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A Hierarchical Framework for Conserving Biodiversity

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Society recognizes a large variety of values associated with biodiversity including aesthetic, economic, conservation, and educational (McNeely et al. 1990, Heywood and Watson 1995). These values are all ultimately related to the definition of biodiversity as a manifestation of genetic diversity, the primary raw material that is filtered by natural selection, resulting in evolutionary and ecological adaptation of biota to environmental conditions. Minimizing additional loss of biodiversity will provide the best assurance that biota will adapt to the increasing rate and spatial extent of environmental change (Pratt and Cairns 1992), and that societal values will be sustained.

Traditionally, the management of biodiversity has focused on rescuing rare, threatened or endangered species. Huge sums have been spent on recovery programs for a small number of species. Although strong conservation arguments exist for preserving these species, the effort expended can easily become out of proportion to the contribution that these species make to genetic diversity, and therefore to the fitness of the biota to adapt to environmental change. In a time when resources for environmental management are decreasing, prioritizing effort so that resources are allocated in proportion to risk and value can optimize conservation effectiveness (Pulliam and Babbitt 1997).

Multiple-scale, hierarchical approaches are needed for conserving biodiversity (Freemark 1995, Freemark et al. 1995, Davis and Stoms 1996). Such approaches should be inter-disciplinary, including contributions not only from biology and ecology but also from other applied sciences such as hydrology, agriculture and forest science, and from social sciences and arts as well. With collaboration from many perspectives, richer databases and analytic approaches can be formulated. More significantly, a multi-facetted approach promises better linkage between scientific perspectives and the spatial, temporal, and political structure of decision-making (Lubchenco 1995). Clarifying the scientific status of biodiversity can set the stage for moving the biodiversity debate from one primarily about the facts of the issue to one about values.

This chapter presents a hierarchical framework for assessment and management of biodiversity. The framework advocates (1) understanding associations of biodiversity with environmental factors over large regions, (2) identifying those areas within large regions having species assemblages which contribute the greatest diversity to the biota, and (3) evaluating alternative approaches for managing those important areas in order to explicitly include conservation of biodiversity in land use decisions.

Interaction of Political and Ecological Hierarchies

Hierarchical Structure of Human Decision Making

In Western societies, the hierarchy of sociopolitical entities often follows a common structure, with five to seven levels: villages, towns, or city precincts at the lowest level (smallest human populations); townships or cities at the next level; then counties; states or provinces; multiple state or interstate regions; nations; and finally continents. The boundaries of these entities bear no direct relationship to the spatial boundaries of ecological units, though those at larger extents (e.g., continents) may approximate each other.

Value-based policy about natural resources is usually located at one or more levels in the political hierarchy. For example, an assessment of the implications of alternative biodiversity conservation policies for a state or province must be ultimately constrained to the area within their jurisdiction. However, biodiversity policy for a state or province is more likely to be effective if considered in the context of ecological or biotic regions, of which the state or provincial biota is only a subset for many taxa. Once adopted, a policy applies and is generally implemented by smaller administrative units, such as counties. Therefore the policy must also consider the roles and relative intensity of effort required by smaller units in allocating appropriate resources to get the job done. As a general rule of thumb, ecological policy assessment needs to look both upward for the context at a larger extent and downward for implications of implementation.

The intent of ecological policy assessments varies in emphasis somewhat as a function of scale. Larger government units (nation, state or province) need to efficiently allocate scarce resources to a complex array of ecological issues that they face. While political considerations will always be important, objective policy analysis that suggests priorities in the allocation of resources is particularly useful. To do this one needs an objective way to compare a variety of different issues in common terms. Comparability is a prime criterion.

Smaller political units have less resources to allocate but greater responsibility for management and implementation of policy. Land-use decisions that are likely to affect biodiversity are traditionally made at the county

and municipal level, particularly in the United States. These administrative units may be asked and funded by the nation or state or province to cooperate in a coordinated effort to achieve a larger goal within a relative set of priorities. Ecological management activities at this scale in the hierarchy are likely to be directed much more towards effective, on the ground, conservation activities. For these activities, understanding the particular history and nature of human institutions is important in achieving effective results.

Hierarchical Structure in Ecology

Biodiversity is usually measured at different levels of biological organization: organisms that are composed of cells that contain genes; species populations (or the set of local populations forming a metapopulation) that are composed of individual organisms; communities that are groups of populations interacting with each other; ecosystems that are communities together with their abiotic environment; landscapes that are spatial groupings of ecosystems, and so on to the biome and biosphere. Spatial and temporal scales are conceived as increasing up the hierarchy from genes to biosphere. However, quantifying spatio-temporal scales can be problematical because levels such as populations, communities, and landscapes are open systems with spatiotemporal domains that vary widely among species and processes (Turner 1989, Wiens 1989).

From a different perspective, levels of organization can be viewed as alternative, conceptual constructs that are not hierarchical per se (Allen and Hoekstra 1992). Ecosystem and community conceptions can be compared across a landscape of a given area as well as at larger and smaller spatial extents. A given landscape can be seen to contain smaller landscapes, while itself being a part of a larger landscape. Lastly, community patterns at a given scale may be related to the landscape context at a larger extent. In practice, spatio-temporal scaling is done by the observer so that, at a particular scale, the biological levels of interest appear most cohesive, explicable, and predictable. For adequate understanding, it is necessary to consider three levels and/or scales at once: the one in question, the one below that gives mechanisms, and the one above that gives context, role or significance (Pickett et al. 1994).

The implications of the biological levels of biodiversity for assessment and management are profound. At large spatial extents, biodiversity priorities should take into account the properties of sets of species. A component of prioritization through complementarity analysis is spatial comparison of sets of species to determine those subsets of the whole that give the greatest representation of total diversity in the least number of samples (Williams and Humphries 1994, but see Faith and Walker 1996 for an alternative view). At small extents, assessment and management of biodiversity are more concerned with the functional interaction among the

local set of species. Understanding the mechanisms causing local problems is crucial to solving them.

Subsets of species with similar ecological capabilities provide a functional redundancy that buffers against changes in capacity of any one species of the subset. Since species must co-occur in space to provide redundancy and functional substitution, spatial patterns in diversity are one important descriptor of biodiversity at any scale. Maps of spatial pattern can be useful in setting priorities for biodiversity conservation and in suggesting management options. Spatial pattern recognition is crucial to assessment of risk to values derived from biodiversity and ultimately to managing those risks. Pattern is used as a surrogate measure of process because process is presumed to produce pattern but is more costly and difficult to observe at the large spatial extents relevant to biodiversity (Brown 1995). Therefore, we describe and evaluate patterns of species diversity and anthropogenic and natural modifying factors, and interpret these in the light of processes that are thought to be important at the spatial scale of the study.

