LINKING MODELS OF SPECIES OCCURRENCE AND LANDSCAPE RECONSTRUCTION

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Ecologists and land managers around the world are charged with first arresting and then reversing declines in native species. Revegetation has been proposed as one of the mechanisms by which landscapes can be rehabilitated to support viable populations of native wildlife. Because large-scale revegetation often proves to be technically difficult and costly, it is critical to evaluate the likely outcome of alternative proposals for landscape reconstruction. Here we describe a new approach for examining the potential effects of spatially extensive ecological restoration on species of concern. Our method links validated models of species occurrence with GIS-based models of various revegetation scenarios to estimate the range of biodiversity responses under each option.

Explaining and predicting species occurrence long has been a major goal in ecology, conservation biology, and wildlife management (Rosenzweig 1995, Mac Nally 1995, Bell 2001). There are many possible ways to predict species occurrence. Traditional 'habitat modeling'-predicting occurrence as a function of resource requirements, such as food sources or nesting sites-may have a high probability of success (Hanski 1999, Miller and Cale 2000), but obtaining such data can be expensive, particularly over extensive areas. Therefore, predicting species occurrence as a function of environmental variables that can be quantified easily, at small spatial grains, and over large areas, is appealing (Austin et al. 1990, Guisan and Zimmerman 2000, Jackson et al. 2000).

We recently developed a statistically rigorous framework for examining the generality of predictors of species occurrence using an iterative process of model building, testing, and refinement (Fleishman et al. 2001, in press). We make extensive use of Bayes-based methods, which facilitate more detailed and practical assessment and improvement of predictions than conventional approaches (Ellison 1996, Sit and Taylor 1998). Our framework seeks to identify predictors of species occurrence at grain sizes on the order of several km^2 over extents of 100s to 1000s of km^2. This corresponds to the scale at which many land-use decisions must be made.

To be useful, the predictions of species-occurrence models must be tested using explicit standards (Guisan and Zimmerman 2000, Jackson et al. 2000). We test our models-which effectively are hypotheses about predictors of species distributions-using independent data that were not used to build the models (Fleishman et al. in press). The process of generating and testing model predictions increases our understanding of relationships between organisms and environmental variables and contributes to the scientific foundation for regional conservation and management (Mac Nally and Bennett 1997, Hawkins et al. 2000, Mac Nally et al. 2000).

Species-specific occurrence modeling has been employed widely in the past (Braithwaite et al. 1989, Lindenmayer et al. 1990, Scott et al. 2002), but occurrence models rarely have been linked with GIS-based models of alternative management strategies or revegetated landscapes (Bennett 1999, Marzluff et al. 2002). The alternatives we develop are based on ecological vegetation classes, which are defined as one or more similar floristic communities that exist under a common regime of ecological processes and that are linked to broad landscape features (Muir et al. 1995). Because ecological vegetation classes are closely connected with broad-scale topographic, edaphic, and climatic variables, they are a useful link between vegetation and landscape-scale planning and management. Alternatives vary with respect to the amount and spatial configuration of different ecological vegetation classes. Our approach recognizes that not only is there a spectrum of habitat quality (McIntyre and Barrett 1992), but also that animals respond to more than one vegetational community (Mac Nally et al. 2002).

Connecting occurrence models with revegetation models allows us to estimate the quantity and distribution of suitable habitat for each species that would be available under each scenario. By treating models for individual species as probabilistic, we can generate ranges of outcomes (i.e., confidence intervals) for each alternative. Thus, we can gauge the overall potential of each alternative to achieve specified ecological objectives.

MODELING FRAMEWORK

Our modeling approach involves 4 main steps. We have successfully applied the first 2 steps to a study system in North America. We currently are laying the biological and collaborative groundwork to apply all 4 steps to a second study system in Australia. First, we develop species-specific occurrence models (Fleishman

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et al. 2001). We derive potential predictors of species occurrence, such as elevation, topographic heterogeneity, and precipitation, from GIS-based models of topography and climate. We have devised a process to exhaustively search through millions of possible models for each species of animal (there are 2^Q models for Q predictor variables). After reducing the set of predictors to a relatively small number of variables (usually ≤ 6), we fit models using Bayesian logistic methods. Bayesian approaches are useful because they generate distributions (rather than point estimates) for the probability that a species will be present in a given location.

Second, we validate the models by conducting new, independent field surveys of species occurrence at locations that were not used to build the models (Fleishman et al. in press). The Bayesian model for each species, with computed regression-coefficient distributions, is used with data for the predictor variables from the new locations to generate probability distributions for occurrences at those new locations. The reliability of species-specific models is assessed by compiling the numbers of successful predictions. This phase also identifies those species whose distributions are either inherently difficult to predict or for which model predictions are poorer than expected. In many cases, validation data can be used to improve models (i.e., to alter values of model parameters or to remove or include different independent variables). Third, we use GIS to specify alternative reconstruction scenarios-to emulate alternative distributions of ecological vegetation classes across the landscape. This approach is applicable to virtually any landscape, and scenarios can be based on any combination of ecological, land management, or economic criteria. For example, we can simulate how the percent cover of native vegetation in the landscape might be increased to a target threshold by replanting (1) different amounts of the most depleted ecological vegetation classes, (2) locations least able to support economic uses such as agriculture, (3) locations that have been subject to the most severe human impacts, or (4) ecological vegetation classes that are least expensive and most biologically feasible to restore. In practice, creation of explicit scenarios will depend on the physical and biological attributes of the planning area and the priorities and constraints of the relevant public or private land managers.

