biodiversity features. Using a series of ranking and weighting exercises, this multispecies information is, in turn, confronted by “risk” models, including fire hazard and post-fire erosion, and alternative management actions, including prescribed fire and mechanical thinning. By manipulating the original model parameters, stakeholders can collectively predict, evaluate, and compare the effects of various risk factors and management scenarios on the conservation of multiple species or their habitats.

RECOMMENDATIONS

We are encouraged by recent advances in quantitative methods to inform multispecies conservation planning—diverse life histories and ecological requirements can now be simultaneously addressed for multiple species. However, we perceive a significant gap between the research and practitioner communities in the arena of public lands conservation. As a result, the innovative methods described in recent scientific literature may not be accessible to most land managers. This suggests a need for increased collaboration between the research and management communities.

Given the sheer number of species that must be managed and conserved on most national forests, national parks, wildlife refuges, or other public land areas in the United States, the use of biodiversity surrogates is inescapable (see Margules and Pressey 2000). Despite significant increases in data availability and modeling methods in recent years, we believe the most feasible approach to multispecies conservation planning on public lands at this time remains a combined coarse filter–fine filter approach applied at broad spatial scales (see Hauffer et al. 1999). Substantial increases in the quality and quantity of spatial data from remote sensing have increased the precision and resolution of coarse filter data. These data may allow the identification and mapping of broad vegetation types and stages that serve as useful habitat surrogates for many species. In addition, for the fine filter we advocate for a judicious selection of focal species based on the principles of complementarity and comprehensiveness similar in concept to their use in reserve selection algorithms. A comprehensive species set has the property of spanning, to the extent possible, the range of niche types, trophic positions, allometrically based spatial and temporal scales, demographics, and movement behaviors that characterize the entire species pool. Given that the size of the focal species set will be constrained by budget and data limits, the minimal species set will have the property that member species maximally complement each other's ecologies and life histories.

The knowledge needed to select an (constrained) optimal set of focal species is incomplete at this time (Favreau et al. 2006), and there is debate on the utility of the surrogate species approach (e.g., Lambeck 2002, Lindenmayer et al. 2002). However, we believe categories of focal species and criteria for their selection may be sufficiently advanced that the goals of complementarity and comprehensiveness can be approximated. In addition to focal species selection methods based on complementary life histories and ecologies, existing species categories long recognized by ecologists as useful concepts should be considered.

Identifying Focal Species

To begin the process of filtering the species pool in search of focal species, one may find it useful to move sequentially through the following steps that

include both ecological and social criteria (cf. with Lambeck 1997, Hilty and Merenlender 2000, Beazley and Cardinal 2004):

1. Determine legal responsibilities of the public land managers relative to sustaining biological diversity and the viability of individual species. That is, clarify the requirements for species protection within the larger context of land-use planning, multiple use, and management.
2. Make a list of all the species in the affected area for which the land manager has a legal responsibility. This list could be prioritized, for example, in terms of risk.
3. Apply an initial filter based on the criteria listed in Table 3-1.
4. From this list, attempt to identify species that fall into one of the focal species categories identified (see earlier list).
5. Cross-classify the species list from (4) according to various ecological attributes, including body size (as a surrogate for many allometric relationships), home range size, demographic characteristics (e.g., life span, generation length, reproductive potential), trophic position, and habitat specialization (and other niche dimensions). This step will allow complementary species sets to be identified within each focal species category.
6. Remove species whose dynamics are largely independent of management activities occurring on public lands.

Table 3-1 Desired Attributes of Focal Species as Surrogate Measures for Multispecies Conservation Planning

1	Taxonomic status is well established
2	Ecology, life history, and demography are sufficiently “known” to allow direct or indirect estimates of relative abundance and spatial distribution
3	Relatively high detectability allowing for precise estimates of population status (presence-absence or abundance)
4	Low sampling variability (consistent and high detectability across time and space)
5	Low process variation in demographic rates, allowing more reliable inferences to causal factors affecting population status
6	Attributes (4) and (5) allow for high statistical power to detect trends in presence-absence or abundance
7	Known relationships between environmental stressors and population status

7. Further filter species by retaining only those that can be monitored with available resources, but retaining several species within each focal category.
8. Select a final set of focal species that spans the range of focal species categories, encompasses a wide range of ecological attributes, and, if possible, represents different taxonomic groups. This list should be critically evaluated to see whether it meets the criteria of comprehensiveness and complementarity.

After one follows these steps, the hope is that a near optimal set of fine filter species will have been identified. The set of focal species should complement and provide an opportunity to evaluate the utility of the vegetation-based coarse filter approach. In addition, if the set of focal species is sufficiently small with well-known distributions, habitat relationships, and demographic characteristics, many of the new methods for multiple species assessment discussed previously may be feasible.