Analysis Methods and Data

Types of Analysis

We have incorporated ideas of biodiversity structure and assessment into a hierarchical framework for analysis. At large spatial extents there are two kinds of analyses studying two different questions. First, what are the possible associations of environmental factors with the spatial distribution of biodiversity? Investigations into this question can help to reveal possible mechanisms, including anthropogenic disturbance, responsible for the patterns in biodiversity. These patterns may help to predict biodiversity patterns for areas for which data do not exist, help to predict biodiversity patterns for other taxonomic groups, or help to guide policy development and management implementation by indicating places at greater risk. The second question is, given the distribution of biodiversity, where are the centers, or most important locations, of biodiversity? In other words, with limited resources to study or conserve biodiversity, where are the best places to start further investigations or conservation activities?

For the first question, one approach is a statistical analysis of a response variable representing some measure of biodiversity against a set of predictor variables representing environmental factors, in an exploratory pattern analysis and hypothesis generating mode, rather than in a confirmatory hypothesis testing mode (Brown 1995). Regression trees using the CART methodology (Breiman et al. 1984) are a powerful method for this exploratory analysis. Regression trees can reveal hierarchical spatial structure in the relationship between the explanatory variables and the response, therefore assisting in formulation of hypotheses about mechanisms of control

of the distribution of the response at multiple spatial scales. In regression tree development, the midpoints between all values of all of the predictor variables that are present in the data form the possible splits for the tree. In the first step, sums of squares of differences between the observation response values and their means are computed for all binary divisions of the observations formed by all of the splits. The minimum sum determines the split. The observations are then divided into two sets based on the split and the process recursively repeats on the two descendent sets. Splitting continues until a stopping criterion is reached. We used the cross-validation pruning techniques of Breiman et al. (1984), as implemented by Clark and Pregibon (1992), to determine the optimal size of trees.

The second question can be rephrased as which places in the study area jointly contain the greatest number of species? This is different than the question, which places individually contain the greatest number of species? The answer to the latter is simply those places with the highest total numbers. The most species-rich places will likely have a high overlap in their species lists and may also be concentrated in one part of the study area so that policy targeted there would ignore other less rich but important parts. Places with the greatest joint species richness tend to be located in different parts of a study area, reflecting the contributions of complementary faunas or floras. The complementarity question can be posed with a limit on the number of places, in the manner of an optimization problem. For example, what is the greatest number of species that can be found in any four places? A related question is what is the least number of places to jointly contain all species?

Using optimization methodology, sets of varying numbers of places can be determined as possible answers to questions about important places (Church et al. 1996). We used integer programming optimization techniques (Csuti et al. 1997) to obtain solutions for our case studies. For Oregon the problem size was computing joint species richness for all combinations of 441 hexagons taken 8 at a time (selecting the best eight places), a total of approximately 3.3×10^{16} computations. In Pennsylvania the problem size was all combinations of 211 hexagons taken 6 at a time, a total of 1.1×10^{11} computations. (The number of species is not an important factor in the computational complexity.)

When multiple combinations of places provide optimal coverage of species, this methodology identifies those places that are singularly valuable or irreplaceable because they occur in all combinations, and those places that are optimal but also interchangeable with other optimal places, offering options for conservation activities (Pressey et al. 1993).

Giving all species in an indicator group, such as vertebrates, equal weight in a complementarity analysis invokes the fewest additional assumptions. On the other hand, methods for solving the complementarity problem can be adapted to use species weights based on phylogenetics, ecological function, or conservation ranks (see Chapter 9). If species have

different levels of importance because of different roles in different places, then spatially varying weights could be used.

At the level below the analyses described above, assessment focuses on the question of what are the consequences of possible land use changes at the places identified as important at the higher level, larger area, through the complementarity analysis? Given several places of importance, what should be done about them? One answer is to study the impacts of possible change on the biodiversity of these places. This type of study constitutes a change in scale, now focusing on a local (place or places) scale of concern. Biological data are combined with land use and habitat maps for the existing or current conditions and for one or more alternative scenarios about how the region might change. The alternative scenarios are created to represent a range of possible changes in the amount and spatial distribution of land use and habitat (Harms et al. 1993). With these data, risk statistics can be calculated for various measures of biodiversity, showing the proportion of habitat gained or lost in each alternative scenario relative to the current conditions. This approach can also be used to study change between the current conditions and a reconstruction of past conditions.

Spatial Accounting Units

Different spatial frameworks are appropriate for different levels of analysis. For the larger area studies of environmental associations and of complementarity of biodiversity distributions, a structure that provides comparability is most appropriate (see Conroy and Noon 1996 on issues of using habitat patches). We have used a spatial framework that was designed to provide a regular, systematic, hierarchical spatial structure for environmental monitoring and assessment (White et al. 1992). The basic structure of this framework is a tessellation, or grid, of hexagons of approximately 640 square kilometers in size, with a point-to-point (center-to-center) spacing of approximately 27 kilometers. In the eastern part of the conterminous United States, from about the 103rd meridian eastward, where counties are of a moderately uniform size, this density corresponds, on the average, to about two and two-thirds hexagons per county.

The hexagon sampling cells provide an accounting mechanism that serves several purposes. First, a single set of analysis units facilitates comparison of different data sets. Second, some of the uncertainty in species occurrence data obtained from range maps can be accounted for by limiting the precision of location assignment to this grid. But in addition, concerns about the confidentiality of precise locations of occurrence for certain rare species may be alleviated by generalizing the location assignment to the grid. Finally, there is a theoretical argument for generalizing species distributions from the precise data of field observations in order to account for the biases in observation locations and the presumed broader distributions over time.

It is an advantage to use equal area accounting units, other things being the same. The equal area grid provides a common spatial unit for comparison of diverse data types whereas ecoregions, for example, are not comparable, rather they are by definition unique. Equal area units also minimize confounding due to species-area relationships, a potential problem if units such as counties in the USA are used (for example, Dobson et al. 1997). A hexagon tessellation minimizes spatial distortion and provides an equal area sample (if constructed on an equal area map projection). Furthermore, hexagons are generalizable to both larger and smaller spatial scales. This becomes important for extending assessments to continents and the globe.

The size of the accounting units reflects a compromise between the desire for spatial detail, on the one hand, and the constraints of reasonable spatial representation of species life histories, of data collection, of confidentially, and of computational feasibility, on the other hand. Solutions to statistical analyses of associations and to complementarity analyses can depend, of course, on the size selected (Stoms 1994).

For the assessment of impacts of alternative futures in a smaller area, a more appropriate spatial structure is the ecological units that comprise the study area, usually patches of habitat. Patches may be defined as polygons or aggregates of remote sensing pixels, depending on the source of data.

Biodiversity Response Variables

In choosing how to represent biodiversity in analyses, one principle is that it is preferable to base the response variable on well-defined concepts. In this view genes and species should form the basis for the mapping and monitoring. Because of the practical impossibility of using the gene level we are led to using species. Although there is considerable controversy about the details of the theory of species (biological species concepts versus evolutionary species concepts, for example, see Rojas 1992; Bush 1993), in our applications it is clear in most cases how to decide which species to consider. For a contemporary assessment, where we have a single slice through time, the biological and evolutionary species concepts largely overlap and species are considered to be more or less independent collections of genes (among other things). Hence species have their own identity and are good surrogates for genetic diversity. So our metric of choice to quantify biodiversity for analysis is species richness.

