Research Article

Developing and Applying Habitat Models Using Forest Inventory Data: An Example Using a Terrestrial Salamander

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Abstract

We provide a framework for developing predictive species habitat models using preexisting vegetation, physical, and spatial data in association with animal sampling data. The resulting models are used to evaluate questions relevant to species conservation, in particular, comparing occurrence estimates in reserved and unreserved lands. We used an information–theoretic approach to develop and evaluate a priori models to predict the occurrence of the Del Norte salamander (Plethodon elongatus) *within its geographic range on national forests in California. We then evaluated the association of* P. elongatus *to federal reserved lands using both an empirical and model-based assessment. For the model-based assessment, we calculated the probability of occurrence at existing Forest Inventory and Analysis (FIA) plots that we sampled for salamanders and those that were unsampled within our study area. The Del Norte salamander was more likely to be detected at plots with steeper slopes, older trees, more hardwood basal area, more canopy cover of conifers, more rock, and in areas receiving more precipitation and slightly warmer mean annual temperatures. Only the relationship of percent rock cover to probability of occupancy by* P. elongatus *was linear. Our best multivariate predictive model explained 66.2% of the deviance, and it correctly classified 96% of the plots at which* P. elongatus *was detected and 94% of the plots at which it was not. Ten-fold, cross-validation results revealed that the best model was relatively robust with correct classification rates of 87% and 89% for locations at which* P. elongatus *was detected and not detected, respectively. Our empirical results revealed no strong association with reserved lands. However, when we used our best model to estimate* P. elongatus' *probability of occupancy at both sampled and unsampled plots, the mean probability of occupancy within reserved lands was greater than in unreserved lands, suggesting that reserved lands have higher-quality habitat relative to nonreserved lands. Overall, our results indicate that systematically collected forest inventory data can have significant value in developing wildlife habitat models when combined with samples of animal occurrence. Robust, empirically derived habitat models, such as the one we developed, may be useful tools for managers for monitoring the quantity, quality, and distribution of a species' habitat.* (JOURNAL OF WILDLIFE MANAGEMENT 70(3):671–681; 2006)

Key words

Akaike's Information Criterion, Del Norte salamander, forest inventory and analysis, generalized additive model, management, Plethodon elongatus, *wildlife habitat modeling.*

Although wildlife–habitat modeling has a long history (see Verner et al. 1986), there exists a gap between researcher-generated models and the needs of land managers (Stauffer 2002). Stauffer (2002) stated that many habitat models were developed for small areas and required data inputs that were typically unavailable to managers. We sought to develop, compare, and test predictive habitat models using animal sampling coupled with predictor variables that can be associated with animal distribution and abundance, and that are readily available to land managers and regularly resampled. We also evaluated the use of the best resulting model for addressing questions of conservation interest to forestland managers throughout the U.S. Pacific Northwest.

Regional surveys for rare organisms are extremely useful for delineating geographic ranges (extent of occurrence; sensu Gaston 1991) and assessing relative abundances throughout large areas. However, the time and expense of conducting such surveys often precludes the simultaneous sampling of habitat variables. Thus, development of habitat models based on large-scale surveys often is constrained to use preexisting and remotely sensed data such as broad vegetation categories (e.g., shrub, forest, grassland), elevation, slope, topographic position, and climatic and spatial variables (see Austin and Meyers 1996, Fleishman et al. 2001). Within national forests and Bureau of Land Management forestlands in California and elsewhere, finer-scale data on the vegetation and physical features of a georeferenced 1-ha plot are periodically sampled within Forest Inventory and Analysis (FIA) plots (Roesch and Reams 1999, U.S. Forest Service 2000). Such plots occur on an ~5.5-km grid across the entire forest landscape of the Pacific Northwest. The FIA data are gathered and used to assist in planning and monitoring forest structure and plant communities at large scales (e.g., a region or a national forest). By sampling for other organisms at FIA plots, we have the benefit of using fine-scale physiographic, physiognomic, and floristic data that are preexisting (but of recent vintage) at FIA plot locations, and thus of tremendous economic savings during development of species-habitat models.

However, the coupling of broad-scale surveys and preexisting habitat variables for developing models to predict species occurrence is relatively uncommon, especially for rare species

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(for exceptions, see Wiser et al. 1998, Pearce and Ferrier 2000, Gustafson et al. 2001, Dunk et al. 2004). For most ecological studies that evaluate habitat associations, a species-specific set of habitat variables is measured at sample plots, and those explanatory variables are thought to relate to the organism's occurrence, reproduction, or survivorship. The FIA plots are periodically resampled, and thus if good species-habitat models can be developed, they can be applied to updated FIA data to address questions of estimated habitat quantity, quality, distribution, and trends in these metrics.

In 1994, a bioregional plan was developed to manage public forest lands in the Pacific Northwest (the Northwest Forest Plan [NFP]; U.S. Forest Service and U.S. Bureau of Land Management 1994). Part of the NFP was to address the needs of >300 rare and little known species, which were to be managed within the Survey and Manage provision of the plan. Survey and Manage species were assumed by the authors of the NFP to 1) occur with the NFP area; 2) be associated with late-successional or old-growth forests; and 3) not be adequately protected within the reserve system set up under the NFP, a system designed primarily to assure the persistence of the northern spotted owl (*Strix occidentalis caurina*; U.S. Forest Service and U.S. Bureau of Land Management 1994). The Del Norte salamander (*Plethodon elongatus*) was on the original Survey and Manage list in 1994 because it was considered a rare/uncommon, endemic, terrestrial amphibian associated with late-seral forests (Welsh 1990, Welsh and Lind 1995), and it was not sufficiently protected by either the reserved lands or the aquatic conservation component of the NFP. *Plethodon elongatus* can be very abundant within individual forest stands (Welsh and Lind 1992) and may play an important role in nutrient dynamics and overall forest ecosystem stability (resilience-resistance) where it is the dominant salamander species (see Davic and Welsh 2004). Its densities are clearly sensitive to alterations of forest structure and re-setting of the successional stage (Welsh 1990, 2005; Welsh and Lind 1995; but see Diller and Wallace 1994). Nevertheless, it was removed from the Survey and Manage list (U.S. Forest Service and U.S. Bureau of Land Management 2001) prior to the discontinuation of that entire program (U.S. Forest Service and U.S. Bureau of Land Management 2004), based on the decision by land managers that there were sufficient numbers of populations on federal reserved lands to provide for species persistence.

