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RESEARCH ARTICLE

Habitat suitability of patch types: A case study of the Yosemite toad

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Abstract Understanding patch variability is crucial in understanding the spatial population structure of wildlife species, especially for rare or threatened species. We used a well-tested maximum entropy species distribution model (Maxent) to map the Yosemite toad (*Anaxyrus* (= *Bufo*) *canorus*) in the Sierra Nevada mountains of California. Twenty-six environmental variables were included in the model representing climate, topography, land cover type, and disturbance factors (e.g., distances to agricultural lands, fire perimeters, and timber harvest areas) throughout the historic range of the toad. We then took a novel approach to the study of spatially structured populations by applying the species-environmental matching model separately for 49 consistently occupied sites of the Yosemite toad compared to 27 intermittently occupied sites. We found that the distribution of the entire population was highly predictable (AUC = 0.95±0.03 SD), and associated with low slopes, specific vegetation types (wet meadow, alpine-dwarf shrub, montane chaparral, red fir, and subalpine conifer), and warm temperatures. The consistently occupied sites were also associated with these same factors, and they were also highly predictable (AUC = 0.95±0.05 SD). However, the intermittently occupied sites were associated with distance to fire perimeter, a slightly different response to vegetation types, distance to timber harvests, and a much broader set of aspect classes (AUC = 0.90±0.11 SD). We conclude that many studies of species distributions may benefit by modeling spatially structured populations separately. Modeling and monitoring consistently-occupied sites may provide a realistic snapshot of current species-environment relationships, important climatic and topographic patterns associated with species persistence patterns, and an understanding of the plasticity of the species to respond to varying climate regimes across its range. Meanwhile, modeling and monitoring of widely dispersing individuals and intermittently occupied sites may uncover environmental thresholds and human-related threats to population persistence.

Keywords species distribution models, Maxent, habitat patch, patchy populations, Yosemite toad, *Anaxyrus canorus*, *Bufo canorus*

1 Introduction

Knowledge of species distributions is fundamental to ecology and the distribution of species is largely determined by the environment. Species distribution models are an increasingly common tool to investigate suitable habitat and species distributions (Phillips et al., 2004; Elith et al., 2006). Species distribution models are statistical models that quantify species-environment relationships by relating species occurrences to environmental predictor variables. The models use various algorithms to model the distribution of the known locations (response variable), select significant predictor variables and determine their fit, evaluate the strength of association between predictors and response, and predict habitat suitability in areas where the distribution is unknown (output is known as a habitat suitability map). The advancement of modeling methods has led to the wide-spread use of species distribution models in addressing issues in biogeography, ecology and evolution, and for species conservation and management. For example, species distribution models have been used to quantify the environmental niche of a species (Phillips et al., 2004; Elith et al., 2006; Kumar et al., 2009), predict species invasions (Evangelista et al., 2008; Giovanelli et al., 2008), estimate species distributions in the past (Svenning et al., 2008; Waltari and

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Guralnick, 2009) and in future climates (Jarnevich and Stohlgren, 2008) or under different land uses (Riley at al., 2005), and in conservation planning and reserve selection (Pawar et al., 2007; Fuller et al., 2008).

However, species distribution models commonly assume that all recorded locations of a species are qualitatively the same, and do not take into account habitat heterogeneity such as in spatially subdivided local populations. We found no publications where species distribution models have been used specifically to assess spatially structured populations in discrete habitat patches. Spatially structured populations can be organized in a variety of ways along a continuum of connectivity and patch structure (Harrison and Taylor, 1997). Three main population structures, listed in order of decreasing connectivity, are: patchy population, metapopulation, and isolated populations. In a patchy population, multiple patches are well connected by dispersal and there is little potential for local extinction within individual patches. In a metapopulation, multiple local populations are reciprocally linked by less frequent dispersal (Levins, 1969). Local populations are prone to extinction from both stochastic and deterministic causes and persist only at the regional level through recolonization (Hanski, 1999). In isolated populations, there is no movement between patches and patches that go extinct will not be recolonized (Frankham et al., 2002). These structures are based on connectivity but do not take into account variation in local patch size, location or quality.

Patch variability leads to variants of the patchy population or metapopulation structure, which differ in their mechanisms of persistence and coexistence. In a mainland-island population system, there is substantial variation in the size of patches or populations (Harrison and Taylor, 1997). Larger "mainland" populations are less prone to extinction whereas smaller "island" populations are more susceptible to stochastic extinction. In a source-sink population system, there is variation in the quality of patches with higher quality "source" patches and lower quality "sink" patches (Pulliam, 1988). The quality of the patch is identified by the before-dispersal population growth rate, which is positive in source patches and negative in sink patches. Dispersal from mainland or source patches supports the island or sink patches, and recruitment in the islands or sinks is from immigration rather than from within the local patch. Mainland-island and source-sink systems can apply to both patchy population and metapopulation structures.

Spatially structured population models have been applied to the study of a number of taxa including wetland-breeding amphibians. Breeding areas are discrete habitat patches that can be connected by migrating individuals and the rate of migration is often low due to high site fidelity, low vagility and physiologic constraints that restrict movement to moist areas. This has led to the generalization that many amphibians have a metapopulation structure (Alford and Richards, 1999) although this generalization may be overstated (Marsh and Trenham, 2001; Smith and Green, 2005) and some species are in patchy populations rather than metapopulations (Petranka and Holbrook, 2006). However, regardless of the exact population structure, the patch is an important feature that needs to be considered in any research, management, restoration, or conservation effort (Marsh and Trenham, 2001; Petranka and Holbrook, 2006). Patch variability results in sites that are more consistently occupied (mainland or source sites) versus sites that are more intermittently occupied (island or sink sites). Patch type is likely determined by environmental heterogeneity and local environmental factors.

The Yosemite toad (*Anaxyrus* (= *Bufo*) *canorus*) provides an ideal case study of a species that is spatially structured in discrete patches. It is endemic to the Sierra Nevada mountains in California at elevations above 6,400 ft (1,950 m) and is associated with wet mountain meadows and adjacent forests (Karlstrom, 1962). The Yosemite toad breeds in late spring in areas of shallow water such as wet meadows, margins of ponds and lakes, and slow-moving streams. Breeding usually only lasts 1–2 weeks after which adults typically move to upland areas. Eggs and larvae develop in the shallow water areas and metamorphosis occurs by late summer of the same year. Adults tend to breed in a single site and appear to be highly philopatric, although individuals can move between breeding areas (CT Liang, *pers. obs*.). Breeding sites exhibit variation in year-to-year occupancy and some sites are consistently occupied while others are intermittently occupied. There also is variation in population sizes at the breeding sites. It appears highly likely that mainland-island or source-sink dynamics are occurring in this species though the exact population structure is not known. Regardless, it is evident that patch types vary for the Yosemite toad throughout its range.