Our objective was to describe the distribution of biological species across the conterminous United States. We have chosen to work with The Nature Conservancy and its cooperating network of state Natural Heritage Programs to begin developing the first comprehensive nationwide database that includes standard range information from published literature and expert sources plus specific location data on plants and animals of conservation concern that has been assembled by TNC (Master 1996). These

data sets include all vertebrate species, butterfly and skipper species, tree species, and freshwater mussel species for hexagons covering the states of Washington, Oregon, California, Pennsylvania, Maryland, Delaware, West Virginia, and Virginia. For each species in each hexagon of states initially sampled, the following information was recorded: the occurrence status (confidently assumed or known, probable, possible, or not present); the origin of the species in the hexagon (native, introduced, reintroduced, or unknown); the best source of information for the occurrence information; and residency (year-round/seasonal) and breeding (confirmed, probable, nonbreeder) status for migrant species (e.g., birds, bats). The occurrence status is more precisely defined as "confident or certain" (> 95% chance of occurrence), "predicted or probable" (80% - 95% chance of occurrence), "possible" (10% - 80% chance of occurrence; this category may not be used), and "not significant" (< 10% chance of occurrence). Taxonomic experts in each state extensively reviewed the assignments of species to hexagons.

Explanatory Variables

Among the processes that have been hypothesized to account for spatial patterns of species diversity are climatic extremes, climatic stability, productivity, and habitat heterogeneity (Brown and Gibson 1983, Wickham et al. 1997). Data sets were assembled from existing sources to represent these processes.

Data were compiled for topographic elevation, January and July temperatures, and annual precipitation on a rectangular grid at a resolution of 1 kilometer for the conterminous United States. The elevation data were derived from a 15 arc second digital elevation model obtained from Sue Jensen at the USGS EROS Data Center, by projecting and resampling to the coarser resolution. January and July mean temperature data were modeled and compiled using the method of Marks (1990). The initial data values were the means, over the 40 year period from approximately 1948 to 1988, of the means, over the respective month, of the daily mean temperatures at approximately 1,200 stations in the Historical Climate Network database. These values were first corrected to potential temperatures at a reference air pressure of 1,000 mb using the station elevations and assuming a normal adiabatic lapse rate. The potential temperatures were then interpolated to the 1-km grid using a linear model. Finally, the interpolated values were then converted to estimated actual temperatures from the adiabatic lapse rate correction using the corresponding elevation values at each grid point. Annual precipitation data were compiled from the 10-km resolution dataset prepared by Daly et al. (1994). These authors used a locally adaptive regression model to estimate annual precipitation values for unknown locations from known stations and from the elevation structure in the local

region. The 10-km data were interpolated to 1 km using a linear model.

Data for stream density were developed from the USGS/EPA River Reach File, version 3, corresponding to, and derived from, in part, the USGS 1:100,000 Digital Line Graphs for hydrography. The USGS AVHRR land classification (Loveland et al. 1991) and the USGS Gap Vegetation Classification Map for Oregon (Kagan and Caicco 1992) provided representations of land cover and vegetation heterogeneity. The AVHRR data also provided a measure that estimates net primary productivity, the Normalized Difference Vegetation Index (NDVI) (Reed et al. 1994). Data for road density and human population density were developed by Wickham et al. (1997).

All data not collected by hexagon cells were aggregated or summarized by cell with several statistics, including the mean, median, minimum, maximum, range, and standard deviation. The AVHRR and Gap Vegetation data were converted to class richness values by cell. Slope statistics were calculated from the elevation values in each cell.

Results of Analyses

We will describe examples of analyses at two scales. The regional analyses of environmental associations and complementarity of biodiversity distributions were done in the states of Oregon and Pennsylvania (Fig. 8.1). Based partly on these analyses, landscape level analyses were conducted within the two states, one in a county of Pennsylvania, and the other in a small watershed in Oregon.

Environmental Associations

This analysis investigated the relationship between bird species richness in Oregon and climatic, topographic, hydrographic, land cover, and anthropogenic variables. Richness values were the sum of native summer resident breeding bird species in each hexagon, from a total of 252 species for the state as a whole. Regression tree analysis was used to predict the number of bird species by hexagon grid cell across the state.

The final tree had 6 leaves, or terminal nodes, and used 4 of 19 possible predictor variables to explain 73% of the variation in the response variable (Fig. 8.2). To interpret the tree, a map (Fig. 8.3) of the cases belonging to each leaf is very helpful (O'Connor et al. 1996, White and Sifneos 1997). The most important predictor variable for the data for the state as a whole was minimum elevation which separated a lower richness area in most of western Oregon and the Columbia Plateau from the rest of the state. This split confirmed the strong east-west division in Oregon formed by the Cas-
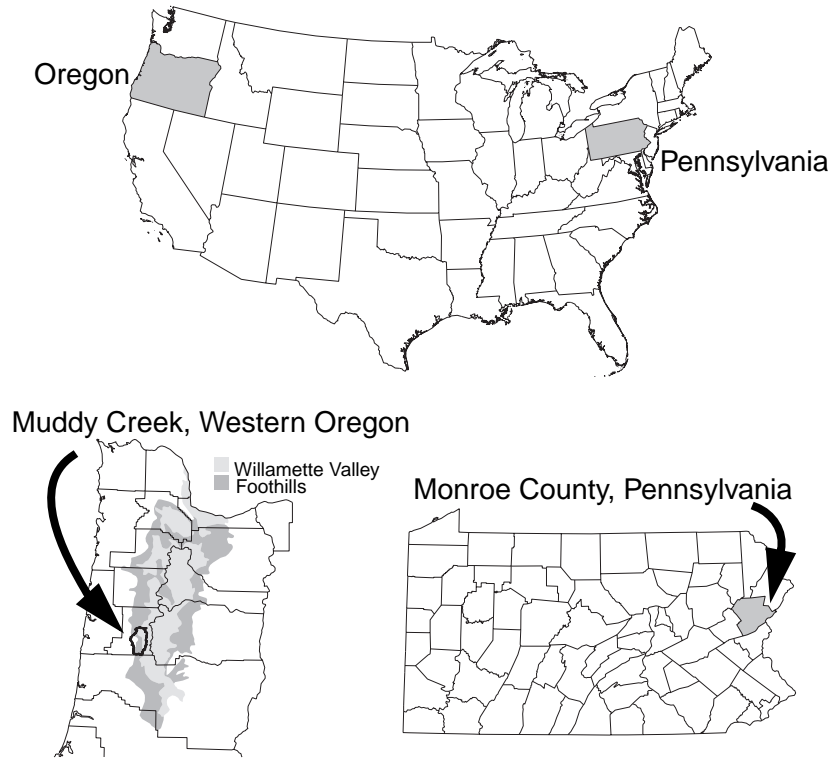
FIGURE 8.1. Locations of study areas for biodiversity analyses are Oregon and Pennsylvania. One landscape level study is set in Monroe County, Pennsylvania and the second in the Muddy Creek watershed in western Oregon.

cades Mountains. Lower species richness in the west was not expected, however. The second split was based on AVHRR-derived total NDVI and separated the drier, less-productive parts of eastern Oregon having lower species richness from the remainder of the hexagons that were more forested and had greater species richness. The drier part of the eastside was further split by the number of Gap vegetation classes into a larger group of hexagons that was less rich both in vegetation and in bird species, and into the remaining hexagons associated with playas, permanent lakes, or higher elevation mountain ranges, hexagons that had a higher average species richness. The other two splits in the tree were based on annual precipitation. The first of these separated higher precipitation, higher elevation hexagons in the Cascades and other high mountains having lower species richness from the remainder. Hexagons remaining from this split were separated by the final split into dry, less rich areas at the margins of the forested part of the eastside, and the core of the forested areas of the eastside

that, among all the groups identified, had the highest average value species richness.