We revisit this issue, in part, by evaluating the association of *P. elongatus* with specific habitat characteristics and with lands reserved for nonconsumptive purposes (hereafter reserved lands). Our analyses, build upon the work of Diller and Wallace (1994) and Welsh and Lind (1995), which evaluated the habitat associations of *P. elongatus*.

These earlier efforts, while informative, are somewhat limited in their usefulness to forest managers. Diller and Wallace (1994) worked on commercial timberlands in the marine-influenced coastal zone of northwest California, which limits the applicability of their results to coastal areas of the range only. Welsh and Lind (1995) sampled across the species' range in California and at multiple spatial scales, but their model would be more difficult for managers to apply on the ground without collecting additional site information, and the level of detail in their study would not be practical for managers to duplicate. Furthermore, both of these studies predated the NFP and, therefore, made no attempt to evaluate the usefulness of the NFP land-allocation system for maintaining the persistence of this species on the landscape. We used our empirical data on *P. elongatus* presence–absence at FIA plots to evaluate its distribution in reserved and nonreserved lands, and we used our best predictive model to evaluate the relative quality of its habitat in reserved and nonreserved lands. If reserved lands contribute more to *P. elongatus* presence, we would expect a higher mean probability of *P. elongatus* occupancy on reserved lands than on those lands available for resource extraction. (e.g., Nauman 2001, Cutler et al. 2003).

Study Area

We conducted this study on those parts of the 3 national forests in northwestern California, USA, that include portions of the range of the Del Norte salamander (Stebbins 2003), the Shasta-Trinity, the Six Rivers, and the Klamath, sampling for salamanders at predetermined FIA points (Fig. 1).

Methods

Salamander sampling occurred within 1 hectare circles centered on the georeferenced FIA points, under appropriate climatic conditions (see below), in 1999, 2000, and 2001. Data on salamander occurrence came from 2 sources: first, salamanders were sampled concomitant to mollusk sampling as part of a large-scale regional sampling effort (see Dunk et al. 2002). For that effort, the sample was drawn from FIA plots using a stratified random design, with each of the 3 national forests as strata. Of 308 selected FIA plots, 105 fell within the known range of *P. elongatus* (Stebbins 2003). However, many FIA plots within *P. elongatus*' known range were not sampled as part of the joint mollusk–salamander sampling because they were not part of the initial random draw. We augmented the sample by adding 54 of the 181 remaining FIA plots within the salamander's range that were not included in the original sample, and that were accessible by road or trail and were below the known maximum elevation of the species (~1,570 m; Ollivier and Welsh 1999). This was a justifiable means of increasing our sample size because the entire set of FIA plots falling within the range of *P. elongatus* represented a random systematic sample relative to the potential occurrence of this salamander and its habitat. Ten of the sampled plots were missing associated FIA data, and thus our final sample included 149 plots. The 149 plots constituted 52% of the FIA plots within the range of *P. elongatus* (Fig. 1). Prior to combining the 2 salamander data sets, we evaluated whether they differed in the proportion of sample points at which *P. elongatus* was detected, using a chi-square analysis, to assure ourselves that there was no bias introduced by the differences in the field crews or methods of plot selection.

We conducted salamander sampling during the spring and fall under limited temperature (air: 4.5–25°C, soil: 4.5–20°C) and moisture conditions (relative humidity ≥45%; see Ollivier and Welsh 1999) to maximize the likelihood of detecting surface-active salamanders, with the protocol calling for 2 visits per site (105 sites) or the same total sampling effort during 1 visit to the more inaccessible sites (54 sites). Our sampling consisted of a 2- or