APPLICATION TO FEDERAL PUBLIC LANDS

Conservation practice on public land areas in the United States is constrained by a plethora of often conflicting legal statutes and by profound limits on data availability. These points can be illustrated by considering the management of Forest Service lands in the United States. Probably the most important statute to consider is the NFMA, which requires the Forest Service to maintain biological diversity in perpetuity. Thus, the Forest Service has a formal legal mandate to engage in multispecies conservation. Between 1982 and 2005, the biodiversity requirements in NFMA were interpreted to mean maintaining the viability of native vertebrate species across their ranges. The approach was to choose “management indicator species,” similar in intent to focal species, and to manage for and monitor their populations. Although the efficacy of this approach has been questioned (Landres et al. 1988, Landres 1992), there is no way to evaluate its effectiveness because the requirements were never fully implemented. To the best of our knowledge, the Forest Service has never monitored the populations of the indicator species designated in their management plans in a manner that would allow a rigorous and comprehensive assessment of their response to management and the degree to which unmeasured species were being conserved.

In 2005, the Forest Service issued new regulations to implement the NFMA, dropped their requirements for viability assessments of selected vertebrate species, and shifted over to a coarse filter model for conservation (Noon et al. 2005). The agency asserts that maintaining a diversity of natural vegetation

community types will maintain ecological systems and their component species (Federal Register, 70:3:1023). As a result, the agency is no longer required to implement mesofilter or fine filter approaches to conservation planning, or to directly monitor species responses to management actions.

While maintaining a diversity of vegetation types is far easier to implement and monitor than is the maintenance of viable populations of multiple species, there is little guidance concerning how vegetation diversity alone can be used to infer the conservation status of unmeasured species. The reality is that the composition and configuration of vegetation types and successional stages needed to sustain multiple species over the long term is unknown (Cushman et al. 2008). The challenge of managing multiple animal species through vegetation surrogates is further complicated by current data limitations. Without additional funding, vegetation will be mapped based almost exclusively on spectral imagery with little ground-truthing. Forest vegetation data, such as species composition and structure, collected over large spatial extents are generally limited to Forest Inventory and Analysis (FIA; U.S. Forest Service 2003) data collected at plots located on a 4.8 km grid (see www.fia.fs.fed.us). These data are designed to provide broad-scale assessments of forest resources and have only secondarily been modified to include additional measurements believed relevant to wildlife populations. While more than adequate for their designed purpose, FIA plots carry little spatial information, do not extend to nonforested areas, and primarily measure trees instead of providing comprehensive floristic information. Further, statistical models relating the coarse-grained habitat data available from satellite imagery or FIA data and fauna presence and/or abundance have not been generated (however, see Fitzgerald et al., this volume). Thus, land management agencies have little quantitative information to provide even an indirect check on whether the populations of specific species are likely being maintained by use of vegetation surrogates as a coarse filter.

In recent years, public land management agencies have seen reduced budgets while fixed costs have steadily risen. This trend is not likely to reverse in the near future, and therefore proposals that require large infusions of money are likely dead on arrival. Thus, for the near term, public land management agencies in the United States will need primarily to work within the confines of existing data. This is unfortunate, as virtually all the promising new approaches to multiple species conservation cannot be implemented given these data. Although we believe that a mix of coarse and fine filter approaches likely has the greatest merit, we acknowledge that, given the existing data and knowledge base, federal land management agencies may be able to implement only coarse filter approaches. Under this scenario, the emphasis should be on validation of the coarse filter approach (see Schulte et al. 2006), identification of mesofilter elements, and selection of fine filter species based on the criteria for focal species selection discussed previously. With these constraints in mind, we propose the following steps to improve multispecies conservation on federal public lands:

1. Make sure that existing data are fully utilized. For many species, mesofilter elements will likely have the greatest relationship to habitat quality; therefore, plot inventory data should be expanded such that these elements can be mapped and spatially evaluated. Currently, a variety of approaches that would serve as a coarse filter are under development, including gradient modeling and machine-learning or expert-system methods (Frescino et al. 2001, Moisen and Frescino 2002, Ohmann and Gregory 2002, Olden and Jackson 2002, Stockwell 2006). Although the general efficacy of these methods is unknown, priority should be given to this area of research.
2. Recognize that certain habitat elements and landcover classes have been greatly reduced from their historical levels (e.g., large diameter trees and old-growth forest). Identify, and prioritize for conservation, species associated with these elements and classes. Where large, relatively pristine areas of rare habitats exist, manage to ensure their persistence.
3. Recognize that it will be some time before more complete data on species distributions and habitat relationships become available. In the interim, give conservation priority to habitat elements and landscape classes, such as older forests or large diameter trees, which cannot be rapidly replaced.
4. Given uncertainties about the relationships between vegetation mosaics and fauna populations, any multispecies conservation strategy must be considered an untested hypothesis. Testing the hypothesis is a formidable task, but it may be possible to use currently collected fauna information as a check on land management. For instance, at the landscape scale, FIA plot composition has been correlated with breeding bird survey data (Fearer 2006) and with the distribution of forest carnivores (Zielinski et al. 2006b). Similarly, population information on game species collected by state Fish and Game agencies can be correlated to broad landscape vegetation characteristics.
5. Take advantage of new monitoring methodologies. Genetic monitoring methods (Schwartz et al. 2007, Zielinski et al. 2007) allow the population attributes of many species to be inferred at greatly reduced costs, potentially providing direct feedback. Agencies therefore should prototype genetic collection and analysis approaches to accelerate adoption of this technology.
6. Based on the methods discussed previously, choose to monitor a small group of focal species with complementary and comprehensive ecologies. Develop detailed habitat relationships for these species, manage for their viability, and track their populations. If the set of focal species is small enough, and sufficient data exist on their ecologies and life history, optimization methods based on maximizing their combined persistence

likelihoods may be possible (Nicholson and Possingham 2006, Nicholson et al. 2006). Because of the limited nature of this fine filter, and because of the requirement of additional funding for this work, for pragmatic reasons we suggest that the set of focal species include some of public interest, such as game species or those listed species under the ESA.

SUMMARY

Federal land managers in the United States are responsible for sustaining native biodiversity and obligated not to put any species at risk of extinction. In other words, they must manage in a way that benefits and sustains multiple species. However, even assuming well-intentioned and adequately funded managers, difficulties arise because most species are poorly known, and the quantitative methods and technologies that allow the concurrent evaluation of ≥ 2 species are just now being developed. These novel methods are significant, but their data requirements and technical challenges currently limit their utility to the conservation manager. As a result, conservation planning now, and in the foreseeable future, will depend on the continued use of broad-scale environmental proxies and species-based surrogates. These surrogate measures, encompassing both coarse filter and fine filter elements, must be judiciously selected so as to allow inference to the viability of all the unmeasured species.

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.
- Aurambout, J. P., A. G. Endress, and B. M. Deal. 2005. A spatial model to estimate habitat fragmentation and its consequences on long-term persistence of animal populations. *Environmental Monitoring and Assessment* 109:199–225.
- Bailey, R. G. 1995. Descriptions of the Ecoregions of the United States. U.S. Forest Service, Miscellaneous Publication number 1391, Washington, D.C., USA.
- Bailey, T. C., and A. C. Gatrell. 1995. *Interactive spatial data analysis*. Addison-Wesley Publishers, Reading, Massachusetts, USA.
- Barry, S., and J. Elith. 2006. Error and uncertainty in habitat models. *Journal of Applied Ecology* 43:413–423.
- Beazley, K., and N. Cardinal. 2004. A systematic approach for selecting focal species for conservation in forests of Nova Scotia and Maine. *Environmental Conservation* 31:91–101.
- Beyers, M., J. Hof, B. Kent, and M. G. Raphael. 1995. Sustainable forest management for optimizing multispecies wildlife habitat: A coastal Douglas-fir example. *Natural Resources Modeling* 9:1–23.
- Block, W. M., L. A. Brennan, and R. J. Gutiérrez. 1987. Evaluation of guild-indicator species for use in resource management. *Environmental Management* 11:265–269.
- Bonham-Carter, G. F., F. P. Agterberg, and D. F. Wright. 1989. Weights of evidence modeling: A new approach to mapping mineral potential. Pages 171–183 in F. P. Agterberg and G. F. Bonham-Carter, editors. *Statistical applications in the earth sciences*. Geological Survey of Canada paper 89-9, Ottawa, Ontario, Canada.