How does this prediction geography in Oregon correspond to knowledge of patterns in other areas?   At a global scale, higher species richness is generally associated with areas that are: (1) warmer rather than colder, (2) wetter rather than drier, (3) less seasonal rather than more, (4) more varied in topography and climate rather than less, and (5) larger rather than smaller (Caldecott et al. 1996, but also see Scheiner and Rey-Benayas 1994). The last condition does not apply because equal area accounting units were used. Three of the other global patterns were contradicted in the study. Western Oregon is distinguished from eastern Oregon by having greater annual precipitation, less seasonality, and slightly greater mean annual temperature, yet bird species richness was lower in western Oregon than in large areas in eastern Oregon. Only association (4) may have been par-

Elevation.Minimum <> 343.5
134 species; 391 cases; 28.3%

A

117 species
115 cases

AVHRR.Total.NDVI <> 40.6
141 species; 276 cases; 28%

GAP.Veg.Classes <> 10.5
123 species; 95 cases; 3.8%

Annual.Precip.Mean <> 1300.5
150 species; 181 cases; 8.4%

B

121 species
85 cases

C

146 species
10 cases

Annual.Precip.Mean <> 292
153 species; 157 cases; 4.1%

F

128 species
24 cases

D

131 species
12 cases

E

155 species
145 cases

Total variation explained = 73%

FIGURE 8.2. The regression tree for bird species richness has five splits using four different predictor variables resulting in six leaves. Each split indicates the splitting value of the splitting variable, the number of cases considered at the split, the mean value of the response variable for those cases, and the amount of variation explained by the split.

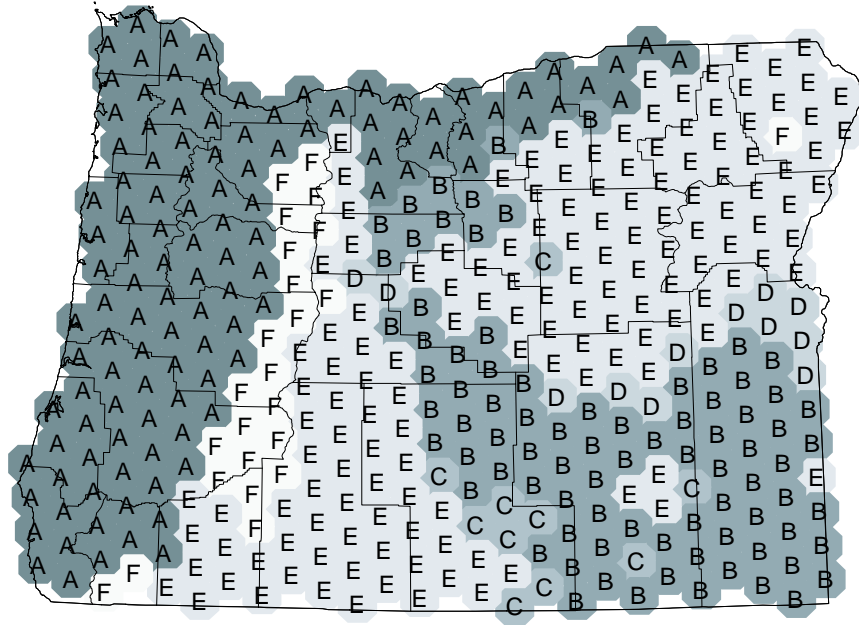## Prediction Geography for Bird Species Richness

FIGURE 8.3. The map of the cases belonging to each leaf has a highly structured geography. The boundary between western and eastern Oregon is usually considered to be the crest of the Cascade Mountains. This boundary appears on the map, for the most part, as the boundary between "F" and "E" hexagon cells trending primarily north-south about one-third of the distance from west to east across the state.

tially demonstrated by the split on Gap vegetation class richness.

So how is the prediction pattern to be explained? Leaves "A" and "E" covered much of the forested area in Oregon, but "E" hexagons had a mean response that was 38 species greater than "A" hexagons. One hypothesis is that, historically, conifer forest cover in western Oregon was so continuous and homogeneous in flora and structure that bird habitat was limited compared to the more open and varied habitat in eastern Oregon forests. The eastern Oregon areas represented by leaf "A" in the Columbia Plateau have an environment more like that of leaf "B" hexagons, and, in this study, had a similar richness level. Other splits in the tree suggest other mechanisms. The split on AVHRR Total NDVI is consistent with studies showing that species richness is positively correlated with higher available energy (e.g., Wright et al. 1993), indicated in this case by higher net primary productivity which is correlated with higher total NDVI (Reed et al. 1994). The first

split on precipitation separated high precipitation, higher elevation hexagons much of whose precipitation is in the form of snow; their lower richness values compared to the other half of the split may correspond not to absolute precipitation but to cooler temperatures and reduced winter habitat due to snow cover. The second split on precipitation separated very dry hexagons with lower richness values from the large group of high richness value hexagons. This split was consistent with theory.

Three anthropogenic variables were included in this study, human population density, road density, and number of introduced species, but none entered into the model. Reasons for the lack of association with indicators of human disturbance may be that the scales of disturbance do not coincide with the scale of study (for example, disturbances at a smaller grain than 640 km^2), that Oregon is not affected by such disturbance, or that Oregon is not yet affected by such disturbance. In a related study (Rathert et al. 1999), richness in introduced fish species was positively associated with richness in native fish species. This finding could correspond to the hypothesis that in the initial stages of intensive human occupation (as in the past 150 years or so in the western United States) humans are positively associated with biodiversity since humans are attracted to the same places as many other vertebrate species. Only after humans come to dominate a landscape for some decades or perhaps centuries in duration, does their disturbance eventually reduce native species presence by a significant amount. If, during the initial period of human occupancy, species diversity is increased by increased habitat heterogeneity, or by introduced species such as in the fish example, then it may be reasonable to think of a regional analogue of the intermediate disturbance hypothesis (Connell 1978). Effects like these on diversity may sometimes be captured by statistical modeling techniques (Wickham et al. 1997).

Complementarity of Species Distributions

Studies of complementarity used species lists in cells of the hexagon grid in Oregon and Pennsylvania. In Oregon the study included all native vertebrate species, divided into two groups: fish (67 native species) and all others (457 native amphibian, reptile, bird, and mammal species, hereafter called "terrestrial," recognizing that a number of species could also be considered aquatic, e.g., frogs). In Pennsylvania 323 native terrestrial vertebrate species (same definitions as in Oregon) were studied.

