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Modelling butterfly species richness using mesoscale environmental variables: model construction and validation for mountain ranges in the Great Basin of western North America

Ralph Mac Nally[a,*], Erica Fleishman[b], John P. Fay[b], Dennis D. Murphy[c]

[a]*Australian Centre for Biodiversity: Analysis, Policy and Management, School of Biological Sciences, Monash University 3800, Australia*
[b]*Center for Conservation Biology, Department of Biological Sciences, Stanford University, Stanford, CA 94305-5020, USA*
[c]*Department of Biology/314, University of Nevada, Reno, NV 89557, USA*

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Abstract

If species richness can be modelled as a function of easily quantified environmental variables, the scientific foundation for land-use planning will be strengthened. We used Poisson regression to develop a predictive model of species richness of resident butterflies in the central Great Basin of western North America. Species inventory data and values for 14 environmental variables from 49 locations (canyon segments) in the Toquima Range (Nevada, USA) were used to build the model. We also included squares of the environmental variables to accommodate potential non-linear relationships. Species richness of butterflies was a significant function of elevation and local topographic heterogeneity, with the selected model explaining 57% of the total deviance of species richness. Predictive variables can be derived efficiently from GIS-based data for areas in which species inventories have not yet been conducted. Therefore, in addition to evaluating the ability of the model to explain observed variation in species richness, we generated and tested predictions of species richness for 'new' locations that had not been used to build the model. Predictions were effective for five new segments also located in the Toquima Range, but not for 22 new segments in the nearby Shoshone Range. We discuss issues related to generalizability and data quality in model development.
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1. Introduction

Richness of native species is a widely used criterion for land-use and conservation planning. Managers of natural resources often must determine which locations preferentially should be protected from anthropogenic impacts, where to concentrate more intensive human activities, and how to maintain or maximize species diversity across the landscape. Information on species richness across broad areas is an important consideration in making these decisions (Freitag et al., 1997; Heikkinen, 1998; Tardif and DesGranges, 1998; Ricketts et al., 1999). Ideally, data on current species richness are obtained from comprehensive field inventories. However, inventory data for many regions are sparse, and logistics and funding limit acquisition of new data (Stohlgren et al., 1995; Faith et al., 2001a, b).

Development of predictive models of species richness may be valuable in light of practical obstacles to conducting spatially and temporally extensive inventories and the need to weigh the potential ecological and economic benefits and risks of management alternatives (Oliver and Beattie, 1996; Longino and Colwell, 1997; Niemi et al., 1997; Simberloff, 1998). If species richness can be modelled successfully as a function of easily quantified environmental variables, then the scientific foundation for making land-use decisions will be strengthened. Managers would then be able to predict the species richness of particular locations on the basis of the biophysical attributes of the locations. If the attributes can be modified by human activities, then it should be possible to anticipate the effect of different management strategies on species richness. The capacity to forecast potential shifts in species richness can contribute to land-use planning even if key environmental

* Corresponding author. Tel.: +61-3-9905-5642; fax: +61-39-905-5613.
E-mail address: ralph.macnally@sci.monash.edu.au (R. Mac Nally).

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variables cannot be managed directly (Peters and Lovejoy, 1992). For example, if species richness of certain locations is likely to be modified by global climate change, it may be possible to limit urbanization along potential migration routes. The outcome of predictive models (both species-richness values and identification of critical environmental variables) also can help to set priorities for locations for field inventories, monitoring efforts, and more detailed empirical studies (Parmesan et al., 1999).

Here, we analyse and develop forecasting methods for species richness of butterflies in the central Great Basin of the western United States of America. Modelling species richness patterns in the Great Basin is valuable for several reasons. First, more than 75% of the region is federally owned and managed under multiple-use mandates. Second, although managers currently are revising land-use plans for much of the landscape, they frequently lack even the most basic data on species distributions. And third, patterns of species richness in the Great Basin are likely to be modified by impending climate change (McDonald and Brown, 1992; Murphy and Weiss, 1992; Fleishman et al., 1998). We chose to focus on butterflies because they are well understood biologically, fairly easy to study and monitor, have relatively short generation times (thus may exhibit rapid responses to management), and often have been suggested as surrogate measures of overall species richness or ecosystem attributes (e.g. Ehrlich and Davidson, 1960; Scott, 1986; New, 1991; Kremen, 1992; Prendergast et al., 1993; Holl, 1995; Blair and Launer, 1997).