- Cabeza, M., and A. Moilanen. 2003. Site selection algorithms and habitat loss. *Conservation Biology* 17:1402–1413.
- Caro, T. M., and G. O'Doherty. 1999. On the use of surrogate species in conservation biology. *Conservation Biology* 13:805–814.
- Carroll, C., R. F. Noss, P. C. Paquet, and N. H. Schumaker. 2003. Use of population viability analysis and reserve selection algorithms in regional conservation plans. *Ecological Applications* 13:1773–1789.
- Carroll, C., W. J. Zielinski, and R. F. Noss. 1999. Using presence-absence data to build and test special habitat models for the fisher in the Klamath Region, USA. *Conservation Biology* 13:1344–1359.
- Christianou, M., and B. Ebenman. 2005. Keystone species and vulnerable species in ecological communities: Strong or weak interactors? *Journal of Theoretical Biology* 235:95–103.
- Clark, J. D., J. E. Dunn, and K. G. Smith. 1993. A multivariate model of female black bear habitat use for a geographic information system. *Journal of Wildlife Management* 57:519–526.
- Committee of Scientists (COS). 1999. Sustaining the people's lands: Recommendations for stewardship of the national forests and grasslands into the next century. U.S. Forest Service, COS report. <<http://www.fs.fed.us/forum/nepa/rule/cosreport.html>>.
- Cotgreave, P., and P. H. Harvey. 1992. Relationships between body size, abundance, and phylogeny in bird communities. *Functional Ecology* 6:248–256.
- Cushman, S. A., and K. McGarigal. 2004. Hierarchical analysis of forest bird species-environment relationships in the Oregon Coast Range. *Ecological Applications* 14:1090–1105.
- Cushman, S. A., K. S. McKelvey, C. H. Flather, and K. McGarigal. 2008. Do forest community types provide a sufficient basis to evaluate biological diversity? *Frontiers in Ecology and the Environment* 6:13–17.
- Cushman, S. A., K. S. McKelvey, J. Hayden, and M. K. Schwartz. 2006. Gene flow in complex landscapes: Testing multiple hypotheses with causal modeling. *American Naturalist* 168:486–499.
- Early, R., and C. D. Thomas. 2007. Multispecies conservation planning: Identifying landscapes for the conservation of viable populations using local and continental species priorities. *Journal of Applied Ecology* 44:253–262.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. C. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.
- Fauth, J. E. 1997. Identifying potential keystone species from field data—An example from temporary ponds. *Ecology Letters* 2:36–43.
- Favreau, J. M., C. A. Drew, G. R. Hess, M. J. Rubino, F. H. Koch, and K. A. Eschelbach. 2006. Recommendations for assessing the effectiveness of surrogate species approaches. *Biodiversity and Conservation* 15:3949–3969.
- Fearer, T. M. 2006. *Evaluating population-habitat relationships of forest breeding birds at multiple spatial and temporal scales using forest inventory and analysis data*. Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24:38–49.
- Fischer, J., and D. B. Lindenmayer. 2006. Beyond fragmentation: The continuum model for faunal research and conservation in human-modified landscapes. *Oikos* 112:473–480.
- Fischer, J., D. B. Lindenmayer, and A. Cowling. 2004a. The challenge of managing multiple species at multiple scales: Reptiles in an Australian gazing landscape. *Journal Applied Ecology* 41:32–44.
- Fischer, J., D. B. Lindenmayer, and I. Fazey. 2004b. Appreciating ecological complexity: Habitat contours as a conceptual landscape model. *Conservation Biology* 18:1245–1253.
- Fleishman, E., R. B. Blair, and D. D. Murphy. 2001. Empirical validation of a method for umbrella species selection. *Ecological Applications* 11:1489–1501.