In the analysis for Oregon, we computed complementarity for eight places for both fish and terrestrial vertebrates. In eight places, about 96% of the terrestrial vertebrates were included but only about 76% of the fish species. The locations of the places that comprised the sets of eight places were different for fish than for vertebrates and were positioned in different parts of the state (Figs. 8.4 and 8.5). In complementarity analyses, there is often more than one optimal or exact solution for a given number of places.
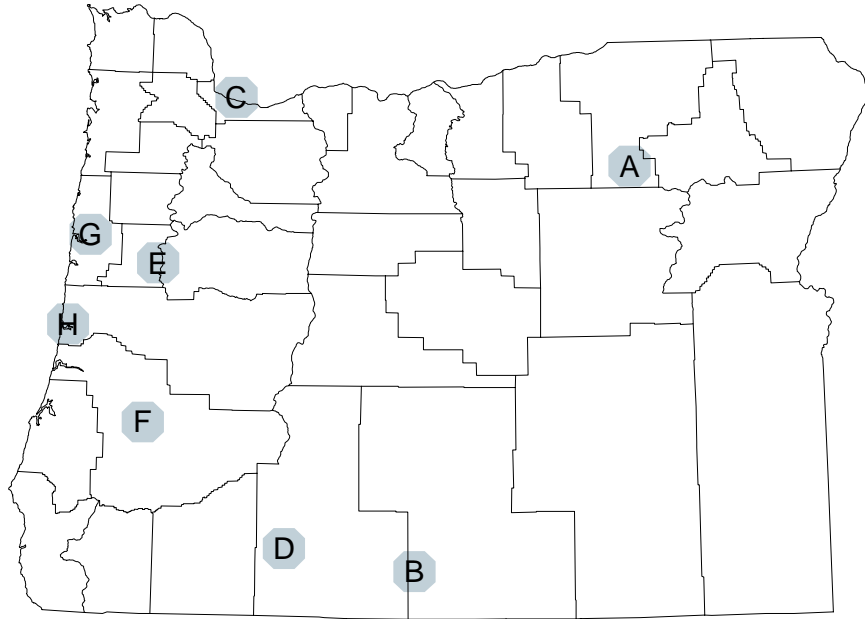
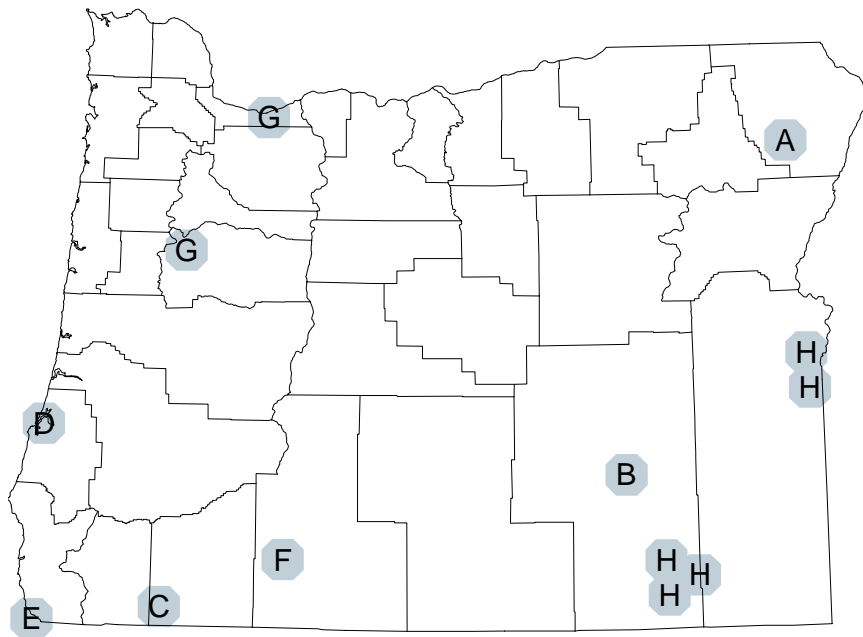Eight places cover 76% of 67 species

FIGURE 8.4. One combination of eight hexagons covers (i.e., contains in the joint species list) 76% of the native fish species in Oregon. There is no necessary priority to the eight hexagons; collectively their complement of species is the greatest for any combination of eight hexagons. Of course, some hexagons have more unique species than others.

Thus the five hexagons labeled "H" and the two labeled "G" in Figure 8.5 made similar, though not necessarily identical, contributions to the joint species richness. Each combination that has the highest joint richness included only one of the two "G" hexagons and one of the five "H" hexagons. When the solutions for the sequence of one place, two places, and following are examined, the pattern often resembles a recursive partitioning of the study area (see Kiester et al. 1996). These optimal coverage solutions had a quite different geography than the sets of the eight highest individually rich hexagons. For terrestrial vertebrates, for example, the eight richest hexagons were all in the south central and southwestern part of the state (Fig. 8.6). Also, the total coverage for the eight richest hexagons was substantially less than the optimal coverage: 72% for vertebrates and 31% for fish.

Because the optimal solutions for terrestrial vertebrates are located in different places than those for fish, it is fair to ask how well do the solutions for one set of species cover the other. For a single group, the percentage of species covered, by the sequence of solutions from one place to the number of places required to totally contain all species increases steeply in the initial

steps but levels off as the total number of species is approached. The first step accounts for the most species and each additional step captures successively fewer. Now, in each step of the solution for one group of species, for example, terrestrial vertebrates, we can compute how many species of the other group are covered in the hexagons that comprise the solution, and vice-versa (Figs. 8.7 and 8.8). These "sweep" analyses (Kiester et al. 1996) tell different stories. Terrestrial vertebrates are completely covered in 20 hexagons, but a mean of only about 50% of the fish species are covered in the set of solutions for complete terrestrial coverage (Fig. 8.7). Conversely, in the set of solutions that completely cover all fish species, also requiring 20 hexagons, coincidentally, a mean of about 93% of the terrestrial vertebrate species are covered (Fig. 8.8). However, the number of species not covered is about the same in both cases: 34 terrestrial vertebrate species not covered by fish and 33 fish species not covered by terrestrial vertebrates.