Finally, we link the alternative reconstruction scenarios with the species-specific models to evaluate the potential effectiveness of each scenario in sustaining or increasing native biodiversity. Again using GIS, we compute species-specific logistic models corresponding to each alternative reconstruction scenario. This step provides probability fields of occurrence across the landscape based on the pertinent environmental variables. For each species, we estimate the total area that would be "highly likely" (say, $\geq$ 70% probability) to support the species according to each reconstruction scenario. After the species-specific results have been computed, we can estimate the biological success of alternative scenarios using a variety of criteria. For example, we might simply calculate total area with a high probability of supporting occupancy. We also might differentially weight taxa by conservation concern-e.g., high weightings for threatened species, no weighting for ubiquitous species.

CASE STUDIES

We focused on butterflies in the Great Basin of western North America as our initial study system. In temperate ecoregions, butterflies are well understood ecologically, easy to study and monitor, and may respond rapidly to management (New 1991, Holl 1995, Blair and Launer 1997). Biological research in the Great Basin has yielded landmark contributions to ecology and biogeography (e.g., Brown 1971, Lomolino 1996). The Great Basin also is an appropriate focal system from a natural resource perspective, as more than 75% of the ecoregion is public land that is managed under multiple-use mandates.

We used 14 topographically based, GIS derived environmental variables (and, to capture possible non-linear responses, their squares) from 49 locations in the Toquima Range (Lander and Nye Counties, Nevada, USA) and species inventories conducted over 4 years (1996-1999) to model logistically occurrence of resident butterfly species in the Great Basin. We obtained statistically significant models for 36 of the 56 species (Fleishman et al. 2001). To test the models, we collected new validation data from 39 locations in the nearby (ca 40 km) and ecologically similar Shoshone Mountains. We conducted inventories of butterflies in 22 locations in 2000-2001 and in another 17 locations in 2001.

Validation tests (Fleishman et al. in press) showed that success rates for predicted absences were uniformly higher than for predicted presences. Increasing the temporal extent of data from 1 to 2 years elevated success rates for predicted presences but decreased success rates for predicted absences, leaving the overall success rates essentially the same. Model fit (measured by the explained deviance) was an indicator of the probable success rate of predicted presences. Occurrence rates for several species differed dramatically between the model-building and model-validation data sets, suggesting that some of the locations used to build models should be inventoried again during the validation phase to discriminate between temporal and spatial sources of variability in occupancy. To refine the models, we will use existing and new validation data to 'update' model parameter estimates to improve the fit and/or predictive success of models for species that were not modeled well in the first iteration.

Our work in the Great Basin serves as a template for conducting parallel exercises with other taxonomic groups or in different study areas. We have initiated comparable assessments of birds and mammals in the box-ironbark forests of central Victoria, Australia, in which 85% of presettlement vegetation has been lost (Environment Conservation Council 2000). Managers in the 2 ecoregions confront similar patterns of landscape degradation and its impacts on native wildlife. However, the study areas have different management and legislative infrastructures, biotas, and evolutionary histories. These correspondences and contrasts allow us to evaluate the generality of our approach and, therefore, the practical applicability of its outcomes.

In the box-ironbark forests, we have surveyed birds in 160 locations in a 30,000 km^2 region over 2 full years (Mac Nally et al. 2000, 2002). 80 of these locations also have been surveyed for mammals, including bats (Mac Nally et al. 2002). We have categorized all locations with respect to ecological vegetation classes using GIS-based maps of topography, soils, and geology and groundtruthing. We are in the process of collecting validation data from 80 new locations and from 40 of the original locations. Simultaneously, we are collaborating with the Victorian Department of Natural Resources and Environment and other stakeholders to develop a suite of alternative reconstruction scenarios.

Landscape reconstruction offers a potential means to mitigate pervasive losses of native species and promote future ecological sustainability. The focus of revegetation and other types of ecological restoration has usually been on either relatively small areas or reestablishment of ecosystem functions, such as releasing enough water at the appropriate point in time to support fish spawning in a river. The theoretical and conceptual basis for creating vegetational communities that will be sufficient in extent and geometry to support viable native populations of native wildlife, however, is relatively weak (Lindenmayer et al. 1990).

Our approach will bridge existing gaps between modeling current occurrence patterns of individual species and analyzing the costs and benefits of alternative future scenarios for landscape reconstruction. Our methods allow us to consider the potential effects on species of concern if a landscape were managed for a specified allocation and spatial configuration of various vegetation classes or land uses. For example, we can ask how the distribution of 1 or more endangered species might be affected if 25%, 60% or 90% of each presettlement ecological vegetation class was restored. Although our work has focused on native species, a similar process could be followed to predict the occurrence of non-native invasive species. We believe that our approach has promise for using ecological information to more effectively target conservation and restoration of locations with the greatest potential for achieving explicit biodiversity objectives.

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