The Yosemite toad is a candidate for federal listing as endangered or threatened and a California state species of special concern due to its apparent disappearance from over 50% of its historic range even in seemingly undisturbed areas. In addition, remaining populations appear to be in decline (Sherman and Morton, 1993; Drost and Fellers, 1996; Davidson et al., 2002). The cause(s) of the disappearance and decline are not known, although potential factors include airborne pesticides and other toxins, infectious disease, climate change, and habitat modification due to anthropogenic changes. Habitat modification related to livestock grazing, roads, timber harvest, vegetation and fire management activities, recreation, and dams and water diversion are all considered threats to the species (USFWS, 2002).

Our objectives were to: 1) determine the Yosemite toad's response to environmental variables throughout its range to develop better conservation strategies for this rare species; and 2) demonstrate the general utility of modeling species-environmental relationships separately for consistently occupied sites compared to intermittently occupied sites to understand patch variability and potential threats to the species' persistence.

2 Methods

2.1 Yosemite toad locations

Numerous surveys related to the Yosemite toad have been conducted in the national forests and parks within its range. Visual encounter survey for any life stage is the typical method. Some sites have been repeatedly visited over the past 10–15 years to survey for breeding adults, eggs and/or tadpoles. Based on available survey information, 49 consistently occupied sites and 27 intermittently occupied sites were identified in the Inyo National Forest, Sequoia and Kings Canyon National Park, Sierra National Forest, Stanislaus National Forest, and Yosemite National Park (Fig. 1). Consistent sites were defined as being occupied on a yearly basis in $\geqslant 50\%$ of total surveys for the site and with a relatively robust population in all occupied years; intermittent sites were not occupied on a yearly basis in $< 50\%$ of site surveys and had relatively few individuals when occupied. A site was considered occupied if any Yosemite toad life stage was found during the survey. The classification of "consistent" and "intermittent" was based on the best available knowledge of the sites although sites were not necessarily surveyed consecutively over multiple years or with standardized levels of effort. The classification was used only to identify two different patch types which the Yosemite toad occupies and does not make any assumptions about the population structure (e.g., patchy population, metapopulation), which cannot be determined from the available data and is not the focus of this paper.

2.2 Environmental variables

Twenty-six environmental variables were originally considered for the models representing climate, topography (elevation, aspect and slope), land cover type, and disturbance factors (distances to agricultural lands, fire perimeters, and timber harvest areas) throughout the historic range of the Yosemite toad (Appendix 1). Nineteen bioclimatic variables defining ecophysiological tolerances of species based on annual mean temperature and precipitation were calculated from PRISM climate data (http://www.prism.oregonstate.edu) using an ARC AML script (mkBCvars.aml; http://www.worldclim.org/mkBCvars.aml). Vegetation type was based on the California Wildlife-Habitat Relationships (WHR) classification. All environmental variables were gathered in a geographic information system (GIS) and resampled to 30 m resolution to match the digital elevation model layer. GIS analyses were conducted using Environmental

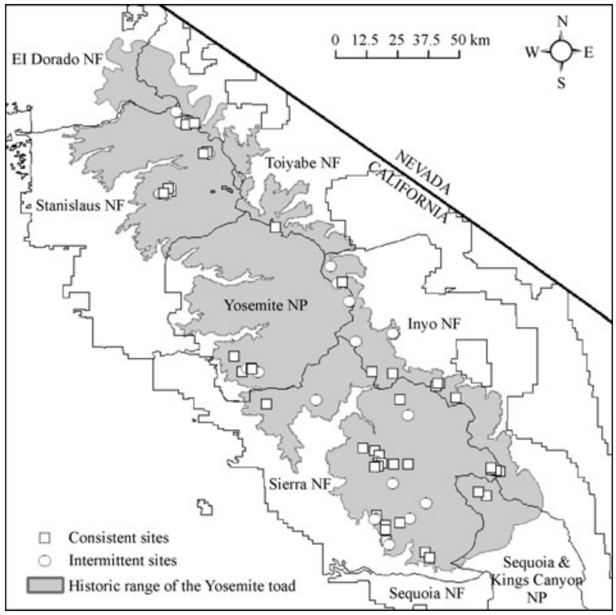

Fig. 1 Yosemite toad locations, classified into consistent and intermittent sites

Systems Research Institute's (ESRI, Redlands, California, USA) ArcGIS 9.2.

Multicollinearity was tested by examining cross-correlations for all variables. Only one variable from a highly correlated set of variables (Pearson's correlation coefficient $\geqslant \pm 0.80$) was included in the analyses, based on contribution to potential distribution and ecological relevance to the Yosemite toad. For example, many of the bioclimatic variables were correlated such as mean diurnal range, isothermality, and temperature annual range; only mean diurnal range was included in the analyses and the other variables were excluded. Subsequently, only six of the 19 bioclimatic variables (mean diurnal range, temperature seasonality, maximum temperature of warmest month, annual precipitation, precipitation of driest quarter, and precipitation of coldest quarter) were included in the analyses. Overall, a total of 12 environmental variables that were not correlated were used in the models (Appendix 1).

2.3 Maxent model

There are numerous species distribution modeling methods, but the purpose of this paper was not to compare them. Instead, we used one relatively newer method which has consistently fared well in model comparison studies (Elith et al., 2006; Kumar et al., 2009; Li et al., 2008). The maximum entropy model, Maxent, is a general purpose predictive model that uses presence-only data (Phillips et al., 2004, 2006b). It is based on the principle of maximum entropy, using available information as constraints and obtaining the least-biased inferences when insufficient information is available. This method estimates the probability distribution of a species by finding the probability distribution of maximum entropy, which is a probability that is closest to uniform (Phillips et al., 2006b). Maxent 3.3.0 was used for the modeling and is freely available from the authors (www.cs.princeton.edu/~schapire/maxent/).

2.4 Model development and validation

Three separate Maxent models were run for 1) all occurrence locations (with all 76 sites); 2) the 49 consistent sites, and 3) the 27 intermittent sites, using the 12 environmental predictors. We ran each model 25 times with a 25-fold cross-validation, and model results were averaged for all runs. The validation of predictive model outputs from Maxent is accomplished in several ways. First, the user has the option of defining a percentage of the data which: 1) allows for testing and training omissions against threshold; 2) provides predicted area against threshold; and 3) calculates the receiver operating characteristic curve (ROC). The area under the ROC curve (AUC) is calculated for each. Second, a jackknife option allows the estimation of the bias and standard error in the statistics, and tests of variable importance (Phillips et al. 2004, 2006b). Finally, Maxent generates response curves for each predictor variable. Maxent has had favorable reviews with predicting species distributions from small sample sizes (e.g., geckos in Madagascar, *Uroplatus sp*., Pearson et al., 2007; American bullfrogs across the globe, *Rana catesbeiana*, Ficetola et al., 2007).