In Pennsylvania, the solution for six places for terrestrial vertebrates spreads the solution sites across the state much as in Oregon (Fig. 8.9). In this case there are also multiple combinations, using one of the two "E" hexagons and one of the four "F" hexagons. (All combinations of the iden-

Eight places cover 96% of 457 species

FIGURE 8.5. There are multiple combinations of eight hexagons that cover 96% of the native terrestrial vertebrate species in Oregon. Hexagons with the same letter comprise a group from which only one participates in any of the optimal combinations. Often, but not always, members of such groups are located in proximity.
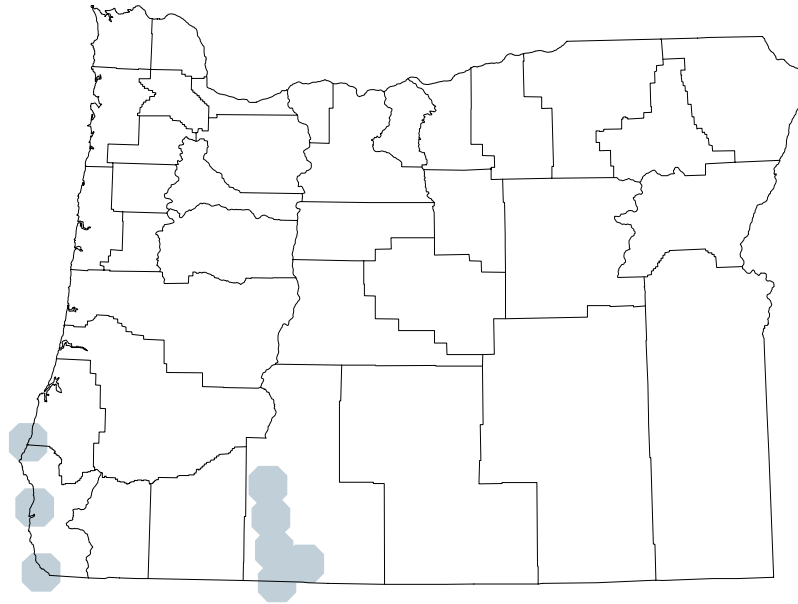
Eight individually richest places

FIGURE 8.6. The eight hexagons with the greatest richness values for native terrestrial vertebrate species in Oregon are concentrated in the Klamath Falls area and along the south coast. The maximum value of richness is 275 species.

tified hexagons may not be maximal solutions; in the Pennsylvania example, there are eight possible combinations of six hexagons, taking one from each letter group, but only six of these contain the maximum number of species.)

Because the size of the accounting units in the complementarity studies are a compromise, some species will be better represented through this process than others. The solutions are not absolute spatial locations for conservation activities, but initial approximate representations of complementary biodiversity assemblages. Thus, it is important to ask what happens next after producing these solutions. We will focus on two studies at a finer scale whose locations in Oregon and Pennsylvania were partly identified through complementarity analyses at the larger extents. The target areas are suggested by the "E" hexagon in northeastern Pennsylvania (Fig. 8.9) and by the "E" hexagon of the fish solution in west central Oregon (Fig. 8.4).

Assessment of Alternative Future Landscapes

Monroe County is located in the Poconos region of Pennsylvania (Fig. 8.1). This region has been a vacation and second home destination since

the nineteenth century and has recently begun to increase more rapidly in human population through suburban development. Projections to the year 2020 suggest that population may double in the county. These changes threaten some of the natural values of the region, including its contribution to state level biodiversity as indicated in Figure 8.9. With respect to these projected changes, the impacts of possible future land development patterns on biodiversity were investigated (White et al. 1997).

Land cover data for this study included a remote sensing derived map of the current habitat in the county developed initially at Cornell University (Smith and Richmond 1994) and refined at Harvard University (Steinitz et al. 1994). The Harvard group also developed six maps of future habitat distributions resulting from different land development scenarios envisioned in consultation with stakeholders within the county. Biodiversity was represented as lists of 147 bird, 44 mammal, 20 reptile, and 20 amphibian species, all considered to be native to the study area, and the habitat associations for these species (obtained from Smith and Richmond 1994). In addition, White et al. (1997) estimated breeding area requirements for
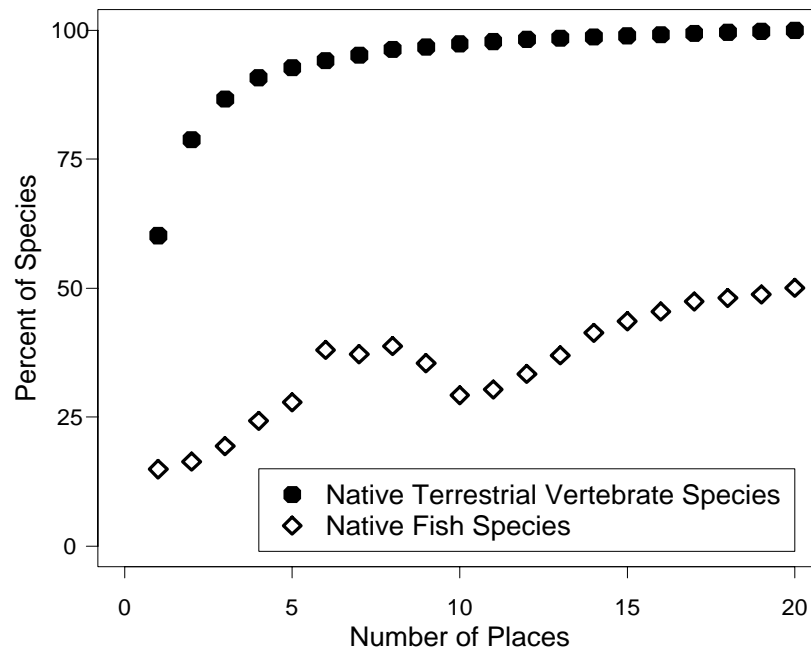

FIGURE 8.7. The solid symbols trace the accumulation of percentages of terrestrial vertebrate species covered in successive optimal solutions for joint species richness. With one hexagon about 60% of the species are covered; with two about 79%, and so on to 100%. In the hexagons that comprise these solutions, the corresponding percentages of fish species covered ("swept" along and symbolized in the open symbols) are 15%, 16%, and so on, up to a maximum of 50%.
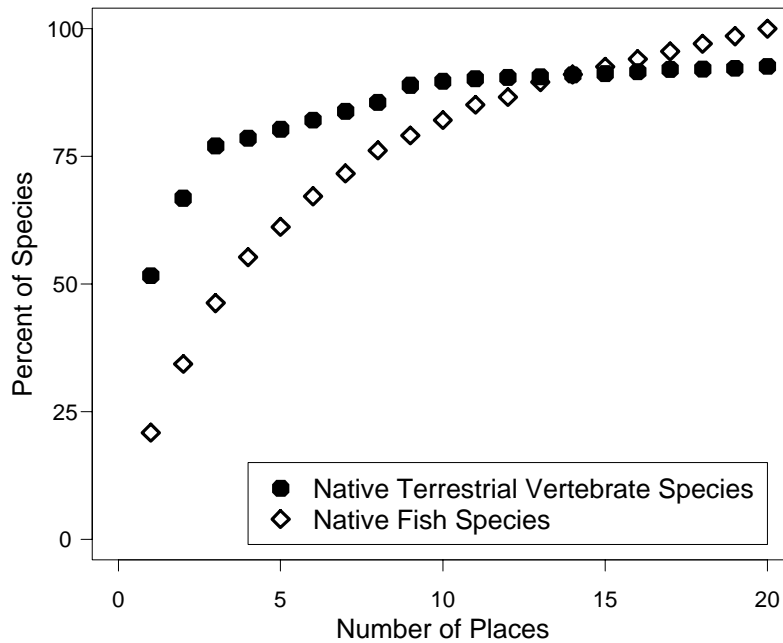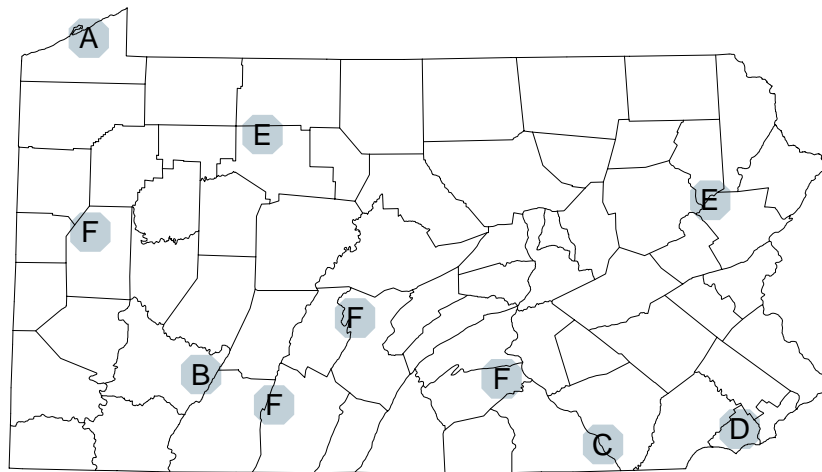
FIGURE 8.8. The counterpart to Figure 8.7 shows that when fish are optimized, coverage starts at about 21%, then 34% and so on to 100%. The corresponding percentages of vertebrates swept along are about 52%, then 67%, and so on up to a maximum of 93%.