- Fleishman, E., D. D. Murphy, and P. F. Brussard. 2000. A new method for selection of umbrella species for conservation planning. *Ecological Applications* 10:569–579.
- Forest Ecosystem Management Assessment Team. 1993. Forest ecosystem management: An ecological, economic, and social assessment. U.S. Government Printing Office, Report number 1993-793-071, Washington, D.C., USA.
- Frescino, T. S., T. C. Edwards, Jr., and G. G. Moisen. 2001. Modeling spatially explicit forest structural attributes using generalized additive models. *Journal of Vegetation Science* 12:15–26.
- Gardner, R. H., and E. J. Gustafson. 2004. Simulating dispersal of reintroduced species within heterogeneous landscapes. *Ecological Modelling* 171:339–358.
- Goble, D. D., and E. T. Freyfogle. 2002. *Wildlife law*. University Case Book Series, Foundation Press, New York, New York, USA.
- Groves, C. R., D. B. Jensen, L. L. Valutis, K. H. Redford, M. L. Shaffer, J. M. Scott, J. V. Baumgartner, J. V. Higgins, M. W. Beck, and M. G. Anderson. 2002. Planning for biodiversity conservation: Putting conservation science into practice. *Bioscience* 52:499–512.
- Groves, C., L. Valutis, D. Vosick, B. Neely, K. Wheaton, J. Touval, and B. Runnels. 2000. *Designing a geography of hope: A practitioner's handbook for ecoregional conservation planning*. Second edition. The Nature Conservancy. <<http://conserveonline.org/docs/2000/11/GOH2-v2.pdf>>.
- Guisan, A., A. Lehmann, S. Ferrier, M. Austin, J. M. C. Overton, R. Aspinall, and T. Hastie. 2006. Making better biogeographical predictions of species' distributions. *Journal of Applied Ecology* 43:386–392.
- Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135:147–186.
- Haight, R. G., B. Cypher, P. A. Kelly, S. Philips, H. P. Possingham, K. Ralls, A. M. Starfield, P. J. White, and D. Williams. 2002. Optimizing habitat protection using demographic models of population viability. *Conservation Biology* 16:1386–1397.
- Hanski, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* 63:151–162.
- Haufler, J. B., C. A. Mehl, and G. J. Roloff. 1996. Using a coarse-filter approach with species assessment for ecosystem management. *Wildlife Society Bulletin* 24:200–208.
- Haufler, J. B., C. A. Mehl, and G. J. Roloff. 1999. Conserving biological diversity using a coarse-filter approach with a species assessment. Pages 107–125 in R. K. Baydack, H. Campa, III, and J. B. Haufler, editors. *Practical approaches to the conservation of biological diversity*. Island Press, Washington, D.C., USA.
- Hilty, J., and A. Merenlender. 2000. Faunal indicator taxa selection for monitoring ecosystem health. *Biological Conservation* 92:185–197.
- Hof, J. G., and M. G. Raphael. 1993. Some mathematical programming approaches for optimizing timber age class distributions to meet multispecies wildlife population objectives. *Canadian Journal of Forest Research* 23:828–834.
- Holzkämper, A., A. Lausch, and R. Seppelt. 2006. Optimizing landscape configuration to enhance habitat suitability for species with contrasting habitat requirements. *Ecological Modelling* 198:277–292.
- Hooper, D. U., F. S. Chapin, III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Hosmer, D. W., and S. Lemeshow. 2000. *Applied logistic regression*. Second edition. John Wiley and Sons, New York, New York, USA.
- Hunter, M. L., Jr. 1991. Coping with ignorance: The coarse filter strategy for maintaining biodiversity. Pages 266–281 in K. A. Kohm, editor. *Balancing on the brink of extinction: The Endangered Species Act and lessons for the future*. Island Press, Washington, D.C., USA.
- Hunter, M. L., Jr. 2005. A mesofilter conservation strategy to complement fine and coarse filters. *Conservation Biology* 19:1025–1029.

- Hunter, M. L., Jr., G. L. Jacobson, Jr., and T. Webb, III. 1988. Paleoecology and the coarse-filter approach to maintaining biological diversity. *Conservation Biology* 2:375-385.
- Hutchinson, G. E. 1957. Concluding remarks. Cold Springs Harbor Symposium. *Quantitative Biology* 22:415-427.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373-386.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78:1946-1957.
- Jordán, F., A. Takács-Sánta, and I. Molnár. 1999. A reliability theoretical quest for keystones. *Oikos* 86:453-462.
- King, A. W., and K. A. With. 2002. Dispersal success on spatially structured landscapes: When do spatial pattern and dispersal behavior really matter? *Ecological Modelling* 147:23-39.
- Kintsch, J. A., and D. L. Urban. 2002. Focal species, community representation, and physical proxies as conservation strategies: A case study in the Amphibolite Mountains, North Carolina, U.S.A. *Conservation Biology* 16:936-947.
- Klute, D. S., M. J. Lovallo, and W. M. Tzilkowski. 2002. Autologistic regression modeling of American woodcock habitat use with spatially dependent data. Pages 335-344 in J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. *Predicting species occurrences: Issues of accuracy and scale*. Island Press, Washington, D.C., USA.
- Knick, S. T., and D. L. Dyer. 1997. Distribution of black-tailed jackrabbit habitat determined by GIS in southwestern Idaho. *Journal of Wildlife Management* 61:75-85.
- Lambeck, R. J. 1997. Focal species: A multi-species umbrella for nature conservation. *Conservation Biology* 11:549-551.
- Lambeck, R. J. 2002. Focal species and restoration ecology: Response to Lindenmayer et al. *Conservation Biology* 16:849-856.
- Landres, P. B. 1992. Ecological indicators: 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.
- Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species: A critique. *Conservation Biology* 2:316-328.
- Lawler, J. J., D. White, and L. L. Master. 2003. Integrating representation and vulnerability: Two approaches for prioritizing areas for conservation. *Ecological Applications* 13:1762-1772.
- Lindenmayer, D. B., A. D. Manning, P. L. Smith, H. P. Possingham, J. Fischer, I. Oliver, and M. A. McCarthy. 2002. The focal-species approach and landscape restoration: A critique. *Conservation Biology* 16:338-345.
- Lindenmayer, D. B., C. R. Margules, and D. B. Botkin. 2000. Indicators of biodiversity for ecologically sustainable forest management. *Conservation Biology* 14:941-950.
- MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence and divergence of coexisting species. *American Naturalist* 101:377-385.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. *Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence*. Elsevier Academic Press, Amsterdam, The Netherlands.
- MacNally, R., A. F. Bennett, G. W. Brown, L. F. Lumsden, A. Yen, S. Hinkley, P. Lillywhite, and D. A. Ward. 2002. How well do ecosystem-based planning units represent different components of biodiversity? *Ecological Applications* 12:900-912.
- Manel, S., M. K. Schwartz, G. Luikart, and P. Taberlet. 2003. Landscape genetics: Combining landscape ecology and population genetics. *Trends in Ecology and Evolution* 18:189-197.
- Manly, B. F. J., L. L. McDonald, D. A. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource selection by animals: Statistical design and analysis for field studies*. Second edition. Kluwer Academic, Dordrecht, The Netherlands.
- Marcot, B. G., R. S. Holthausen, M. G. Raphael, M. M. Rowland, and M. J. Wisdom. 2001. Using Bayesian belief networks to evaluate fish and wildlife population viability under land management