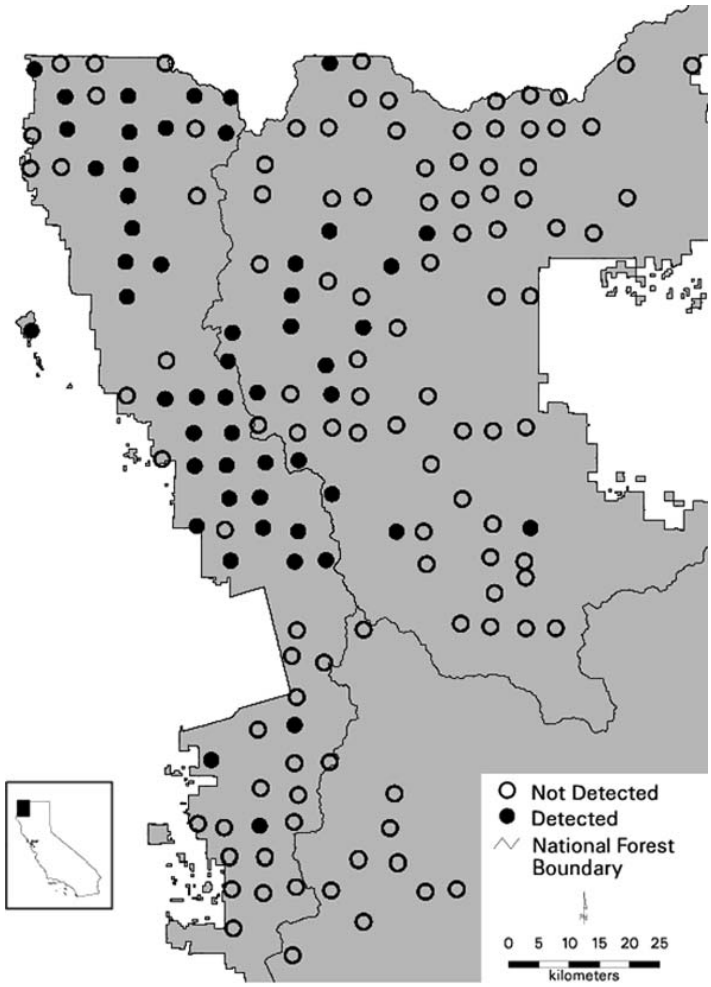

Figure 1. Distribution of FIA points sampled within the range of the Del Norte salamander (*Plethodon elongatus*) on the Six Rivers, Shasta-Trinity, and Klamath national forests of northern Calif., USA, in 1999, 2000, and 2001. Closed circles indicated detections of the target species.

4-person-hour, respectively, visual encounter survey (VES; Crump and Scott 1994) of surface cover objects within each 1-ha FIA plot. Given the potential for high variability in the detectability of plethodontid salamanders (Hyde and Simons 2001), we estimated detection probabilities using 43 plots that were sampled on 2 occasions and at which *P. elongatus* was detected during at least 1 of the visits. The probability of failing to detect the species after 2 visits was 0.0914, yielding a detection probability of greater than 90%, which exceeded the $\geq$80% recommended for habitat suitability modeling (Williams 2003). Our rigorous sampling protocol (Ollivier and Welsh 1999) was an attempt at keeping detectability constant over space and time, as recommended by Pollock et al. (2002), and the high detection probability we found suggests that we succeeded.

Analyses

Explanatory variables.—We derived candidate explanatory variables from 3 sources: 1) the vegetation variables collected at FIA plots during 1998 and 1999; 2) macroclimate variables from Parameter-elevation Regressions on Independent Slopes Model (PRISM; Daly et al. 1994); and 3) spatial coordinates (northing and easting). We restricted the large number of available FIA variables to only those that have been found to be correlated with the presence of *P. elongatus* in other studies in northern California (Diller and Wallace 1994, Welsh and Lind 1995) or were considered surrogates for these established predictive variables (see below). This included macroclimatic variables we thought might influence *P. elongatus* occurrence at a finer scale of resolution (see Spotila 1972, Feder 1983). The 8 PRISM climatic variables (Table 1), derived from USGS regional weather station data, represent mean values over a 30-year period from the mid-1960s to the mid-1990s (Daly et al. 1994). These data are at a 2-km resolution, which allowed for a reasonable estimation of the macroclimatic conditions associated with individual FIA plots 5.5 km apart.

Predictive models.—We used generalized additive models (GAMs; Hastie and Tibshirani 1990), with a logit-link function, using *P. elongatus* occurrence (detected, or not) as the binary response variable. We conducted all analyses using S-Plus 2000 statistical software (MathSoft 1999). The GAMs allow the data to define the functional form (shape) of the relationship between dependent and independent variables, rather than forcing the analyst or researcher to do so. For many organisms, so little is known of their relationship to biotic and abiotic features of the environment that searching for all possible or conceivable functional forms simply adds (often tremendously) to the number of models being compared with little additional benefits. We had confidence in our choice of explanatory variables, but for many of the variables, we could conceive of several functional forms. GAMs employ the data to determine the correct functional form and are an excellent tool for data exploration (Yee and Mitchell 1991) as well as prediction (Pearce and Ferrier 2000).

Because we used preexisting vegetation data at FIA plots and did not measure microclimatic variables (e.g., relative humidity), we lacked measurements of all variables included in the best models reported by previous investigators (Diller and Wallace 1994, Welsh and Lind 1995). However, we did include available surrogates for important variables that were not measured as a part of the FIA program (e.g., we substituted PRISM mean annual precipitation and temperature values for relative humidity). We developed and compared 167 subsets of possible predictor variables (hereafter models) that varied from 1 explanatory variable to those containing up to 8 variables. We developed models based on an evaluation of the literature, consideration of various combinations of variables that represented conditions found in late-seral forests (specifically relevant to the NFP), and field experience. We did not include in the same model variables we believed were highly correlated with one another (e.g., tree diameter and tree height). However, many of the models were nested subsets of other models. Due to the political, social, and management sensitivity of issues regarding wildlife associated with late-seral or old-growth forest, we sought to thoroughly evaluate several models that included these variables. It is important to note, however, that the form of these models would also be able to detect a lack of association with such conditions. Although 167 models may initially appear to be a data dredging exercise (sensu Anderson et al. 2001), an all possible subsets analysis (dredging at its truest) with 29 covariates would result in >250,000,000 models. We generally concur with the analytical philosophy of

Table 1. Mean and SE of variables at FIA plots from the Six Rivers, Shasta-Trinity, and Klamath national forests of northern Calif., USA (Fig. 1), where *Plethodon elongatus* was and was not detected. Data were collected in 1999, 2000, and 2001.