2.5 Patch connectivity and patch size

Patch connectivity and size are important components in defining a spatially structured population and may play a role in identifying patch type. However, patch connectivity (measured by distance to nearest occupied site) and patch size (measured by site acreage) were not included in the Maxent model because they do not have meaningful measurable values in the landscape outside the sites, and thus cannot be modeled by the maximum entropy probability distribution. To evaluate the importance of these variables in determining patch type, classification and regression trees (CART) method was utilized with a 10-fold cross-validation. The two patch types were classified by CART using the 12 uncorrelated environmental variables plus distance to nearest occupied site and site acreage. Distance to nearest occupied site was calculated in a geographic information system (ArcGIS 9.3) based on known occupied sites. Site acreage was gathered from the survey data set of Yosemite toad locations. Statistical analysis was performed with R software (version 2.11.0; http://www.r-project.org) using the rpart package.

3 Results

3.1 All-sites species distribution model

The Maxent model results for all sites showed suitable habitat for the Yosemite toad in areas from El Dorado National Forest in the north, through Yosemite National Park and down to Sierra National Forest and Sequoia-Kings Canyon National Park in the south (Fig. 2). Highly suitable habitats primarily have low slopes, are in specific vegetation types (wet meadow, alpine-dwarf shrub, montane chaparral, red fir, and subalpine conifer), and have warm temperatures; greater distance to fire perimeter, low aspect classes and mean diurnal temperature range between approximately 10–14°C are also associated with suitable habitat to a lesser degree (Table 1). The Maxent model performed well for all the Yosemite toad sites (AUC = 0.95±0.03 SD). Variable response curves for the top six predictors showed mostly nonlinear responses for the factors, excepting vegetation type and aspect which were categorical factors (Fig. 3). Slope displayed a reverse sigmoid response with a fairly steep decline. The bioclimatic variables showed unimodal responses, with a fairly broad range of suitability for these variables. Distance to fire perimeter showed a linear response until it reached a threshold value.

3.2 Consistent-sites species distribution model

The Maxent model results for consistent sites showed more limited suitable habitat for the Yosemite toad for the same study area (Fig. 2). Similar to the model for all Yosemite toad occurrence sites, highly suitable consistent-site habitats have low slopes, specific vegetation types (primarily wet meadow, alpine-dwarf shrub, montane chaparral, red fir, and subalpine conifer), and warm temperatures; low aspect-classes, precipitation range between approximately 500–800 mm during the coldest quarter, and mean diurnal temperature range between approximately 9–15°C further define consistent-site habitat (Table 1). The Maxent models performed well for the Yosemite toad consistent sites (AUC = 0.95±0.05 SD). Variable response curves for the top six predictors show similar nonlinear responses as the all-occurrence model for most of the factors as well as similar results for the categorical variables (Fig. 4).

3.3 Intermittent-sites species distribution model

The Maxent model results for intermittent sites differed markedly from the models for all-occurrence sites and consistent sites (Fig. 2). Intermittent-site habitat is more extensive throughout the range of the Yosemite toad than for consistent sites. The primary factors associated with intermittent-site habitat included distance to fire perimeter,