- alternatives from an environmental impact statement. *Forest Ecology and Management* 153:29–42.
- Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* 405:243–253.
- McArdle, B. H., K. J. Gaston, and J. H. Lawton. 1990. Variation in the size of animal populations: Patterns, problems, and artifacts. *Journal of Animal Ecology* 59:439–454.
- McDonnell, M. D., H. P. Possingham, I. R. Ball, and E. A. Cousins. 2002. Mathematical methods for spatially cohesive reserve design. *Environmental Modeling and Assessment* 7:107–114.
- McRae, B. H. 2006. Isolation by resistance. *Evolution* 60:1551–1561.
- Mills, L. S., M. E. Soulé, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. *Bioscience* 43:219–224.
- Moilanen, A., A. M. A. Franco, R. I. Early, R. Fox, B. Wintle, and C. D. Thomas. 2005. Prioritizing multiple-use landscapes for conservation: Methods for large multi-species planning problems. *Proceeding of the Royal Society of London, Series B* 272:1885–1891.
- Moisen, G. G., and T. S. Frescino. 2002. Comparing five modelling techniques for predicting forest characteristics. *Ecological Modelling* 157:209–225.
- Nagle, J. C., and J. B. Ruhl. 2002. *The law of biodiversity and ecosystem management*. University Case Book Series, Foundation Press, New York, New York, USA.
- Nicholson, E., and H. P. Possingham. 2006. Objectives for multi-species conservation planning. *Conservation Biology* 20:871–881.
- Nicholson, E., M. I. Westphal, K. Frank, W. A. Rochester, R. L. Pressey, D. B. Lindenmayer, and H. P. Possingham. 2006. A new method for conservation planning for the persistence of multiple species. *Ecology Letters* 9:1049–1060.
- Noon, B. R., and V. H. Dale. 2003. Broad-scale ecological science and its application. Pages 34–51 in K. J. Gutzwiller, editor. *Applying landscape ecology in biological conservation*. Springer, New York, New York, USA.
- Noon, B. R., and K. S. McKelvey. 1996. A common framework for conservation planning: Linking individual and metapopulation models. Pages 139–166 in D. R. McCullough, editor. *Metapopulations and wildlife conservation*. Island Press, Washington, D.C., USA.
- Noon, B. R., D. D. Murphy, S. R. Beissinger, M. L. Shaffer, and D. DellaSala. 2003. Conservation planning for U.S. National Forests: Conducting comprehensive biodiversity assessments. *Bioscience* 53:1217–1220.
- Noss, R. F. 1996. Ecosystems as conservation targets. *Trends in Ecology and Evolution* 11:351.
- Noss, R. F., and A. Y. Cooperrider. 1994. *Saving nature's legacy*. Island Press, Washington, D.C., USA.
- Noss, R. F., M. A. O'Connell, and D. D. Murphy. 1997. *The science of conservation planning: Habitat conservation under the Endangered Species Act*. Island Press, Washington, D.C., USA.
- Ohmann, J. L., and M. J. Gregory. 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, USA. *Canadian Journal of Forest Resources* 32:725–741.
- Olden, J. D., and D. A. Jackson. 2002. A comparison of statistical approaches for modelling fish species distributions. *Freshwater Biology* 47:1976–1995.
- Østergaard, S., M. M. Hansen, V. Loeschcke, and E. E. Nielson. 2003. Long-term temporal changes of genetic composition in brown trout (*Salmo trutta L.*) populations inhabiting an unstable environment. *Molecular Ecology* 12:3123–3135.
- Panjabi, A. O., E. H. Dunn, P. J. Blancher, W. C. Hunter, B. Altman, J. Bart, C. J. Beardmore, H. Berlanga, G. S. Butcher, S. K. Davis, D. W. Demarest, R. Dettmers, W. Easton, H. G. de Silva Garza, E. E. Iñigo-Elias, D. N. Pashley, C. J. Ralph, T. D. Rich, K. V. Rosenberg, C. M. Rustay, J. M. Ruth, J. S. Wendt, and T. C. Will. 2005. Partners in Flight handbook on species assessment. Version 2005. Partners in Flight Technical Series number 3, Rocky Mountain Bird Observatory website: <<http://www.rmbo.org/pubs/downloads/Handbook2005.pdf>>.
- Patton, D. R. 1987. Is the use of “management indicator species” feasible? *Western Journal of Applied Forestry* 2:33–34.