Species richness potentially can be explained as a function of several distinct suites of environmental variables. The first suite includes location-specific variables related to the resource requirements of the focal species, such as basal area coverage of woody vegetation. This set of variables frequently yields successful results (Hanski and Gilpin, 1997), but obtaining the necessary data can present logistic obstacles akin to those encountered in species inventories. A second approach employs variables that can be quantified over large spatial scales from topographic models. A key advantage to this technique is that the variables can be derived efficiently and potentially cheaply, generally from remotely sensed data and geographic information systems (GIS) (Caicco et al., 1995; Edwards et al., 1995). We believe that if this second approach proves successful, even for the single system upon which it is based, then the advantages for land-use planning may be considerable.

Predictive models for the distributions of species given information on current or past occurrence have been developed in the past few decades, especially with the advent of modern computers. For example, BIOCLIM (Busby, 1991) has been used to model the distributions of many kinds of organisms in the southern hemisphere, including vertebrates, invertebrates, vascular plants, and fungi (Randolph, 1993; Wardell-Johnson and Roberts, 1993; Brereton et al., 1995; James and Bell, 1995; Martin, 1996; Tyler et al., 1996; Neave and Norton, 1998; Eeley et al., 1999; Jackson and Claridge, 1999). The BIOCLIM model also has been used retrospectively in a paleogeographic context (e.g. D'Costa and Kershaw, 1997; Kershaw, 1997). Like BIOCLIM, most predictive models are based on extensive biogeographic domains with pronounced climatic variation. Because our study included just one dominant biogeographic domain (central Great Basin), there was little grounds for differentiation of locations on a broad climatic basis. Therefore, we chose to employ methods more intimately connected with the topography of the mountain ranges from which the data were collected.

In this paper, we present an approach to explaining and predicting the species richness of butterflies. Ordinary multiple linear regression is not ideal for modelling richness data because the error distribution of richness data is expected to be Poisson rather than Gaussian (normal) (Cameron and Trivedi, 1998). Because one of our goals was to identify explanatory and predictive models with methods that are more effective than multiple linear regression (Mac Nally, 2000), we first used Schwarz's information criterion (SIC, Schwarz, 1978) to locate the probable best model. We then used derived models within the context of Bayesian modelling to predict the species richness of locations that had not been used to build the models. The latter locations were inventoried during the 2000 field season, and the new data were used to test the predictions. Aspects of the derived model were used as components of distributional priors for the new data sets (see Lee, 1989). We tested species richness predictions for (1) locations in Toquima Range that had not been inventoried previously and (2) locations in the nearby Shoshone Range, a range in which virtually no butterfly inventories had been conducted.

We reiterate that confidence in model predictive capacity involves the development of models that produce testable predictions, i.e. predictions for locations for which no information on the dependent variable—species richness—currently exists (see Mac Nally and Bennett, 1997; Mac Nally et al., 2000). Therefore, we see predictive modelling as a process that requires separation of the building and testing phases. If tests of the model are successful, then the model may be used with confidence. Otherwise, the modelling process involves, in decreasing order of severity, either (1) complete abandonment of the initial model, which indicates that the modelling methodology may not be appropriate irrespective of the set of variables that is available for use; (2) refinement of model structure, which implies a major revision of the model, perhaps using a different

suite of variables and/or functions thereof; or (3) refinement of model parameters, which means that the initial set of variables and/or interactions seem justified, but the values of model coefficients were inadequate (i.e. too large or small).

2. Field methods

The Great Basin of western North America includes nearly 430,000 km^2 of internal drainage bounded by the Sierra Nevada and southern Cascades to the west, the Wasatch Range to the east, the Columbia River to the north, and the Colorado River to the south (Grayson, 1993). Topographically, the Great Basin is dominated by more than 200 mountain ranges. After the Pleistocene, these ranges were isolated from the surrounding valleys as the regional climate became warmer and drier (Brown, 1978; Grayson, 1993). Individual mountain ranges, and the canyons that deeply incise many of them, seem to function as discrete islands of habitat for numerous taxa that either are restricted to montane ecotypes or have relatively low mobility, including butterflies (McDonald and Brown, 1992; Murphy and Weiss, 1992). The US Forest Service, which oversees many of the largest and most biologically diverse mountain ranges in the Great Basin, generally develops management plans for individual mountain ranges, and solicits biological data to guide these plans. Within mountain ranges, land uses commonly are delineated at the level of individual or several adjacent canyons. The spatial resolution of our field inventories and analyses therefore was appropriate for the ecology and political realities of our study system.