Variable	Mean detected	SE detected	Mean not detected	SE not detected
% Conifer cover	58.76	4.20	49.64	3.00
% Hardwood cover	51.63	5.99	36.98	4.05
% Shrub cover	35.31	3.50	33.70	2.63
% Forb cover	8.67	1.12	10.27	1.02
% Grass cover	1.43	0.42	6.17	0.83
% Rock cover	6.59	1.22	7.91	1.03
Conifer basal area (m^2/ha)	31.46	2.76	29.32	2.26
Hardwood basal area (m^2/ha)	14.13	2.07	8.69	1.32
Total basal area (m^2/ha)	45.59	3.29	38.01	2.50
Mean tree age	149.67	11.53	111.99	6.74
SD tree age	81.40	8.19	60.24	5.07
DBH of all trees (cm)	37.10	2.46	37.46	1.68
SD DBH of all trees	29.11	1.77	25.91	1.22
DBH of conifers (cm)	49.41	3.77	45.92	2.32
SD DBH of conifers	29.57	1.77	25.74	1.34
DBH of hardwoods (cm)	16.26	1.78	13.36	1.25
SD DBH of hardwoods (cm)	9.93	1.17	9.49	0.94
Mean tree height (m)	17.17	0.82	15.37	0.55
SD tree height	12.53	0.71	11.21	0.51
Mean conifer height (m)	21.25	1.35	18.96	0.90
SD conifer height	13.15	0.79	11.64	0.60
Mean hardwood height (m)	9.14	0.80	6.15	0.54
SD hardwood height	4.45	0.53	3.33	0.32
% Slope	54.49	2.26	45.00	1.95
Transformed aspect	0.44	0.06	0.48	0.04
Vol. of large downed wood (m^3/ha)	35.53	6.12	47.62	5.89
Vol. of Small downed wood (m^3/ha)	13.26	0.81	15.22	0.78
Vol. of downed wood (m^3/ha)	48.79	6.32	62.84	6.14
Elevation (m)	1374.42	159.46	1947.05	149.38
Mean annual temp.	51.97	0.26	50.47	0.23
August max. temp.	85.13	0.75	83.95	0.59
CV precipitation	95.43	0.19	93.84	0.28
Dec. min. temp.	30.16	0.35	28.32	0.28
Dec. min.–Aug. max. temp.	54.97	0.93	55.63	0.67
Mean annual precipitation	85.39	2.95	62.53	2.29
Mean summer temp.	62.93	0.37	61.72	0.28
Mean summer precipitation	8.23	0.05	7.95	0.03

Burnham and Anderson (2001) regarding a priori model selection. However, we also note that it is reasonable to generate and compare a larger set of a priori models for scientific questions (or species in this case) about which less is known; with subsequent efforts narrowing down such candidate model sets. Taper (2004) noted that there may be a substantial cost in the use of small model sets—potentially resulting in underfitting errors and reducing predictive ability. We view our approach as a compromise between these competing philosophies.

We compared models using the bias-corrected Akaike's Information Criterion (AIC_c; Akaike 1973). In addition, we calculated Akaike weights (w_i), cumulative normalized weights of AIC_c values (Burnham and Anderson 1998), and the relative likelihood of the top model being the best model compared to all others (AIC_c weight of the highest-ranking model/AIC_c weight of model *i*). We evaluated each model's deviance reduction relative to the deviance of the null model using adjusted D^2 (sensu Guisan and Zimmerman 2000). Additionally, because the performance of a model (though not AIC values) will be different at different probability cutoff points, we evaluated the distribution of predicted probabilities of salamander presence (P_o) using cutoff points ranging from 0.15 to 0.65, in increments of 0.05. Standard statistical packages use a default cutoff point of 0.5. We determined the best cutoff value that minimized both errors of omission and commission to evaluate our model's correct classification rates (see Neter et al. 1989:609–610).

Model evaluation.—For the best model developed, we conducted a 10-fold cross-validation procedure. We randomly divided the original data into 10 equal-sized segments, estimated the model with 9 segments (training data) and classified the remaining (10%) segment (test data; see Fielding 2002). We repeated this procedure 10 times. To evaluate the stability of the model's predictions, we evaluated the distribution of predicted probabilities for the test data and correct classification rates. Based on the recommendations of Manel et al. (2001), we compared chance-corrected classification rates of our best model using Cohen's kappa, for both the original (full data set model) and the cross-validated data. To evaluate the stability of the model, we visually inspected graphs of each variable's functional form for each of the 10 iterations. Because GAMs require that test data (or new data one wishes to classify) fall within the range of observed variable values in the training data set, the total sample of

classified observations was less for the cross-validation evaluation than for the entire data set.

P. elongatus *and habitat in reserved and nonreserved lands*.—To evaluate the association of *P. elongatus* with reserved and nonreserved lands, we used the occupancy data from all locations that were sampled within our study area ($n = 159$), including those for which FIA data were missing. Each FIA plot within the study area fell within a discrete land allocation category (see U.S. Forest Service and U.S. Bureau of Land Management 1994, Dunk et al. 2002). The reserve category included late-successional reserves (LSR), riparian reserves (RR), congressional reserves (CR; e.g., wilderness areas), and administratively withdrawn areas (AW). We tested the association of *P. elongatus* with reserved and non-reserved land allocations using a chi-square analyses. Under the null hypothesis of no association, the expected number of locations in each land allocation was equal to the total number of plots at which *P. elongatus* was detected ($n = 53$) multiplied by the proportion of sampled plots falling within each land allocation.

To evaluate the relative quality of *P. elongatus*' habitat in reserved and nonreserved lands, we used our best model to estimate *P. elongatus*' probability of occurrence (P_o) at all FIA plots within the salamander's geographic range. Because estimates based on GAMs require the values of all newly classified plots to fall within the range of those values in the developmental model, we were able to produce estimates for the 149 FIA plots we sampled plus the 75 plots we did not sample for salamanders ($n = 224$ plots); ~80% of all FIA plots within *P. elongatus*' geographic range on national forests in California. We tested whether mean P_o values differed between reserved and nonreserved lands using a 2-sample t-test. Because we expected to find the salamander more frequently on reserved lands, we tested the hypothesis that mean P_o on reserved was greater than on nonreserve lands, using a 1-tailed test. We set alpha at $P \leq 0.1$ for all univariate tests (Schrader-Frechette and McCoy 1993).