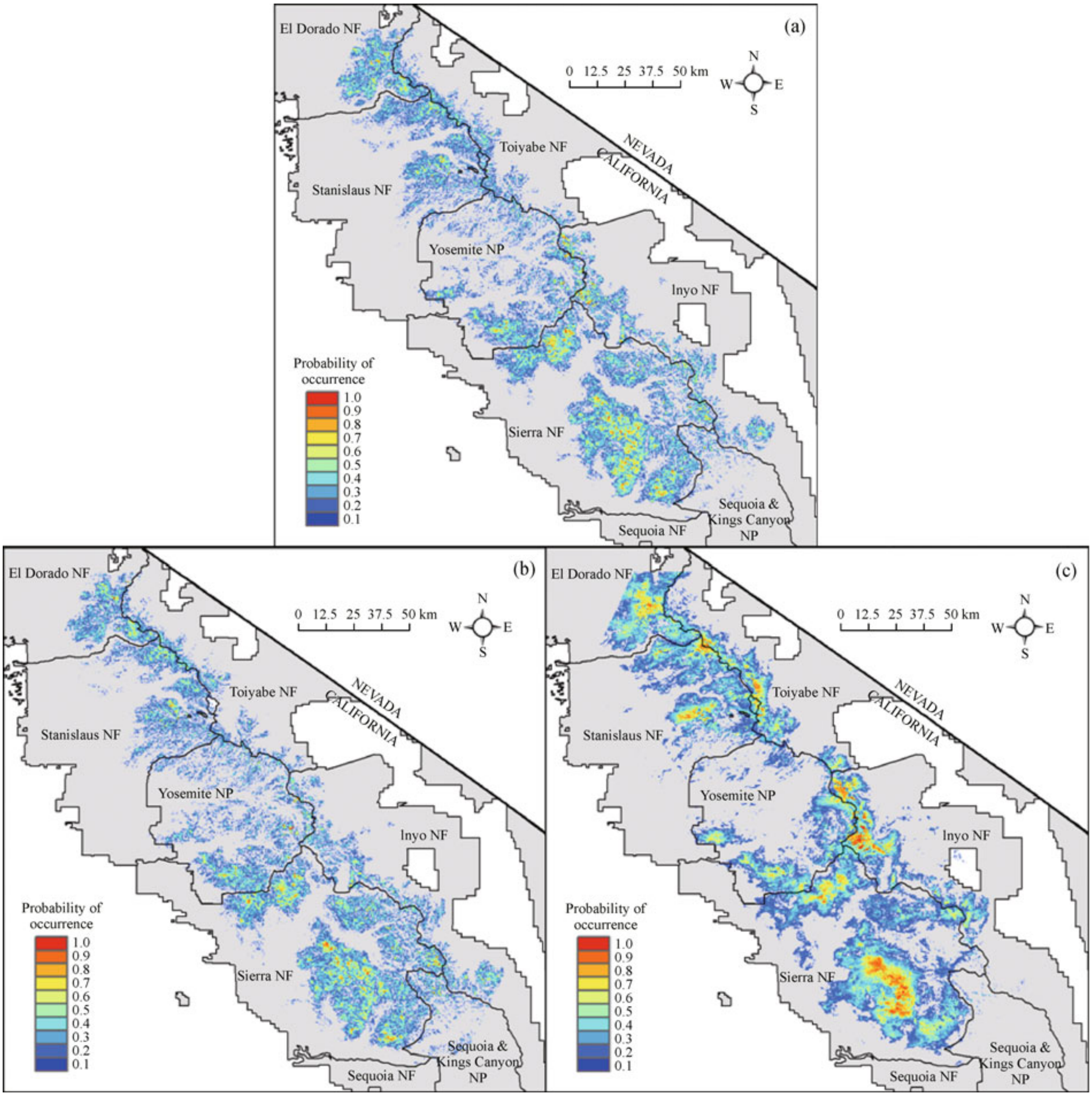

Fig. 2 Predicted potential geographic distribution for Yosemite toad: (a) all sites; (b) sites that are consistently occupied with relatively robust populations (consistent sites); and (c) sites that are intermittently occupied with few individuals when occupied (intermittent sites)

a slightly different response to vegetation types, distance to timber harvest activity, and aspect class (Table 1). More than half of variable contributions to the model were a combination of distance to fire perimeter (41.8%) and distance to timber harvest activity (10.1%). Certain vegetation types such as lodgepole pine were used more by intermittent-site populations than by consistent-site populations, while montane chaparral was used less.

Fewer variables contributed more than 5% to the intermittent-site habitat compared to the all-occurrence habitat and consistent-site habitat (Table 1). Slope was not a significant predictor in the intermittent-site model (4% contribution to the predicted potential geographic distribution), unlike the all-occurrence and consistent-site models where slope had the highest contribution. Intermittent sites were associated with a wider spectrum of slopes, as the slope response curve was more gradual for intermittent sites (Fig. 5) compared to all-occurrence sites (Fig. 3) and consistent sites (Fig. 4). The Maxent models performed well for the Yosemite toad intermittent sites (AUC = 0.90±0.11 SD).

3.4 Area of consistent- and intermittent-site habitats

Results show that habitat suitability for consistent sites is more restricted than either the all-occurrence sites or the

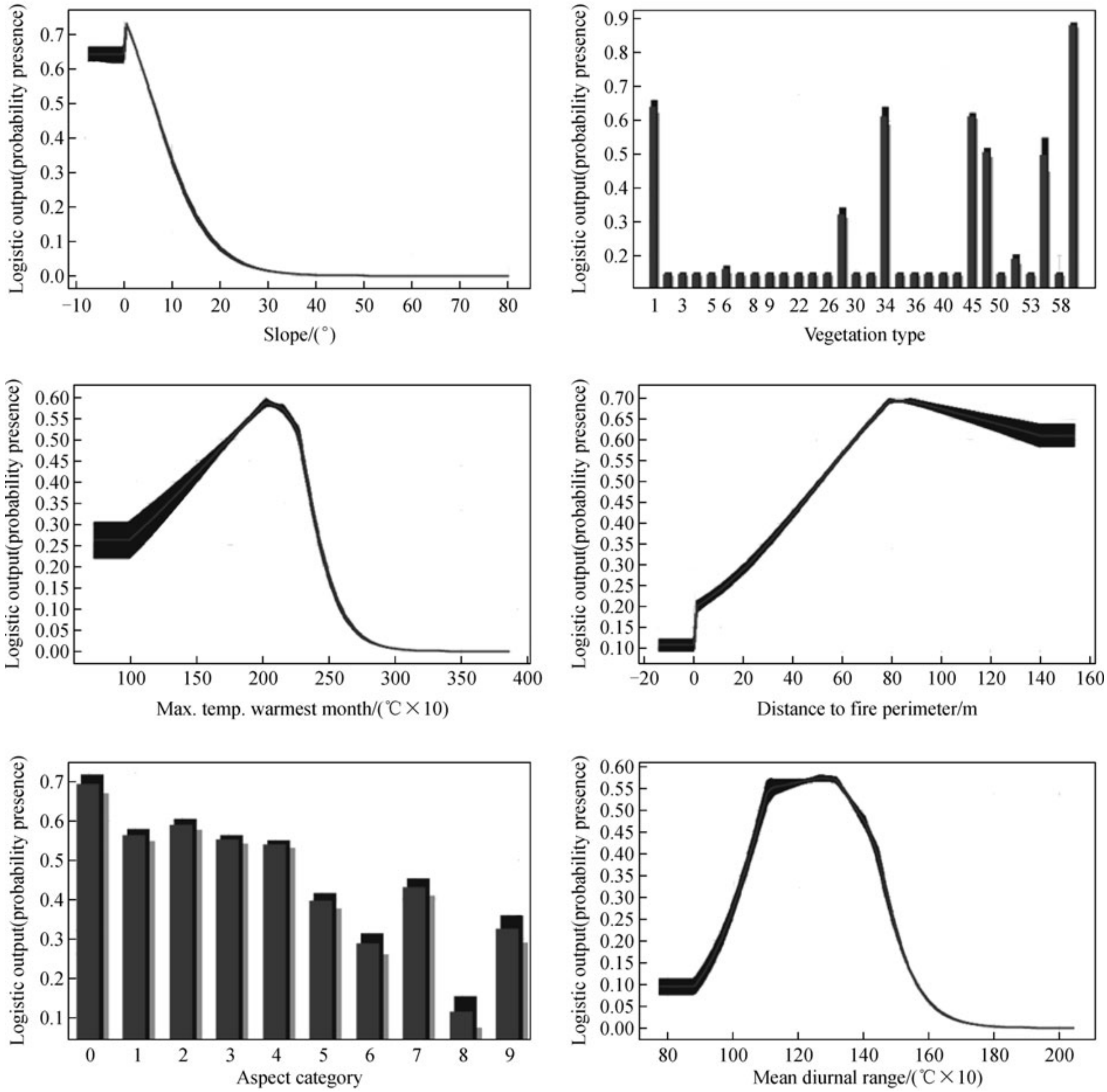

Fig. 3 Variable response curves for the top six predictors in the Maxent model prediction for all Yosemite toad sites (consistent plus intermittent sites)

Table 1 Relative contributions of predictor variables to the three predicted potential geographic distribution models (models using all sites, consistent sites only, and intermittent sites only) for Yosemite toad. Only variables that have greater than or equal to 5% contribution are included in the table