In 1996 and 1997, we conducted comprehensive inventories of butterflies, using standard methods (Shapiro, 1975; Thomas and Mallorie, 1985; Swengel, 1990; Kremen, 1992; Pollard and Yates, 1993; Harding et al., 1995), in 10 canyons in the Toquima Range (Lander and Nye counties, Nevada), a 1750 km^2 mountain range in the central Great Basin. We divided canyons into multiple segments (three to six per canyon), each extending for approximately 100 m in elevation, from base to crest. We inventoried a total of 49 segments, covering an elevational gradient from 1872 to 2750 m. Because the timing and duration of flight varies among butterfly species, locations, and years, we inventoried each canyon approximately every 2 weeks throughout the majority of the flight season. During every canyon visit, we walked the length of each segment at a constant pace (thus, sampling effort was equal per unit area), and recorded the presence of all butterfly species seen. These standard techniques for surveying butterfly assemblages reliably detect species presence and permit assessment of distributional trends across space and time (e.g. Pollard and Yates, 1993; Harding et al., 1995). Fifty-six resident species (taxa that complete their entire life cycle in the Toquima Range, Fleishman et al., 1997, 1999) were recorded in our inventories. Given the average length of our canyon segments (>1.2 km) and the low vagility of most butterflies in our study system (rarely more than several hundred m), it is reasonable to assume that our measurements of butterfly species richness are spatially independent (Fleishman et al., 2000).

It is unlikely that we failed to detect species that actually were present in a given location, at least during the years in which we conducted inventories. Field personnel were very familiar with the regional butterfly fauna, and we restricted our inventories to times when the weather was most favourable for flight. It is reasonable to interpret that a given butterfly species is absent if the area has been searched with these methods during the appropriate season and weather conditions (Pullin, 1995; Reed, 1996). Using these methods in the nearby Toiyabe Range, for example, we recorded 98% of the theoretical total number of resident species expected in the mountain range under a Michaelis–Menten model (Clench, 1979; Raguso and Llorente-Bousquets, 1990; Soberón and Llorente, 1993). Field methods are described in more detail in Fleishman et al. (1998, 1999). Canyon segments were delineated by overlaying differentially corrected global positioning system locations on a 30 m (1:24,000) Digital Elevation Model (DEM) maintained on a Geographic Information System. Sampled area was 50 m on all sides (left, right, and overhead) of the inventory route (generally a hiking trail, recreational access road, or historic mining road).

Fourteen environmental variables were measured for each canyon segment (Table 1). Most were derived from existing electronic sources of data such as DEMs and digital line graphs (DLGs) in combination with ArcView and Arc Macro Language scripts. DEMs and DLGs are available at no charge from the US Geological Survey's EROS Data Centre, http://edc.usgs.gov/doc/edchome/ndcdb/ndcdb.html. We also used the squares of the environmental variables because there may be non-monotonic responses (e.g. declines in species richness at extremes of a variable). Values for environmental variables included in this study also can be obtained for locations that have not yet been inventoried. Therefore, we could make predictions for 'new' canyon segments based on the model, and then inventory the canyon segments to test the efficacy of the model.

3. Model-building and model-testing

3.1. Model variable selection

We fitted species-richness (the dependent variable, DV) by using Poisson regression because non-negative

variables are best modeled using a Poisson-error distribution (Crawley, 1993). With many independent variables (IVs; e.g. 14 in the current study and their squares = 28 in total), many of the 'screening' approaches to identify the most promising set of variables to retain are suspect for statistical reasons (e.g. stepwise methods, naïve screening; Mac Nally, 2000). Mac Nally (2000) recommended using Schwarz's information criterion (Schwarz, 1978) to identify the most efficient model, at least initially. Every possible model involving main IVs and their squares ($2^{28} = 268{,}435{,}456$ here, excluding interactions) in the hierarchy is calculated and SIC for each is computed—the minimum SIC is sought. SIC is an 'optimal' statistic, a compromise between model 'fit' (ability to explain observed variation in the DV) and model complexity (number of IVs). We screened only non-interaction models for tractability—there are $O(2^{2^{28}})$ models including all hierarchical combinations of the 28 IVs, their squares and interactions, so one could not possibly process all models up to and including the 28-way interaction. Moreover, it seems unwarranted to search for the best candidate model consisting of just main effects and then, having found this, to begin including interaction terms. We believe that use of hierarchical partitioning (see later) at least partially addresses the interaction problem.