Results

We found no difference in the proportion of FIA plots at which *P. elongatus* were detected between the original and the augmented data sets ($\chi^2 = 0.002$, $P = 0.999$); thus, we used the combined 149 plots for all analyses. *P. elongatus* were detected at 49 locations and not detected at 100 locations. Descriptive statistics (Table 1) revealed that plots where *P. elongatus* were detected occurred at lower elevations and on steeper slopes; had on average more conifer and hardwood canopy cover and hardwood basal area; had older and taller trees with more variable ages and conifer diameters; and had less small downed woody debris, and less grass cover, than plots where they were not detected. *P. elongatus* were also detected at plots that had greater mean annual and summer temperatures, greater mean annual and summer precipitation, and greater winter minimum temperatures than plots where they were not detected (Table 1). These univariate comparisons, however, assume a linear relationship between each variable and the presence of *P. elongatus*, and we caution against overinterpretation of these univariate relationships because habitat selection is very likely influenced by an interaction of multiple variables (see below).

Multivariate Habitat Models

The 3 top-ranking habitat models differed only slightly from one another, varying by <4 AIC_c units (Table 2). These 3 top models had AIC_c weights of 0.556, 0.340, and 0.096, respectively, and, thus, the cumulative AIC_c weight of these 3 models was 0.992 (the cumulative weight of all 167 models = 1.0). The best (lowest AIC_c) model included percent slope, mean tree age, hardwood basal area, percent canopy cover of conifers, percent rock cover, and the interaction of mean annual precipitation and mean annual temperature. With the exception of percent rock cover, the functional forms of these variables were nonlinear (Fig. 2). The only difference among the top 3 models was that the second-ranking model included percent grass cover and not percent rock cover, and the third-ranked model did not include percent hardwood basal area. Because the top 3 models shared so many covariates and the effect of model averaging on P_o values would be negligible, we only used the top-ranking model to estimate P_o values.

For the top model, the distribution of P_o values was well-separated (i.e., occupied vs. unoccupied sites were readily distinguishable), with 96% of the locations at which *P. elongatus* were detected having $P_o > 0.40$ and 94% of the locations where *P. elongatus* were not detected having $P_o \leq 0.40$ (Fig. 3). A P_o cutoff point of 0.4 provided the best balance of the 2 types of error (Fig. 4). The best model explained 66.2% of the deviance in the data (Table 2).

Our cross-validation tests revealed that the best a priori model continued to have high correct classification rates and visual inspection of the functional forms of covariates for each of the 10 iterations revealed no appreciable changes, suggesting that both the model and its predictions were quite stable for the data we collected. Using P_o of 0.4, cross-validated data had correct classification rates of 87% when *P. elongatus* were detected, 89% when they were not detected, and 89% overall. Cohen's kappa was 0.881 (SE = 0.061) for the full data set model and 0.740 (SE = 0.065) for the cross-validated data.

Associations with Land Allocations

P. elongatus were detected at 53 of 159 FIA plots. Approximately 36% of the sampled plots fell within late-successional reserves (LSR), 26% in nonreserved lands, 21% in congressionally reserved (CR), 11% in riparian reserves (RR), and 6% in administratively withdrawn areas (AW). The pattern of salamander detections did not suggest disproportionate association with either nonreserve or reserve lands ($P = 0.60$; Fig. 5a). However, mean P_o for reserved and nonreserved lands was 0.34 and 0.27, respectively ($t = 1.36$, $P = 0.087$, Fig. 5b) indicating higher habitat quality on reserve lands.

Discussion

We successfully developed, tested, and applied an accurate species-habitat model using data that are widely available to federal land managers. Our best model consisted of 7 explanatory variables, 2 of which occurred in the model as a positive interaction (annual precipitation and annual temperature). The other 5 variables exhibited response forms from approximately linear (rock and canopy closure [the latter following an initial threshold form]), to quadratic (percent slope), and logistic (hardwood basal area and

Table 2. Comparison and ranking (based on AICc) of the 4 top models used to relate habitat features to *Plethodon elongatus* occurrences. Habitat data were collected from FIA plots within the range of *P. elongatus* on the Six Rivers, Klamath, and Shasta-Trinity national forests of northern Calif., USA (Fig. 1), in 1999, 2000, and 2001.

Model[a]	AIC_c	Δ AIC_c	K[b]	w_i[c]	$\sum w_1 - w_i$	w_{ibest}/w_i	$D^{2,d}$
(temp., precip.), % slp, hard. ba, % con. cover, age, % rock cover,	121.60	0	27	0.556	0.556	1.000	0.66
(temp., precip.), % slp, hard. ba, % con. cover, age, % grs. cover,	122.59	0.984	27	0.340	0.897	1.636	0.65
(temp., precip.), % slp, % con. cover, % rock cover,	125.13	3.522	19	0.096	0.992	5.819	0.53
(temp., precip.), % slp, hard. ba, % con. cover, age, % fb cover, % rock cover	130.16	8.556	31	0.008	1.000	72.099	0.68

[a] temp. = mean annual temperature; precip. = mean annual precipitation; slp = percent slope; hard. ba = hardwood basal area; % con. cover = percent canopy cover of conifers; age = mean tree age; % grs. cover = percent grass cover.
[b] K = number of parameters in the model.
[c] w_i = Akaike weights.
[d] D^2 = percent of deviance explained (adjusted D^2, following Guisan and Zimmerman 2000).

forest age; Fig. 2). Among these 7 variables, the entire range of spatial scales, from coarse or landscape to fine or microenvironmental, are represented. The model depicted a habitat niche comprised of topographic, climatic, forest composition and structure, and site substrate attributes. It is important to note that the inclusion of a variable in the best model is not proof of that variable's importance to *P. elongatus*, nor is the absence of a variable from the best model proof of its lack of importance to *P. elongatus*. Rather the presence of a particular explanatory variable suggests an important direct or indirect relationship between that variable and the probability of occurrence; only a controlled experiment can establish unequivocally the requirement for a particular habitat attribute by a species.