Six places cover 95% of 323 species

FIGURE 8.9. The optimal set of solutions for six hexagons in Pennsylvania consists of six solutions of six hexagons having the maximum number, about 95%, of the native terrestrial vertebrate species.

each species using home ranges, sampled population densities, or genetic area requirements that incorporated dispersal distances.

In this study, measures of biodiversity were species richness and indices of population abundance based on availability of suitable habitat. Indices of population abundance for each species were calculated in two ways. First, total habitat area was computed for each species in each landscape. Second, the number of breeding habitat units for each species in each landscape was calculated by dividing the size of each habitat patch in the landscape by the area requirement and summing over all patches. Species richness was based on presence of habitat so that species became locally extinct in the landscape only if they had no habitat area or no habitat units. For each species, ratios of abundance in each future scenario to abundance in the present were computed. The ratio of future to present species richness was also computed. Summary statistics were calculated across all species and subtracted from one to obtain a measure of risk.

Species richness changed little from present to future. However, there were distinctly greater risks to habitat area in scenarios that extrapolated from present trends or zoning patterns (Plan Trend and Build Out) as opposed to scenarios in which land development activities were designed to follow more constrained patterns (Township, Spine, Southern, Park). All taxonomic groups followed similar trajectories; amphibians had the greatest risk across all scenarios (Fig. 8.10). These results were similar for both indices of population abundance. Sensitivity analyses indicated that the results were robust to errors in the estimates of area requirements. Studies in progress refine the initial approach to include the use of habitat quality metrics in the species-habitat association matrix and a more restrictive definition of suitable habitat in relation to area sensitivity and interior/edge habitat preferences of some forest bird species.

The other study took place in the Muddy Creek watershed in western Oregon (Fig. 8.1). This 320 km^2 watershed includes commercial forest land in mid and high elevations, Christmas trees, vineyards, orchards, pasture, and mixed woodlands in mid-elevations, and primarily grass seed agriculture plus a wildlife refuge in low elevations. Current human settlement consists of about 1,200 households, located in one village in the lowlands and scattered rural residences in the low and mid-elevations. Anticipated growth to the year 2025 is between one third and two thirds of current population. (More complete descriptions of all aspects of this project are [in 1998] at the world wide web site http://ise.uoregon.edu).

For this study, University of Oregon researchers assembled a map of current conditions from several sources of remote sensing and from field work, as well as maps of other physical features, state land use zones, and land ownership. They then worked closely with stakeholders in the watershed to formulate a sequence of possible future landscape scenarios, arranged in a gradient from a high development oriented scenario to a high conservation oriented scenario. The midpoint in the gradient was consid-
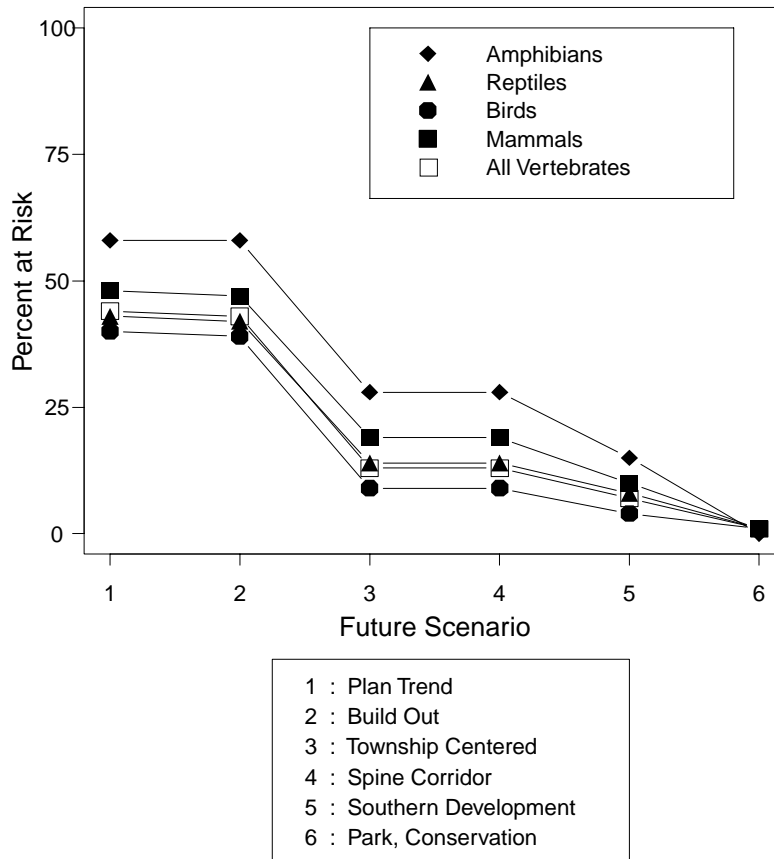
Figure 8.10. The percentage of habitat area at risk of being lost in Monroe County relative to the present conditions varies by taxonomic group and by future scenario.

ered the most likely scenario and labeled Plan Trend. The scenarios incorporated projected human population growth ranging from 10% to 100%. In addition to these future scenarios, the project acquired a map of pre-settlement vegetation for the watershed that was interpreted and interpolated by the Oregon Natural Heritage Program from General Land Office surveyors' notes (Christy et al. 1996-1997).