Automating such exhaustive searching is straightforward when multiple linear regression (MR) is used because MR involves matrix calculations. Most other fitting methods including multiple Poisson modelling (PR, for 'counts' DVs, such as species richness) use iterative methods (e.g. Newton–Raphson), which are difficult to automate for PR. Therefore, we initially used ordinary MR even though the DV is not normally distributed. However, a useful adjunct in this regard is to use $\log_e(1 + \text{richness})$ because the logarithm is the appropriate link function for Poisson-distributed DVs in generalized linear modelling (McCullagh and Nelder, 1989).

All 2^{28} MR models were calculated by using software written by RM based on matrix calculations (Huang, 1970, §4.1.4). The minimum SIC values were found for each level of model complexity. We then investigated models based on variables included in that minimum-SIC model. For example, a minimum often occurs with the inclusion of a variable that accounts for minor variation that might be considered 'noise' in the model-building data-set. Thus, it is critical to evaluate more fully the variables associated with the minimum-SIC models in relation to the amounts of variance they 'explain'.

Model fit in Poisson regression is measured by using the deviance, and differences between the deviances of any two models are distributed approximately as a χ^2 with the difference in the number of IVs used as degrees-of-freedom (d.f.). The residual deviance should be approximately the same as the residual d.f. if the data are adequately modelled by a Poisson DV (Crawley, 1993, § 14.9.1). We used the program GLMStat (Beath, 2000) for calculating the maximum-likelihood estimates.

We also used hierarchical partitioning for establishing which of the variables have the most 'independent'

Table 1
Environmental variables used for Poisson modelling of the species richness of butterflies in the Toquima Range (Lander and Nye counties, Nevada, USA)

Code	mean	SD	min.	max.	Definition
EASTX	3.3	51.3	−74.9	85.1	mean 'eastness' on a scale from −100 (west-facing) to 100 (east-facing)
NORX	16.8	35.9	−56.7	79.5	mean 'northness' on a scale from −100 (south-facing) to 100 (north-facing)
ELEVX	2369	182	1921	2707	mean elevation in m
SLOPEX	10.5	3.7	3.7	19.6	mean slope in degrees
LENGTH	1736	927	441	4441	segment length in m
PRECIP	423	74	283	612	mean annual precipitation in mm for the 4×4 km cell in which the canyon segment falls, or weighted mean of the cells in which the canyon segment falls (derived from PRISM, Daly et al., 1994)
EQINX	14970	1273	11290	17586	mean solar insolation in kJ at the vernal equinox
EQINS	1718	770	346	3631	standard deviation of solar insolation in kJ at the vernal equinox
EX300X	−17.3	11.1	−38.7	9.2	mean topographic exposure within a 300 m radius. Compares the elevation of the canyon segment with the mean elevation of a specified neighbourhood around that segment. If the segment is in a valley, value < mean; if on a ridge, value > mean; if on an open slope, value = mean, slope ≠ 0; if flat, value = mean, slope = 0
EX300S	8.9	5.2	1.7	25.9	standard deviation of topographic exposure within a 300 m radius
EX150X	−6.2	4.2	−14.3	3.9	mean topographic exposure within a 150 m radius
EX150S	5.0	2.3	1.9	11.6	standard deviation of topographic exposure within a 150 m radius
H_2OX	401	187	34	500	mean distance in m from the centre of the canyon segment to running or standing water; maximum set at 500
H_2OM	319	229	0	500	minimum distance to running or standing water

SD, standard deviation; min., minimum; max., maximum

explanatory power (see Chevan and Sutherland, 1991; Mac Nally, 2000), i.e. those that independently account for the most variance in the DV. As with conventional multiple linear regression, multiple Poisson regression can be adversely influenced by collinearity among independent variables (Chevan and Sutherland, 1991). Hierarchical partitioning is a arithmetico-statistical method that estimates the amount of variation in the dependent variable explained by each independent variable (e.g. I_{tot}) without the problems inherent in multiple regression (Chevan and Sutherland, 1991). Variation attributable to the joint influence of two or more independent variables is distinguished from variable-specific explained variance (Chevan and Sutherland, 1991), so that one can isolate those IVs most likely having the strongest independent influence on the dependent variable.

3.2. Modelling process

The process used for Bayesian modelling of species richness involves model-building and model-testing phases.