Plethodontid Biology and the Best Model

Our best model described many habitat features that would be expected based on the ecological physiology of terrestrial plethodontid salamanders (Feder 1983), particularly their association with biotic and abiotic attributes that provide cool, moist, stable microclimates. Lungless salamanders respire through their skin and buccopharyngeal region, which must remain moist to transport oxygen. Consequently, they require cool, moist environments that allow respiration while simultaneously limiting moisture loss (Spotila 1972). Even under cool conditions, sufficient moisture is critical for these salamanders, and activities such as foraging can be curtailed if humidity is too low (see Jaeger 1978, 1979). Four of 7 variables in our model directly influence and control the range and/or stability of forest microclimates (i.e., forest age, canopy closure, precipitation, and temperature; see Chen et al. 1999). The remaining variables all can have an important indirect effect on microclimates. For example, deciduous hardwood trees produce leaf litter that stores and modulates the release of moisture as well as provides the primary source of food for much of the invertebrate fauna that salamanders eat (e.g., Wyman 1998). Rock substrates provide cover from predators and maintain equable temperature and moisture for retreat sites (see Maiorana 1978). Slope influences both interception of precipitation and the speed and magnitude of surface and subsurface drainage, as well as influencing the accumulation of leaf litter and rock substrates.

Comparisons with Previous Modeling Efforts

Our best model is consistent with a number of aspects of previous work (Diller and Wallace 1994, Welsh and Lind 1995). However, important differences existed among these 3 efforts. For example, while the variables that comprised our best model were a close match to 6 of the 11 important predictor variables determined by Welsh and Lind (1995), the nonlinear nature of most of our responses (Fig. 2) were not in agreement because their approach allowed for only linear responses from the data. Here, it is important to note that the response surfaces reflect the influence of one variable in the presence of the other variables in the model. Thus, a graph of a single-variable model might exhibit a much different functional form than when that variable is one of several in a model. That said, mean forest age—in the presence of the other variables in the model—appears to show 2 response peaks, one between zero and about 50 years, and a second peak between ~100 and 200 years of age (Fig. 2). The first peak, with confidence intervals that fall below zero on the logit scale (= P_o of 0.5), indicating a rather weak relationship, probably reflects that Del Norte salamanders occasionally occur in young stands (Raphael 1988, Welsh and Lind 1995), particularly on north aspects. The second peak, with the 95% confidence intervals above the zero, reflects a stronger relationship and is more consistent with the previously established relationship of this salamander with greater forest age (e.g., Welsh 1990, Welsh and Lind 1995:table 2; mean forest age = 215.8).

Conifer canopy cover exhibited a logistic relationship with *P. elongatus* from ~0 to 60%, after which the response curve appeared to be linear (Fig. 2), and P_o values exceeded 0.5 at ≥70%. This result is consistent with Welsh and Lind (1995), who found that detections were uncommon below, then increased markedly above, 75% canopy closure (see their fig. 4a). However, Diller and Wallace (1994) reported no significant relationship with canopy in the marine-influenced coastal redwood zone.

The probability of salamander occurrence increased with increasing percent slope in the range of 40–80% slope, with the optimum occurring between 50 and 60% (Fig. 2). Our results indicated a greater range of slope preferences and one that was steeper than that reported by Welsh and Lind (1995:table 2; mean slope for sites with salamanders = 30.30%), but it was consistent with Diller and Wallace (1994) who reported a mean slope of 60.94% (SD 25.72) for sites with salamanders. The relationship between predicted salamander occurrence and the variable percent rock cover appears to be linear, starting at a minimum of about 5% rock cover, with P_o increasing with increasing amounts of rock (Fig. 2). The wide confidence intervals here suggest that as long as some rock was present there would be a positive effect on