In consultation with local experts, Freemark et al. (1996) compiled lists of historical and current breeding species for the watershed (including 135 bird, 71 mammal, 16 reptile, and 14 amphibian species), and a species-habitat association matrix. Of the 236 species, 1 amphibian, 3 bird, and 4 mammal species had been permanently extirpated from the watershed since the time of European settlement; 8 bird and 2 mammal species native to the watershed were deemed rare (including currently extirpated); 1 am-

phibian, 1 reptile, 6 bird, and 6 mammal species were introduced. Using the methodology of the Monroe County study, risks for each species were calculated from habitat area in the future (or pre-settlement past) compared to the present, for various groups of species, subset by taxonomy, conservation status, and ecological function.

For all native species groups except reptiles, risk was greatest in the high development scenario and declined across the gradient of future scenarios (Fig. 8.11). Values for non-reptile species for the two conservation scenarios and for the pre-settlement scenario were negative, indicating improvement over the present. The trend across future scenarios was similar for all taxa except reptiles; amphibians had the greatest change, from risk
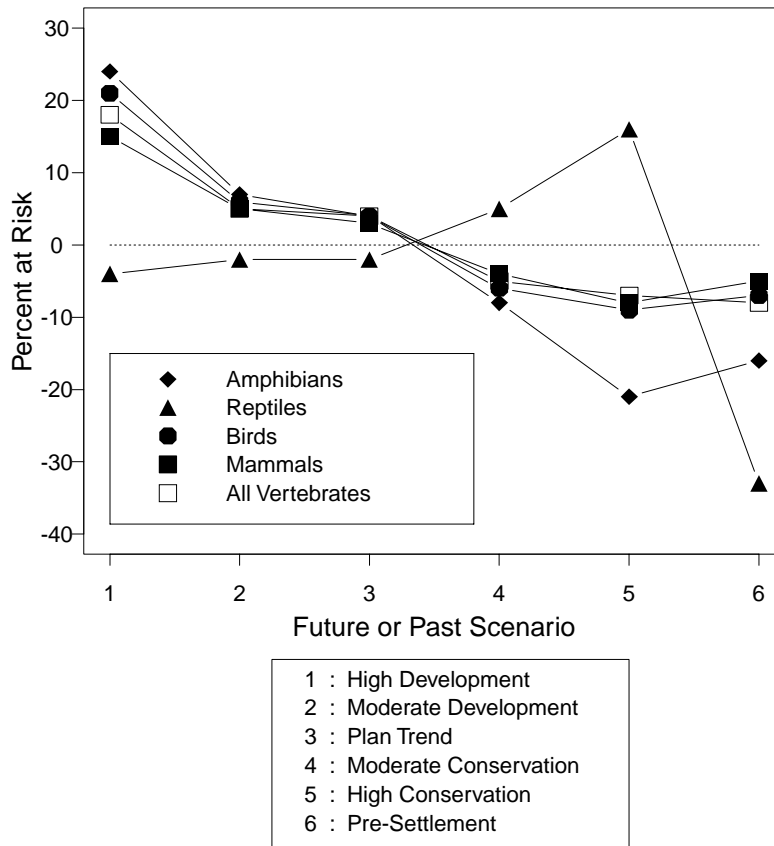
FIGURE 8.11. The percentage of habitat area at risk of being lost in the Muddy Creek watershed also varies by taxonomic group and by future scenario. All groups show a loss, indicated as a negative risk, between the reconstructed past landscape pattern and the present. Reptiles in Muddy Creek respond oppositely to the other taxonomic groups.

in high development to improvement in high conservation. Reptiles had the greatest loss from the pre-settlement to the present. The contrary response of reptiles is due primarily to their preferential assignment to non-forested, open habitat types. These habitat types were less abundant in the conservation scenarios than in other scenarios and much more abundant in the pre-settlement scenario.

These two studies demonstrate methods to discriminate the effects of potential changes in land development on biodiversity and thereby help inform the decision-making process. It is important to note that the modeling methodology begs the question of the viability of populations for any particular species. Abundant species with small ranges, or small area requirements for breeding, may be assessed much better than rare species or those with wide ranges or large area requirements. To look at all species adequately requires a hierarchical scope of study ranging from local to global. To look at the viability of any individual species in detail requires demographic modeling (Dunning et al. 1995).

Summary

The hierarchical framework presented suggests that understanding the distribution of species over large areas and then selecting important subareas for conservation actions can be usefully followed by looking at the consequences of possible landscape changes in those important subareas. Consequences at the landscape level can help to inform policy decisions over the larger area by providing additional information on risks for specific subareas. When a complementarity analysis over the larger area includes options of multiple subareas, understanding specific consequences can help to further prioritize where to initiate actions.

We believe the hierarchical framework makes several contributions to biodiversity conservation. First, it helps improve knowledge regarding the importance of different areas and environmental factors in contributing to the biodiversity of species, habitats and ecosystems at different spatial scales. Many investigators have studied the distribution and possible causes of biodiversity. Our work has had a specific focus of understanding the hierarchical structure of prediction and the geography of explanatory relationships. Within Oregon, for example, the relationship between bird species distributions and environmental factors appears to depend more on regional history and mechanisms than on global patterns. An important research direction is the identification of the possible effects of human activities over a national or continental extent (O'Connor et al. 1996).

Second, the framework helps to identify species and regions that are poorly represented by current conservation activities, and that may benefit from applying integrated planning for biodiversity conservation. This aspect of our work is very similar to goals and methods of the USGS Biolog-

ical Resources Division's Gap Analysis Program (Scott et al. 1993; Csuti and Kiester 1996). Complementarity analyses explicitly show important areas of biodiversity. Combining this with knowledge of existing protection areas reveals gaps in coverage and targets for conservation planning.

Third, the focus of biodiversity conservation is extended beyond rare, threatened or endangered species or ecosystems to more comprehensive sets of species. This methodology has included comparing the effectiveness of determining conservation priorities by one taxonomic group versus another. For states for which there are vegetation maps, similar analyses can be conducted to determine how conservation priorities based on habitat coverage compare to animal or plant species priorities. In this way the approach contributes to integrating species-based and ecosystem-based assessments.

Fourth, the kinds of assessments are expanded to include the evaluation of alternative conservation strategies through collaboration with landscape planners (Rookwood 1995). These alternative future scenario projects provide a reasonable cost method for considering future impacts of human activities on biodiversity. The concerns of local stakeholders can be incorporated into the future visions and a range of future options can be considered, including restoration to earlier more pristine conditions or development to total urbanization, as appropriate. In addition to synthesized designs for alternative future scenarios, more formal allocation rule systems offer a more objective and controlled method for generating future possibilities (Bettinger et al. 1996).

Additional research projects associated with the work reported here seek to improve knowledge of the economic feasibility and sociopolitical acceptability of alternative conservation strategies (protection, mitigation, restoration). Another project is combining complementarity analyses of species distributions with economic constraints to address the question of where are the best places to conserve biodiversity under a limited budget (see Chapter 9).

Finally, these ideas provide a conceptual and spatial framework for decentralizing resource management decision-making to more local levels, while maintaining the larger spatial perspectives necessary for sustainable resource use. This hierarchical perspective and framework for science, policy, and management responds, we believe, to the challenge of developing more comprehensive strategies for conservation of biodiversity.

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