3.2.1. Model-building phase

1. All IVs are standardized $X'_{ik} = \left(X_{ik} - \overline{X}_{.k}\right)/s_k$, where the means ($\overline{X}$) and standard deviations (s) of variable k are used for each site i. IV standardization was undertaken to reduce potential correlation among model parameters, which may significantly affect model convergence (see Spielgelhalter et al., 1996).
2. The Poisson-regression model is specified by using the BUGS programming framework (see Spielgelhalter et al., 1996). This amounts to the following format:

$$\log(\mu_i) = \alpha_0 + \sum_{k=1}^{g} \alpha_k X'_{ik} + \varepsilon;$$
$$Y_i \sim \text{Poisson } (\mu_i).$$

The αs are the usual regression coefficients, μ_i is the (unobservable true) mean species-richness at site i given the state of the IVs, ε is model error, and Y_i is the observed species richness, which is assumed to be distributed ('$\sim$') as a Poisson variable with mean μ_i. The αs are initially given 'non-informative' normal priors $[\alpha \sim \text{Normal}(\mu = 0, \sigma^2 = 300)]$ which indicates that initially their values are unknown.
3. Markov Chain-Monte Carlo (MCMC) involves repeatedly 'sampling' from distributions specified in a model (see Gilks et al., 1995). Because this is an iterative procedure, initial values of the parameters need to be specified. Depending on model complexity and data quantity, it may take 300–1000 iterations before the parameter estimates have 'settled down' (the 'burn-in'), after which parameter distributions are built for another 2000–10,000 iterations. In the current analyses, the burn-in was 1000 iterations and sampling 3000 iterations.
4. The distribution of μ-values gives a posterior probability distribution of species-richness values for each segment given the values of the IVs. A 95% credible interval for the fitted values for μ can be derived from the posterior distribution. A credible interval refers to the interval in which the given fraction of posterior probability falls.

3.2.2. Model-testing phase

5. Values for the set of IVs from sites for which predictions are to be made ('new sites') are standardized by using the means and standard deviations from step 1. The data for the testing phase should be a subset of values used in the model-building phase for each retained IV. In other words, no values outside the minima and maxima of the data used in the model-building phase are employed in the testing phase.
6. The Bayesian model with regression-coefficient distributions is used in conjunction with the standardized data from the new sites to generate μ-value distributions.
7. Step 6 produces 'updated' estimates for model parameters: the posterior distributions from the model-building phase become the new prior distributions for future modelling (Lee, 1989, p. 35).

3.3. Model-testing data

During the 2000 field season, we conducted inventories of butterflies in five new canyon segments in a new canyon in the Toquima Range and 22 new canyon segments in the Shoshone Range. The 1600 km^2 Shoshone Range lies roughly 40 km west of the Toquima Range. The two ranges have similar climate, a common biogeographic past and ancestral biota, and comparable management histories. Butterfly species composition of the two ranges appears to be largely the same (see Section 5). The new Toquima Range segments were used to assess whether a model developed from information for a particular mountain range was applicable to other segments in the same range. The validation inventories in the Shoshone Range were conducted to determine whether the model was effective for other geographically proximate and ecologically similar mountain ranges. Methods for species inventories and derivation of independent variables (ELEVX and EX150S) were the same as those described for the initial (model-building) inventories.

Values of the independent variables for the new segments were compared with the minima and maxima for previously inventoried segments. None of the new segments had values outside the latter bounds. Therefore, all of the new segments were retained.

To test conformance between predictions and observations, we asked whether the observed values fell within the 95% credible intervals of the predictive distributions derived from the Bayesian modelling (see Lee, 1989).

4. Results

4.1. Model-building phase

The SIC minimum [MR based on log(richness + 1)] was −115.7 for five variables: ELEVX, ELEVX^2, LENGTH, EX300X^2 and EX150S. We computed all $2^5 = 32$ models in the hierarchy based on these five variables, the deviances from which were then used in a hierarchical partition. It was clear that three of the variables (ELEVX, ELEVX^2 and EX150S) had substantially greater potential explanatory power than LENGTH and EX300X^2. The reduction in deviance (effectively a measure of goodness-of-fit; Cameron and Trivedi, 1998) of the five-variable model was 82.18 (126.50 for the null model, 44.32 for the five-variable model). ELEVX (30.3%), EX150S (27.8%) and ELEVX^2 (24.4%) accounted for the lion's share of the reduction. LENGTH contributed virtually nothing (6%), but EX300X^2 (11%) was problematic. The deviance of a four-variable model (i.e. excluding LENGTH) was 55.22 (44 d.f.), while the deviance of a model also excluding EX300X^2 was 59.93 (45 d.f.). The percentage improvement was 4.71/55.22 = 8.5%, and the four-variable model was statistically better (differences in deviances = 4.71, $0.05 < P < 0.025$, χ^2, 1 d.f.). However, we judged that the improvement associated with including EX300X^2 was marginal; moreover its regression-parameter estimate was not statistically significant ($t \approx 1.9$, $P > 0.06$). Given that our goal was predictive capacity, we concluded that the three-variable model was more likely to be generally applicable.