- Pearson, S. M., M. G. Turner, R. H. Gardner, and R. V. O'Neill. 1996. An organism-based perspective of habitat fragmentation. Pages 77–95 in R. C. Szaro and D. W. Johnston, editors. *Biodiversity in managed landscapes: Theory and practice*. Oxford University Press, New York, New York, USA.
- Pereira, J. M., and R. M. Itami. 1991. GIS-based habitat modeling using logistic multiple regression: A study of the Mount Graham red squirrel. *Photogrammetric Engineering and Remote Sensing* 57:1475–1486.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge, United Kingdom.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.
- Pickett, S. T. A., and M. L. Cadenasso. 2002. The ecosystem as a multidimensional concept: Meaning, model, and metaphor. *Ecosystems* 5:1–10.
- Pimm, S. L. 2002. *Food webs*. University of Chicago Press, Chicago, Illinois, USA.
- Poff, N. L. 1997. Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16:391–409.
- Poiani, K. A., B. D. Richter, M. G. Anderson, and H. E. Richter. 2000. Biodiversity conservation at multiple scales: Functional sites, landscapes, and networks. *Bioscience* 50:133–146.
- Possingham, H., I. Ball, and S. Andelman. 2000. Mathematical methods for identifying representative reserve networks. Pages 291–306 in S. Ferson and M. Burgman, editors. *Quantitative methods for conservation biology*. Springer, New York, New York, USA.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. *Bioscience* 46:609–620.
- Pressey, R. L., R. M. Cowling, and M. Rouget. 2003. Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. *Biological Conservation* 112:99–127.
- Pressey, R. L., C. J. Humphries, C. R. Margules, R. I. Vane-Wright, and P. H. Williams. 1993. Beyond opportunism: Key principles for systematic reserve selection. *Trends in Ecology and Evolution* 8:124–128.
- Pressey, R. L., I. R. Johnson, and P. D. Wilson. 1994. Shades of irreplaceability: Towards a measure of the contribution of sites to a reservation goal. *Biodiversity and Conservation* 3:242–262.
- Pulliam, H. R. 2000. On the relationship between niche and distribution. *Ecology Letters* 3:349–361.
- Raphael, M. G., and R. Molina. 2007. *Conservation of rare and little-known species: Biological, social, and economic considerations*. Island Press, Washington, D.C., USA.
- Raphael, M. G., M. J. Wisdom, M. M. Rowland, R. S. Holthausen, B. G. Wales, B. G. Marcot, and T. D. Rich. 2001. Status and trends of habitats of terrestrial vertebrates in relation to land management in the interior Columbia River basin. *Forest Ecology and Management* 153:63–88.
- Roberge, J.-M., and P. Angelstam. 2004. Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology* 18:76–85.
- Root, K. V., H. R. Akçakaya, and L. Ginzburg. 2003. A multispecies approach to ecological valuation and conservation. *Conservation Biology* 17:196–206.
- Sarkar, S., R. L. Pressey, D. P. Faith, C. R. Margules, T. Fuller, D. M. Stoms, A. Moffett, K. A. Wilson, K. J. Williams, P. H. Williams, and S. Andelman. 2006. Biodiversity conservation planning tools: Present status and challenges for the future. *Annual Review of Environment and Resources* 31:123–159.
- Schulte, L. A., R. J. Mitchell, M. L. Hunter, Jr., J. F. Franklin, R. K. McIntyre, and B. J. Palik. 2006. Evaluating the conceptual tools for forest biodiversity conservation and their implementation in the U.S. *Forest Ecology and Management* 232:1–11.
- Schwartz, M. K., G. Luikart, and R. S. Waples. 2007. Genetic monitoring as a promising tool for conservation and management. *Trends in Ecology and Evolution* 22:25–33.
- Scott, J. M., P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Rafael, W. A. Wall, and F. B. Samson, editors. 2002. *Predicting species occurrences: Issues of accuracy and scale*. Island Press, Washington, D.C., USA.