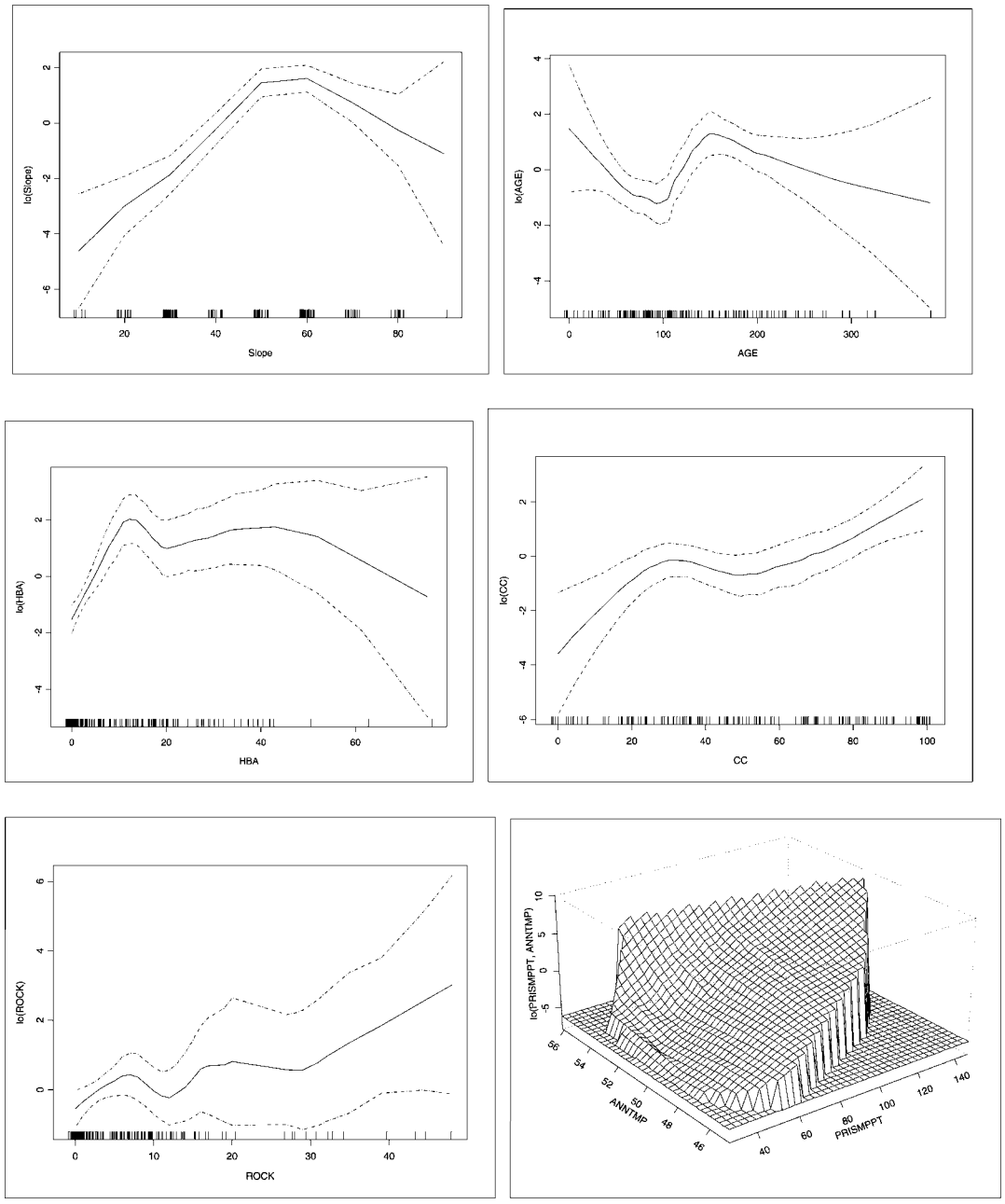

Figure 2. Shape of estimated nonparametric function (solid line) and 95% confidence intervals (dotted line) for the best predictive model. These functional forms describe the relationship of each independent variable to the probability of *P. elongatus* presence given the inclusion of all other variables in the model. The lower right cell illustrates the interaction of mean annual temperature and mean annual precipitation as they act together to influence the probability of salamander presence. Vertical tick marks on the x-axes represent explanatory variable values for each plot. Y-axis values are on the logit-scale. Data on independent environmental variables were collected from FIA plots within the range of *P. elongatus* on the Six Rivers, Klamath, and Shasta-Trinity national forests of northern Calif., USA (Fig. 1), in 1999, 2000, and 2001.

P_o. Diller and Wallace (1994) reported that rock (talus) was the only variable to enter a model to predict the presence of *P. elongatus* in their coastal zone study. Welsh and Lind (1995) reported that a mixture of rock particle sizes was an important characteristic of this cover attribute.

The interaction between temperature and moisture indicated that P_o increased with increase in moisture and temperature, and it decreased with dry conditions regardless of temperature (Fig. 2). Welsh and Lind (1995:table 2) reported a mean relative humidity of 75% for stands with salamanders. Diller and Wallace (1994) did not evaluate temperature and moisture, but they reported that precipitation for the zone of their study was high (102–254 cm annually), and the mean temperatures for both summer and winter were moderate (Elford and McDonough 1974). It would appear that these climatic factors are ameliorated in the coastal zone and therefore of little consequence for limiting the activities of *P. elongatus*.

The relationship depicted with hardwood basal area (Fig. 2) is a logarithmic or threshold relationship, suggesting that the salamanders are uncommon in stands with less than 5 m^2/ha of

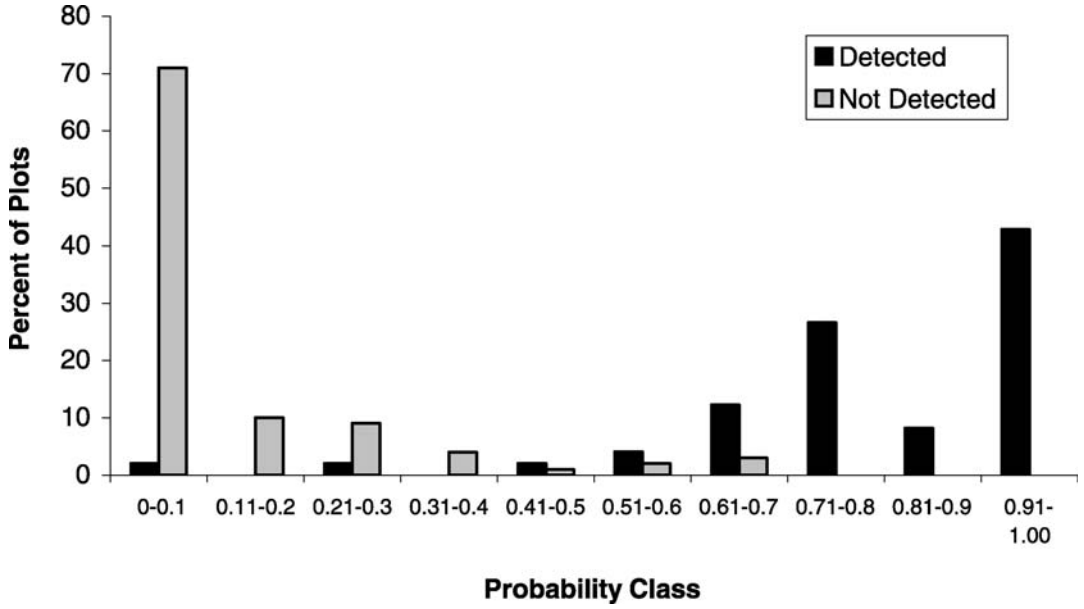

Figure 3. Distribution of predicted probabilities of *P. elongatus* presence from the best model by 10 probability classes, based on whether *P. elongatus* was detected or not. Salamander detection data were collected from FIA plots within the range of *P. elongatus* on the Six Rivers, Klamath, and Shasta-Trinity national forests of northern Calif., USA (Fig. 1), in 1999, 2000, and 2001.

hardwood, with P_o increasing as hardwood reaches 10 m^2/ha (Fig. 2). Beyond 40 m^2/ha, forests tend to become hardwood-dominated, and such stands typically occur where the climate is likely to be too warm and dry for these moisture-requiring animals (see Feder 1983).