Regression-parameter estimates and their standard errors from both maximum-likelihood and Bayesian (BUGS) calculations are listed in Table 2. The estimates are in reasonable agreement, although the Bayes estimates slightly downplay the influence of ELEVX. Mean fitted values and 95% credible intervals of the posterior probability distribution are shown plotted against observed values in Fig. 1a.

4.2. Model-testing phase

Relatively few (12) of the observed values fell within the 95% credible intervals of the predictive distributions for segments surveyed in 2000 (Fig. 1b). However, four of the five Toquima segments fell within the intervals and the other Toquima segment was only just above the 97.5% credible value (Fig. 1b), suggesting that the fitting for new segments in the same mountain range as those from which the model was constructed was good. Values for the Shoshone Range generally fell above the estimates. We also modelled the Shoshone segments alone ($N = 22$) with regression parameter priors having the means from Table 2 but with imprecise variances (100). BUGS modelling produced parameter estimates in which the ELEVX and EX150S terms were no longer statistically different from zero; parameter estimates for the retained terms were constant = 3.049 (0.072 SE), ELEVX^2 = −0.096 (0.044 SE). The effect of this modelling was to shift the credible intervals upwards compared with Fig. 1b, but only 11 of the observed richness values fell within the intervals.

5. Discussion

5.1. The Toquima Range model

We obtained an initial statistically significant model for the species richness of butterflies on the basis of linear and/or quadratic forms of just two environmental variables that are easy to quantify across virtually any landscape. Our validation results suggest that the predictions may hold well for the same mountain range for which the initial model was built (i.e. the Toquima Range), but not necessarily for other mountain ranges (e.g. the Shoshone Range).

Regression models are based upon correlations, and thus do not necessarily identify causes of ecological patterns. Nonetheless, they are useful for planning purposes because they link landscape variables with species distributions and do not require field data from intensive surveys, such as vegetation quadrats (Opdam, 1997). Moreover, we believe we can draw ecological inferences for why elevation and topographic heterogeneity (EX150S) explained significant variance in species richness.

Table 2
Model-building phase parameter values (and standard errors) for Poisson-regression models (maximum-likelihood and Bayesian estimates) for all resident species of butterflies in 49 canyon segments in the Toquima Range (Lander and Nye counties, Nevada, USA)

Variable	MLE (SE)	Bayes (SE)
constant	2.958 (0.047)	2.954 (0.043)
ELEVX	0.180 (0.046)	0.168 (0.044)
EX150S	0.148 (0.037)	0.155 (0.035)
ELEVX^2	−0.154 (0.037)	−0.162 (0.034)

Elevational gradients affect the distributions of numerous taxa, including butterflies, in diverse geographic regions (e.g. Merriam, 1890; Terborgh, 1977; Baz, 1987; Kremen, 1994; Fernández-Palacios and de Nicolás, 1995; Sanchez-Rodriguez and Baz, 1995; Lieberman et al., 1996; Shapiro, 1996; Fleishman et al., 1998, 2000). Elevation is likely to be correlated with species richness of butterflies in mountain ranges throughout the Great Basin, although the functional relationship may vary (Fleishman et al., 2000). In the Toquima Range, species richness and elevation are positively correlated—species richness tends to increase as elevation increases although the negative coefficient associated with the $ELEVX^2$ (Table 2) term indicates a flattening of the curve at lowest and highest elevations. In many mountain ranges, environmental conditions at higher elevations (e.g. increases in cloud cover, precipitation, and wind speed and decreases in ambient temperature) tend to be less conducive to flight. As a result, fecundity often decreases, and risk of local extinction increases, at higher elevations (Kingsolver, 1983, 1989; Springer and Boggs, 1986; Dennis and Shreeve, 1989; Dennis, 1993; Boggs and Murphy, 1997). In the Toquima Range, climatic severity appears to decrease as elevation increases. This may reflect a range-specific gradient in climatic severity (Fleishman et al., 2000). Low elevations in the Toquima Range are arid and floristically depauperate. As a result, larval host-plants, adult nectar sources, and some potential locations for seeking mates are scarce (Scott, 1975, 1986). Because much of the Toquima crest is not extremely high (~2700 m), conditions at upper elevations are not extremely harsh, and thus climate may constrain species richness less at high elevations than at low elevations.