- Segurado, P., and M. B. Araújo. 2004. An evaluation of methods for modelling species distributions. *Journal of Biogeography* 31:1555–1568.
- Shaffer, M. L., and B. A. Stein. 2000. Safeguarding our precious heritage. Pages 301–321 in B. A. Stein, L. S. Kutner, and J. S. Adams, editors. *Precious heritage: The status of biodiversity in the United States*. Oxford University Press, Oxford, United Kingdom.
- Silva, M., and J. A. Downing. 1994. Allometric scaling of minimal mammal densities. *Conservation Biology* 8:732–743.
- Sisk, T. D., J. W. Prather, H. M. Hampton, E. N. Aumack, Y. Xu, and B. G. Dickson. 2006. Participatory landscape analysis to guide restoration of ponderosa pine ecosystems in the American Southwest. *Landscape and Urban Planning* 78:300–310.
- Smith, G. A., and M. V. Lomolino. 2004. Black-tailed prairie dogs and the structure of avian communities on the shortgrass plains. *Oecologia* 138:592–602.
- Stockwell, D. R. B. 2006. Improving ecological niche models by data mining large environmental datasets for surrogate models. *Ecological Modelling* 192:188–196.
- Taylor, P. D., L. Fahrig, and K. A. With. 2006. Landscape connectivity: A return to the basics. Pages 29–43 in K. R. Crooks and M. J. Sanjayan, editors. *Connectivity conservation*. Cambridge University Press, Cambridge, United Kingdom.
- Theobald, D. M., and N. T. Hobbs. 2002. Functional definition of landscape structure using a gradient-based approach. Pages 667–672 in J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Hauffer, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. *Predicting species occurrences: Issues of accuracy and scale*. Island Press, Washington, D.C., USA.
- Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Verner. 1990. *A conservation strategy for the northern spotted owl: Interagency Scientific Committee to address the conservation of the northern spotted owl*. U.S. Forest Service, Pacific Northwest Research Station, Portland, OR.
- Tischendorf, L., and L. Fahrig. 2000. How should we measure landscape connectivity? *Landscape Ecology* 15:633–641.
- Tognelli, M. F. 2005. Assessing the utility of indicator groups for the conservation of South American terrestrial mammals. *Biological Conservation* 121:409–417.
- Tsoar, A., O. Allouche, O. Steinitz, D. Rotem, and R. Kadmon. 2007. A comparative evaluation of presence-only methods for modelling species distributions. *Diversity and Distributions* 13:397–405.
- U.S. Forest Service. 2003. *Forest inventory and analysis*. Pacific Northwest Research Station, Portland, Oregon, USA.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of the Earth's ecosystems. *Science* 277:494–499.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.
- Wilcox, B. A. 1984. *In situ* conservation of genetic resources: Determinants of minimum area requirements. Pages 639–647 in J. A. McNeely and K. R. Miller, editors. *National Parks: Conservation and development*. Smithsonian Institution Press, Washington, D.C., USA.
- Williams, J. C., C. C. ReVelle, and S. A. Levin. 2005. Spatial attributes and reserve design models: A review. *Environmental Modeling and Assessment* 10:163–181.
- Wilson, K., R. L. Pressey, A. Newton, M. Burgman, H. Possingham, and C. Weston. 2005. Measuring and incorporating vulnerability into conservation planning. *Environmental Management* 35:527–543.
- Wintle, B. A., J. Elith, and J. M. Potts. 2005. Fauna habitat modelling and mapping: A review and case study in the Lower Hunter Central Coast region of NSW. *Austral Ecology* 30:719–738.
- Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life stage simulation analysis: Estimating vital rate effects on population growth for conservation. *Ecology* 81:628–641.
- With, K. A. 2004. Metapopulation dynamics: Perspectives from landscape ecology. Pages 23–44 in I. Hanski and O. E. Gaggiotti, editors. *Ecology, genetics, and evolution of metapopulations*. Elsevier Academic Press, Amsterdam, The Netherlands.

- With, K. A., R. H. Gardner, and M. G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. *Oikos* 78:151–169.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.
- Zielinski, W. J., C. Carroll, and J. R. Dunk. 2006a. Using landscape suitability models to reconcile conservation planning for two key forest predators. *Biological Conservation* 133:409–430.
- Zielinski, W. J., R. L. Truex, J. R. Dunk, and T. Gaman. 2006b. Using forest inventory data to assess fisher resting habitat suitability in California. *Ecological Applications* 16:1010–1025.
- Zielinski, W. J., M. J. Mazurek, and J. Zinck. 2007. Identifying the species of bats roosting in redwood basal hollows using genetic methods. *Northwest Science* 81:155–162.

This page intentionally left blank