Variable	Contribution/%		
	All sites	Consistent sites	Intermittent sites
Slope	35.8	35.5	—
Vegetation type	13.4	15.0	20.9
Max Temp. warmest month	10.5	13.7	—
Distance to fire perimeter	9.9	—	41.8
Aspect	8.6	9.2	7.8
Mean diurnal range	8.4	5.0	—
Precip. coldest quarter	—	8.5	—
Distance to timber harvest	—	—	10.1

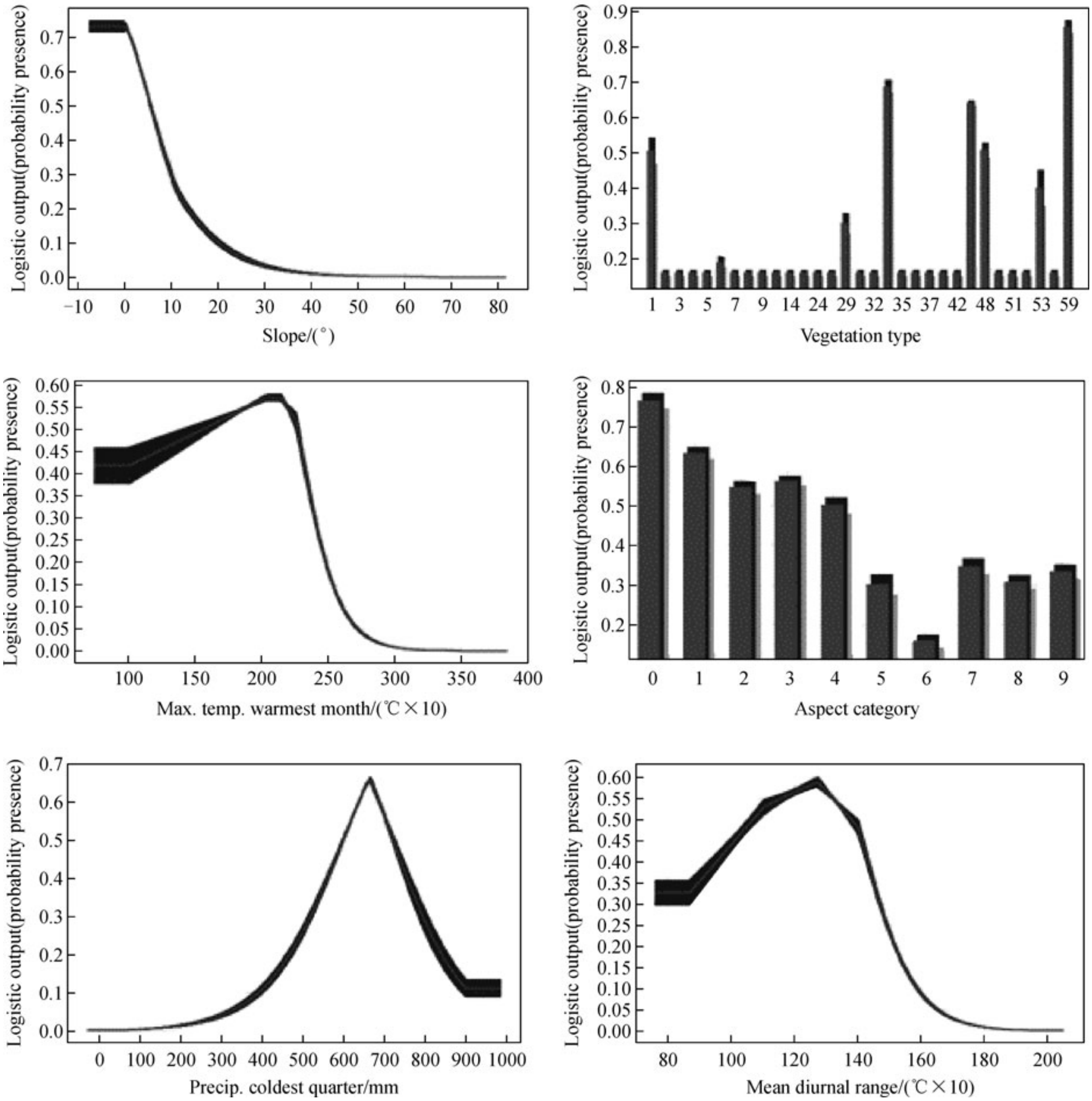

Fig. 4 Variable response curves for the top six predictors in the Maxent model prediction for Yosemite toad sites that are consistently occupied with relatively robust populations (consistent sites)

intermittent sites (Table 2). For probability of occurrence greater than 0.5, consistent sites have 87% of the all-occurrence area and 61% of the intermittent sites area. Intermittent sites have the most extensive habitat suitability, with 141% of the all-occurrence area.

3.5 Patch connectivity and patch size

The classification tree results for predicting patch type (i.e., consistent sites versus intermittent sites) did not include distance to nearest occupied site or site acreage in any of the tree nodes. The root node was split based on distance to fire perimeter (⩾92.9), the second node was separated on the easting coordinates (⩽119.8), the third node was separated on aspect (= south-east, south, south-west, west categories), and the final node was split based on the maximum temperature of the warmest month (⩾201.5). Root node error was 0.355.

4 Discussion

4.1 Consistent- and intermittent- site differences for the Yosemite toad

The two major conclusions from our study were: 1)