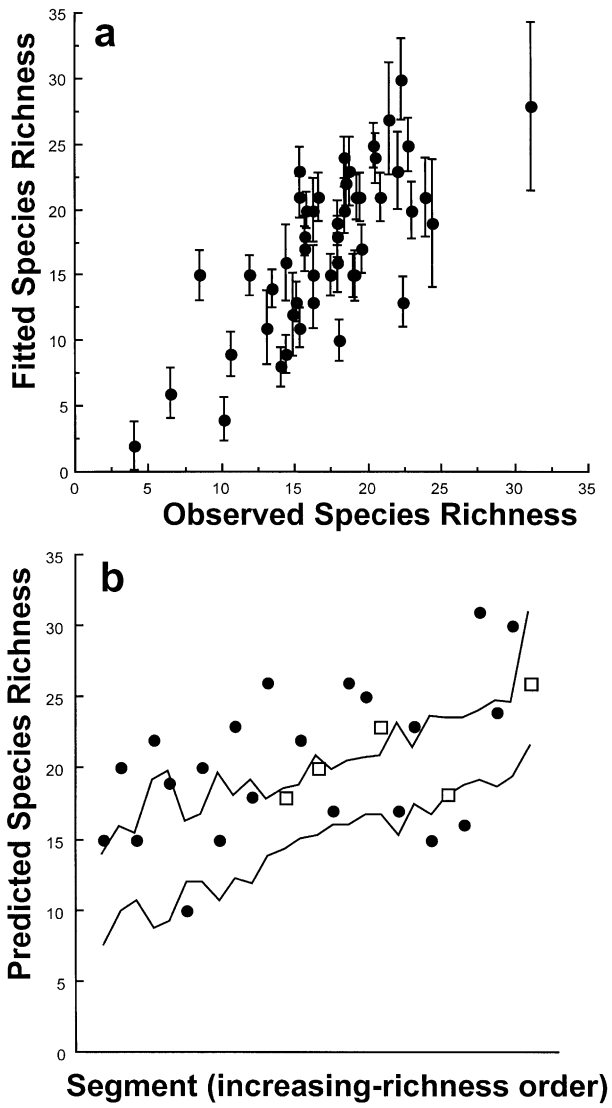

Fig. 1. (a) Mean predicted (with 95% credible intervals) versus observed species richness of all resident species for the 49 segments involved in the model-building phase. (b) Observed species richnesses in relation to 95% credible intervals of the predictive distribution for the 27 segments of the model-validation phase; values are arranged in increasing order of predicted species richness. Open squares are Toquima Range segments and filled circles are Shoshone Mountains segments.

Species richness of butterflies in the Toquima Range also increases with increasing topographic heterogeneity. Varied topography probably supports a correspondingly diverse plant community in terms of both composition and structure. In addition, topographic heterogeneity affords numerous locations for seeking mates and may provide shelter from extreme weather events (Scott, 1975, 1986). While our dependent variable may be sensitive to the spatial scale of our inventories, we believe that the relationship between species richness and the significant independent variables is robust.

The model appeared to predict well the richness of five segments not previously inventoried in the Toquima Range. Model accuracy might be improved further if information on several additional variables that are known to affect butterfly distributions, including local weather and vegetation, could be included in the model-building phase. Currently, data on those variables do not exist for our study area (or for many other remote ecoregions), especially not at the appropriate spatial and temporal resolution. However, the Earth Observing System's Terra satellite and particularly the MODIS (moderate resolution spectroradiometer) instrument will soon provide high-resolution data on relevant variables including timing of snowmelt, plant phenology, and primary productivity (see http://eostc.umt.edu/). We anticipate incorporating such new variables into the future model revisions.

5.2. The Shoshone Mountains and the efficacy of models

The three-term model developed by using data for the Toquima Range did not apply well to the 22 segments surveyed in 2000 in the Shoshone Range. There are several possible reasons why such a result emerged.

First, the different geographic positions of the two ranges may invoke different agents in the determination of species richness. The Toquima and Shoshone ranges have fairly similar area and relief; in fact the Shoshone is slightly smaller and shorter, and has less vegetational diversity. However, the Shoshone and Toquima ranges lie on either side of the Toiyabe Range, which is considerably taller (40% of its crest exceeds 3000 m) and more extensive (3100 km^2) than the Shoshone and Toquima ranges. The Great Basin, within which all three ranges are situated, is a 'cold desert', which means that most precipitation comes from winter snowfall, and winter storms tend to follow an eastward trajectory (Grayson, 1993). Thus, the Toiyabe Range may create a rain-shadow effect, intercepting precipitation before it reaches the Toquima Range. As noted earlier, elevational gradients in species richness in the Toquima Range largely may be associated with a moisture gradient; if water is less limiting in the Shoshone Range, factors other than elevation may be more influential.