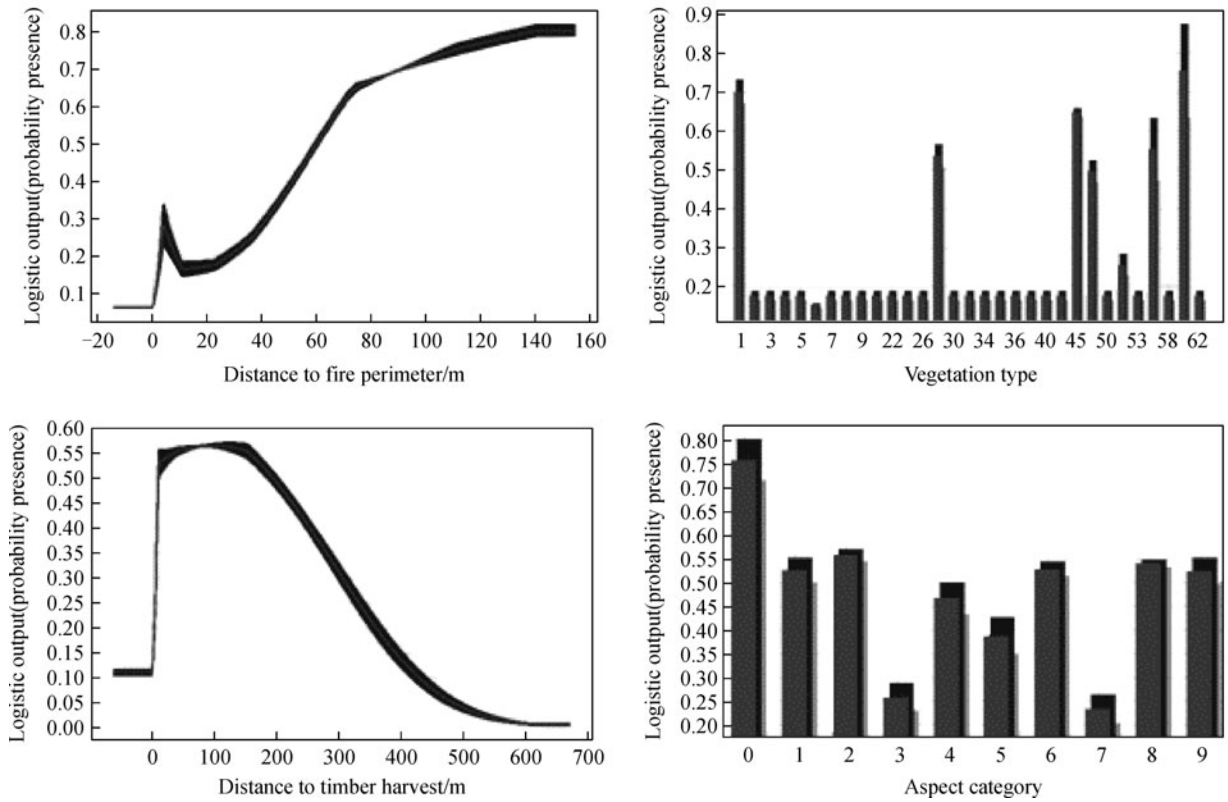

Fig. 5 Variable response curves for the top four predictors in the Maxent model prediction for Yosemite toad sites that are intermittently occupied with few individuals when occupied (intermittent sites)

Table 2 Areas of predicted occurrence for Yosemite toad in the three geographic distribution models (all sites, consistent sites only, and intermittent sites only)

Probability of occurrence	Area/ha		
	All Sites	Consistent sites	Intermittent sites
0.9–1.0	1355	1439	1395
0.8–0.9	6580	6010	9762
0.7–0.8	12564	10312	17522
0.6–0.7	17308	14666	24738
0.5–0.6	23064	20315	32499
Sum	60871	52742	85916

modeling all occurrences of a species may mask important differences in consistent and intermittent sites; and 2) modeling intermittent-site populations may expose threats to population persistence better than models of all-occurrences or consistent sites. Cleary, disturbance factors contributed more to the distribution model for intermittent sites (Table 1). This suggests that highly suitable habitat for breeding populations may be affected by fire and timber harvest. Consistent with what is already known about the Yosemite toad, the models show that the species is generally associated with the wet meadow vegetation type and flat areas. However, modeling consistently occupied sites and intermittently occupied sites separately allowed our first look into the broadening of habitat features associated with marginal habitat. For example, intermittent sites included a broader suite of slopes than consistent sites. In addition, there are fewer significant environmental factors and thus fewer constraints associated with intermittent-site habitat (Table 1). Highly suitable habitat associated with intermittent sites is thus increased relative to that of all-occurrence or consistent sites (Table 2).

For the Yosemite toad, there are several variables that correlate with the presence of the species at both consistent and intermittent sites. This indicates that the species does not have a simple relationship with the environment, and is found within a range of environmental conditions. The distribution of consistently occupied sites is influenced by topographic and bioclimatic factors and shows tolerance for a fairly broad range of temperature and precipitation gradients (Fig. 4). This indicates that the Yosemite toad may be relatively insensitive to changes in bioclimatic conditions within its current elevational range. However, the Yosemite toad may be less able to respond to widespread changes in land management related to fire management and timber harvest (Fig. 5). Fire can have negative effects directly though mortality or indirectly through destruction of habitat. In a review of amphibian responses to fire and fire management practices, Pilliod et al. (2003) found that responses can be spatially and temporally variable. However, the negative effects of fire may be greatest for species in regions with long fire-return intervals (such as in the Sierra Nevada which has been subject to fire suppression activities over the past century) and for habitat specialists like the Yosemite toad. Conversely, timber removal may have a beneficial effect on the species by preventing encroachment of conifers into breeding meadows (Semlitsch et al. 2009) or by changing local mico-climate conditions (e.g., temperature, solar radiation) in cleared areas.

Our study suggests that persistence of the Yosemite toad may depend, in part, on: 1) maintaining highly suitable breeding habitat (and many consistent-site populations) across broad environmental gradients; and 2) reducing threats to consistent-site populations over a smaller area than would be identified if the entire population were modeled (Table 2). Additional monitoring is needed to assess changes in consistent and intermittent sites over time.

4.2 Caveats

There are many caveats associated with species-environmental matching models. All such models are affected by sample size, the clustering of presence points, and the resolution and accuracy of predictive layers (Phillips et al., 2004, 2006b). There are also caveats associated with the data for the Yosemite toad. The classification of "consistent" and "intermittent" sites is somewhat subjective and can be confounded by detectability issues. Sites may only be surveyed once during the year or may not be surveyed in consecutive years, and life-stages other than calling males can be difficult to detect and are easily missed. The classification of a site as consistently occupied versus only intermittently occupied then may not be true in all cases.

In our case study, we had almost twice as many consistent sites (49 vs. 27), but both types of sites were broadly distributed over the same area of interest. A wide range of environmental variables was associated with population distributions, yet the accuracy of models (in terms of AUC) was very high. Thus, we feel that the models performed well enough to provide a preliminary understanding of the primary differences between consistent- and intermittent-type population sites.

4.3 General utility of modeling patch types

There is considerable theoretical interest in patch quality and metrics and increasing empirical evidence that patch quality is influential in species' distributions and spatial population structure (see review by Mortelliti et al., 2010). Though there is recognition that the habitat and quality within patches can vary (Lloyd, 2008; Heisswolf et al., 2009), most studies focus on how patch characteristics relate to overall occupancy (Bradford et al., 2003; Schooley and Branch, 2009). Patch occupancy is treated as a bivariate state (occupied versus not occupied) and once a patch is found to be occupied it remains classified as such. Data gathered from all occupied patches are then typically used in models and analyses. However, occupancy can be intermittent and changeable resulting in different types of occupied patches (e.g., mainlands and islands, sources and sinks). The different patch types vary in their size, location and environmental characteristics and it is not surprising that these variations influence the species-environment relationship and lead to different predictions of suitable habitat. Modeling of patch types separately identifies their associated environmental variables and provides a more complete picture of overall environmental requirements of a species and potential constraints.

Patch type is often thought to be highly related to patch metrics such as connectivity and size since these variables are the principal determinants of the existence and nature of a spatial population structure (Pulliam, 1988; Harrison and Taylor, 1997). Our results, however, indicate that patch type for the Yosemite toad is determined more by environmental variables than by distance to nearest occupied site or site acreage. The results of the CART analysis, similar to the Maxent models, showed that disturbance, topographic and bioclimatic variables are primary factors in differentiating patch type. Although this result may not be true for all species, it illustrates the importance of looking beyond patch metrics when investigating patch types.

Species with spatially structured populations are not uncommon (Pulliam, 1988; Mortelliti et al., 2010), so the lessons learned here may have broad applications. Furthermore, dispersal is a necessary risk for a species to extend its range, with individuals likely moving into intermittently occupied patches first. While dispersal may be risky to the individual, "the long-term survival of populations depends on having a sufficient number of individuals that move, find each other, and locate suitable breeding habitats" (Kokko and López-Sepulcre, 2006). For example, Columbia spotted frogs (*Rana luteiventris*) in the northern Rocky Mountains "had exceptionally high juvenile dispersal rates (up to 62% annually) over long distances (> 5km), large elevation gains (> 750m) and steep inclines (36° incline over 2km)" (Funk et al., 2005). Dispersal increases gene flow, assuming the dispersers survive and reproduce. In addition to extending a species range, and thus extending the environmental gradients associated with range expansion, dispersion may accelerate evolution. For example, the leading edge of invasive Cane toads (*Bufo marinus*) in Australia resulted in longer legs for dispersing individuals (Phillips et al., 2006a). For all these reasons, it may be particularly important to map, model, and monitor dispersing individuals in intermittent-site populations separately from the more stable consistent-site populations of the same species.

We conclude that many studies of species distributions may benefit by modeling patch types separately. Modeling and monitoring consistently occupied sites may provide a realistic snapshot of current species-environment relationships, important climatic and topographic patterns associated with species distribution patterns, and an understanding of the plasticity of the species in response to varying climate regimes across its range. Meanwhile, modeling and monitoring widely dispersing individuals and intermittently occupied sites may uncover environmental thresholds and human-related threats to population persistence. This may be particularly important for rare and threatened species. Model outputs may help guide future data collection, identify suitable habitat, and guide restoration efforts. Iterative mapping, monitoring, and modeling over time may be needed to assure the persistence of sensitive species.

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References

Alford R A, Richards S J (1999). Global amphibian declines: a problem in applied ecology. Annu Rev Ecol Syst, 30(1): 133–165

Bradford D F, Neale A C, Nash M S, Sada D W, Jaeger J R (2003). Habitat patch occupancy by toads (*Bufo punctatus*) in a naturally fragmented desert landscape. Ecology, 84(4): 1012–1023

Davidson C, Shaffer H B, Jennings M R (2002). Spatial tests of the pesticide drift, habitat destruction, UV-B, and climate-change hypotheses for California amphibian declines. Conserv Biol, 16(6): 1588–1601

Drost C A, Fellers G M (1996). Collapse of a regional frog fauna in the Yosemite area of the California Sierra Nevada, USA. Conserv Biol, 10(2): 414–425

Elith J, Graham C H, Anderson R P, Dudik M, Ferrier S, Guisan A, Hijmans R J, Huettmann F, Leathwick J R, Lehmann A, Li J, Lohmann L G, Loiselle B A, Lohmann G, Manion G, Moritz C, Overton J M, Peterson A T, Phillips S J, Nakamura M, Nakazawa Y, Schapire R E, Wisz M S, Zimmermann N E (2006). Novel methods improve prediction of species' distributions from occurrence data. Ecography, 29: 129–151

Evangelista P H, Kumar S, Stohlgren T J, Jarnevich C S, Crall A W, Norman J B III, Barnett D T (2008). Modelling invasion for a habitat generalist and a specialist plant species. Divers Distrib, 14(5): 808–817

Ficetola G F, Thuiller W, Miaud C (2007). Prediction and validation of the potential global distribution of a problematic alien invasive species—the American bullfrog. Divers Distrib, 13(4): 476–485

Frankham R, Ballou J D, Briscoe D A (2002). Introduction to conservation genetics. Cambridge University Press, Cambridge

Fuller T, Morton D P, Sarkar S (2008). Incorporating uncertainty about species' potential distributions under climate change into the selection of conservation areas with a case study from the Arctic Coastal Plain of Alaska. Biol Conserv, 141(6): 1547–1559

Funk W C, Greene A E, Corn P S, Allendorf F W (2005). High dispersal in a frog species suggests that it is vulnerable to habitat fragmentation. Biol Lett, 1(1): 13–16

Giovanelli J G R, Haddad C F B, Alexandrino J (2008). Predicting the potential distribution of the alien invasive American bullfrog (*Lithobates catesbeianus*) in Brazil. Biol Invasions, 10(5): 585–590

Hanski I (1999). Metapopulation Ecology. New York: Oxford University Press

Harrison S, Taylor A D (1997). Empirical evidence for metapopulation dynamics. In: Hanski I, Gilpin M E, eds. Metapopulation Dynamics: Ecology, Genetics and Evolution. New York: Academic Press, 27–42

Heisswolf A, Reichmann S, Poethke H J, Schrader B, Obermaier E (2009). Habitat quality matters for the distribution of an endangered leaf beetle and its egg parasitoid in a fragmented landscape. J Insect Conserv, 13(2): 165–175

Jarnevich C S, Stohlgren T J (2009). Near term climate projections for invasive species distributions. Biol Invasions, 11(6): 1373–1379

Karlstrom E L (1962). The toad genus Bufo in the Sierra Nevada of California. Univ Calif Publ Zool, 62: 1–104

Kokko H, López-Sepulcre A (2006). From individual dispersal to species ranges: perspectives for a changing world. Science, 313 (5788): 789–791

Kumar S, Spaulding S A, Stohlgren T J, Hermann K A, Schmidt T S, Bahls L L (2009). Predicting habitat distribution for freshwater diatom Didymosphenia geminata in the continental United States. Front Ecol Environ, 7: 415–420

Levins R A (1969). Some demographic and evolutionary consequences of environmental heterogeneity for biological control. Bull Entomol Soc Am, 15: 237–240

Li M Y, Ju Y W, Kumar S, Stohlgren T J (2008). Modeling potential habitats for alien species *Dreissena polymorpha* (Zebra mussel) in the