Another possible reason why the Toquima model did not apply well to the Shoshone Range is that annual variation in species richness of butterflies is high, even at one location (Pollard, 1988, 1991; Shapiro, 1996). Estimates of species richness for a single year may be more variable than the total richness observed in the field over several years. Thus, one year 'snap-shots' of segments may be major impediments for both building and validating models. In our first year of inventories in the Shoshone Range, we recorded 48 of the 56 species of resident butterflies present in the Toquima Range. Most of the other eight species are relatively rare in the central Great Basin, and probably will be recorded from the Shoshone Range in future years. Nonetheless, we note that the maximum species richness of any segment in the Shoshone Range (31) was only slightly less than the maximum one year species richness of any Toquima Range segment [33 (1996) or 36 (1997)]. Thus, differences in total species richness should not prevent us from evaluating the predictive ability of the model, at least on a preliminary basis. On the basis of our experience, we think that complete characterization of the butterfly faunas for individual segments probably requires at least 3 years, and that it will be upon such high-quality data that the best models will be constructed. Similarly, validation data based on equally high-quality data is likely to provide the best and most stringent tests of modelling based on mesoscale habitat variables. A reasonable objective is to maximize the number of locations (sample size) used to build and validate models without sacrificing data quality (i.e. recording all species present). In our study system, there is no direct trade-off between sample size and inventory intensity. Each location must be visited at regular intervals (within years) to accommodate interspecific differences in flight phenology, and sampling effort is proportional to area. Our ability to increase sample size instead depends upon accessibility of new locations and personnel.

6. Conclusions

No single tool or method is appropriate for all management challenges (Andelman and Fagan, 2000). The objectives of biodiversity management at the regional level may include maintenance of native species diversity, preservation of rare species, eradication of exotic species, and tracking effects of ecological changes on biological communities. Thus, the process of prioritizing locations for a suite of potential uses is an optimization of a range of considerations. We recognize that analyses of species richness address neither the requirements of individual species of management interest, probabilities of species persistence nor species composition per se. While we have addressed only species richness here, we have shown that a function of the three variables used here is very effective at explaining patterns of biotic nestedness in these butterfly faunas (Fleishman and Mac Nally, 2002), suggesting that not only richness but elements of composition are dependent on these topographic variables.

Environmental variables that influence species richness may have little effect on the distribution of a particular species of concern (Cody, 1986; Thomas, 1995; Fagan and Kareiva, 1997; Freitag et al., 1997), and even locations with relatively low species diversity may serve as key supports for populations in species-rich areas. In addition, management of individual species often relies more heavily upon location- or species-specific data than upon more general and temporally static variables measured over large spatial extents. Ideally, models of both species richness and species occurrence should be developed. In related work, we have used Bayesian logistic modelling to develop predictive models of individual-species occurrence for resident butterflies in the same study system (Fleishman et al., 2001, in press). Using the same environmental variables, we have obtained statistically significant models for 36 species, over half of which include mean elevation.

It is important to develop a range of complementary modelling approaches that can be employed for different purposes than to seek a single panacea for management planning. It also is vital to critically evaluate models that might be used to guide land management (Boone and Krohn, 1999). Although it is tempting to assess a model with respect to its ability to 'explain' observed variation, predictive models must be validated with independent sets of data. Predictive modelling is best represented as a four-stage process: (1) model building, (2) generation of hypotheses (model predictions), (3) hypothesis discrimination, and (4) model

refinement. If stage 3 largely is successful, then the model can be employed with confidence in land-use planning. If the outcome of stage 3 initially is less successful than desired, then newly collected data can be used to revise the model—incorporated into the next model-building phase—and to generate new testable hypotheses. Using a model that is not demonstrably successful clearly offers no advantages.

Species richness of different taxonomic groups often is driven by different environmental factors and may not be correlated at spatial and temporal scales relevant to managers (Erhardt, 1985; Thomas and Mallorie, 1985; Dobkin and Wilcox, 1986; Murphy and Wilcox, 1986; Wilcox et al., 1986; Hafernik, 1992; Kremen, 1992; Prendergast et al., 1993; Launer and Murphy, 1994; Holl, 1995). Nonetheless, a model that is successful for even a single taxonomic group can benefit land-use planning. Not only do managers frequently have a mandate to minimize species losses among all taxonomic groups, but also some taxa, including butterflies, are relatively easy to study and monitor and serve as possible 'flagship species' (New et al., 1995; Simberloff, 1998; Caro and O'Doherty, 1999) for public education.

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