Continental USA. Acta Ecol Sin, 28(9): 4253–4258
Lloyd H (2008). Influence of within-patch habitat quality on high-Andean Polylepis bird abundance. Ibis, 150(4): 735–745
Marsh D M, Trenham P C (2001). Metapopulation dynamics and amphibian conservation. Conserv Biol, 15: 40–49
Mortelliti A, Amori G, Boitani L (2010). The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. Oecologia, 163(2): 535–547
Pawar S, Koo M S, Kelley C, Ahmed M F, Chaudhuri S, Sarkar S (2007). Conservation assessment and prioritization of areas in Northeast India: Priorities for amphibians and reptiles. Biol Conserv, 136(3): 346–361
Pearson R G, Raxworthy C J, Nakamura M, Peterson A T (2007). Predicting species distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar. J Biogeogr, 34(1): 102–117
Petranka J W, Holbrook C T (2006). Wetland restoration for amphibians: should local sites be designed to support metapopulations or patchy populations? Restor Ecol, 14(3): 404–411
Phillips B L, Brown G P, Webb J K, Shine R (2006a). Invasion and the evolution of speed in toads. Nature, 439(7078): 803
Phillips S J, Dudik M, Schapire R E (2004). A maximum entropy approach to species distribution modeling. Brodley C E, ed. In: Proceedings of the 21st International Conference on Machine Learning. New York: ACM Press, 655–662
Phillips S J, Anderson R P, Schapire R E (2006b). Maximum entropy modeling of species geographic distributions. Ecol Modell, 190(3–4): 231–259
Pilliod D S, Bury R B, Hyde E J, Pearl C A, Corn P S (2003). Fire and amphibians in North America. For Ecol Manage, 178(1–2): 163–181
Pulliam H R (1988). Sources, sinks, and population regulation. Am Nat, 132(5): 652–661
Riley S P D, Busteed G T, Kats L B, Vandergon T L, Lee L F S, Dagit R G, Kerby J L, Fisher R N, Sauvajot R M (2005). Effects of urbanization on the distribution and abundance of amphibians and invasive species in Southern California streams. Conserv Biol, 19(6): 1894–1907
Schooley R L, Branch L C (2009). Enhancing the area-isolation paradigm: habitat heterogeneity and metapopulation dynamics of a rare wetland mammal. Ecol Appl, 19(7): 1708–1722
Semlitsch R D, Todd B D, Blomquist S M, Calhoun A J K, Gibbons J W, Gibbs J P, Graeter G J, Harper E B, Hocking D J, Hunter M L Jr, Patrick D A, Rittenhouse T A G, Rothermel B B (2009). Effects of timber harvest on amphibian population: Understanding mechanisms from forest experiments. Bioscience, 59(10): 853–862
Sherman C K, Morton M L (1993). Population declines of Yosemite toads in the eastern Sierra Nevada of California. J Herpetol, 27(2): 186–198
Smith M A, Green D M (2005). Dispersal and the metapopulation paradigm in amphibian ecology and conservation: Are all amphibian populations metapopulations? Ecography, 28: 110–128
Svenning J C, Normand S, Kageyama M (2008). Glacial refugia of temperate trees in Europe: Insights from species distribution modelling. J Ecol, 96(6): 1117–1127
U.S. Fish and Wildlife Service (USFWS) (2002). 12-month finding for a petition to list the Yosemite toad. Federal Register, 67: 75834–75843
Waltari E, Guralnick R P (2009). Ecological niche modelling of montane mammals in the Great Basin, North America: examining past and present connectivity of species across basins and ranges. J Biogeogr, 36(1): 148–161

Appendix 1. Environmental predictor variables considered for the Maxent models. Variables with an asterisk (*) were included in the models after analysis of cross-correlations

Variable	Source
Elevation (m)	USGS National Elevation Data set
*Aspect (category based on degrees)	USGS National Elevation Data set
*Slope (degrees)	USGS National Elevation Data set
*Vegetation (WHR type)	United States Forest Service, Pacific South-west Region GIS Clearinghouse; CALVEG layer
*Distance to agricultural land (m)	California Fire Resources Assessment Program; land cover layer
*Distance to fire perimeter (m)	United States Forest Service, Pacific South-west Region GIS Clearinghouse; FACTS Accomplished Harvest Activities layer
*Distance to timber harvest activity (m)	California Fire Resources Assessment Program; Fire Perimeters layer
Annual mean temperature (BIO1;°Cx10)	PRISM climate data, WorldClim calculation
*Mean diurnal range (BIO2; °C x10)	PRISM climate data, WorldClim calculation
Isothermality (BIO3)	PRISM climate data, WorldClim calculation
*Temperature seasonality (BIO4;SDx100)	PRISM climate data, WorldClim calculation
*Max. temp of warmest month (BIO5; °Cx10)	PRISM climate data, WorldClim calculation
Min. temp of coldest month (BIO6; °Cx10)	PRISM climate data, WorldClim calculation
Temperature annual range (BIO7; °Cx10)	PRISM climate data, WorldClim calculation
Mean temp of wettest quarter (BIO8; °Cx10)	PRISM climate data, WorldClim calculation
Mean temp of driest quarter (BIO9; °Cx10)	PRISM climate data, WorldClim calculation
Mean temp of warmest quarter (BIO10; °Cx10)	PRISM climate data, WorldClim calculation
Mean temp of coldest quarter (BIO11; °Cx10)	PRISM climate data, WorldClim calculation
*Annual precipitation (BIO12;mm)	PRISM climate data, WorldClim calculation
Precipitation of wettest month (BIO13;mm)	PRISM climate data, WorldClim calculation
Precipitation of driest month (BIO14;mm)	PRISM climate data, WorldClim calculation
Precipitation seasonality (BIO15;CV)	PRISM climate data, WorldClim calculation
Precipitation of wettest quarter (BIO16;mm)	PRISM climate data, WorldClim calculation
*Precipitation of driest quarter (BIO17;mm)	PRISM climate data, WorldClim calculation
Precipitation of warmest quarter (BIO18;mm)	PRISM climate data, WorldClim calculation
*Precipitation of coldest quarter (BIO19;mm)	PRISM climate data, WorldClim calculation

Note: WHR is the California Wildlife-Habitat Relationships vegetation classification. BIO represents the 'bioclim' variable calculated from PRISM climate data (http://www.prism.oregonstate.edu) using an ARC AML script (mkBCvars.aml; http://www.worldclim.org/mkBCvars.aml). SD is standard deviation, CV is coefficient of variation