The Environmental Niche of Plethodon elongatus

The endemic status and limited range of *P. elongatus* in the Klamath-Siskiyou Bioregion (Bury and Pearl 1999), and its association with steeper slopes, rocky substrates, older forests with high conifer canopy cover, and hardwood presence (Welsh and Lind 1995, this study) suggests that we modeled the niche of an ecological specialist (Futuyma and Moreno 1988, Van Tienderen 1991). Habitat preferences are based on evolved behavior and thus relate directly to the probability of persistence (Holt 1987, Holt and Gaines 1992). Our results, and that of previous research (Welsh 1990, Welsh and Lind 1995), indicate that *P. elongatus,* outside of a narrow marine-influenced coastal belt (Diller and Wallace 1994), has an ecological dependence (Ruggiero et al. 1988) on, and thus probably an evolutionary association with, mature to late-seral mixed conifer–hardwood forest environments. Such later seral forest environments provide conditions where moist, cool, and stable microclimatic are created and reliably sustained (Welsh 1990).

Land Allocations and the Del Norte Salamander

Our evaluation of the difference in mean P_o between reserve and nonreserved lands asks whether habitat quality is similar between the 2. Although not dramatically different, on average, reserves had higher estimated habitat quality than did nonreserved lands (mean $P_o = 0.34$ and 0.27 for reserved and nonreserved lands, respectively). However, nonreserved lands have habitat value for this salamander (e.g., Ricketts 2001), provided that they include the microenvironmental attributes identified here and are not so fragmented as to preclude dispersal and gene flow (see Lande and Barrowclough 1987, Curtis and Taylor 2003).

The higher P_o values on reserved lands were probably related to the contributions of conifer cover, tree age, and hardwood basal area. Reserved lands had more FIA plots with 41–60%, and 61–80% conifer canopy cover than did nonreserved lands, and nonreserved lands had more FIA plots with 0–20% and 21–40% canopy cover. Mean tree age also differed between the 2 land allocations with reserved lands having more plots >200 years of age than did plots in nonreserved lands (20.9% vs. 8.5% of plots). Similarly, reserved lands had more plots <50 years of age (22.5% of plots) than did nonreserved lands (8.5% of plots). At 50-year intervals from 51 to 200, no appreciable differences were evident. A higher percentage of plots on reserved lands than nonreserved lands (56.2% vs. 34.9%) had <5m^2/ha of hardwood basal area. Similarly, a higher percentage of plots on nonreserved than reserved lands (16.9% vs. 7.2%) had >40 m^2 of hardwood basal area, at intermediate levels, plots in the 2 land allocations had very similar amounts of hardwood basal area.

Modeling Habitat with FIA Data

Although our approach for model building using available FIA data worked well for *P. elongatus*, we believe this may be due, in part, to the fact that we were fortunate that the relevant habitat variables were included for measurement at the FIA plots. Had we been dealing with the habitat requirements of an organism that needed more specific or unmeasured habitat elements (e.g., fern mats that grow in the canopy), we might not have been so fortunate. Nonetheless, we think this approach has merit, and we encourage further evaluation with both common and rare species.

Although we used earlier work to guide our selection of variables for the modeling exercise (Diller and Wallace 1994, Welsh and Lind 1995), the marked success of our best model at predicting occupancy of *P. elongatus* was somewhat surprising given that

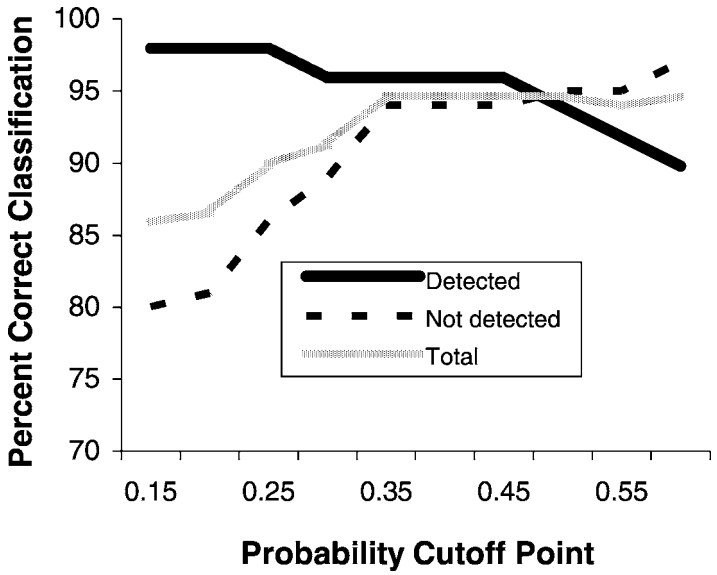

Figure 4. Relationship of probability cutoff point to correct classification rates of *P. elongatus* detection, no detection, and total correct classification for the best a priori model. Salamander detection data were collected from FIA plots within the range of *P. elongatus* on the Six Rivers, Klamath, and Shasta-Trinity national forests of northern Calif., USA (Fig. 1), in 1999, 2000, and 2001.

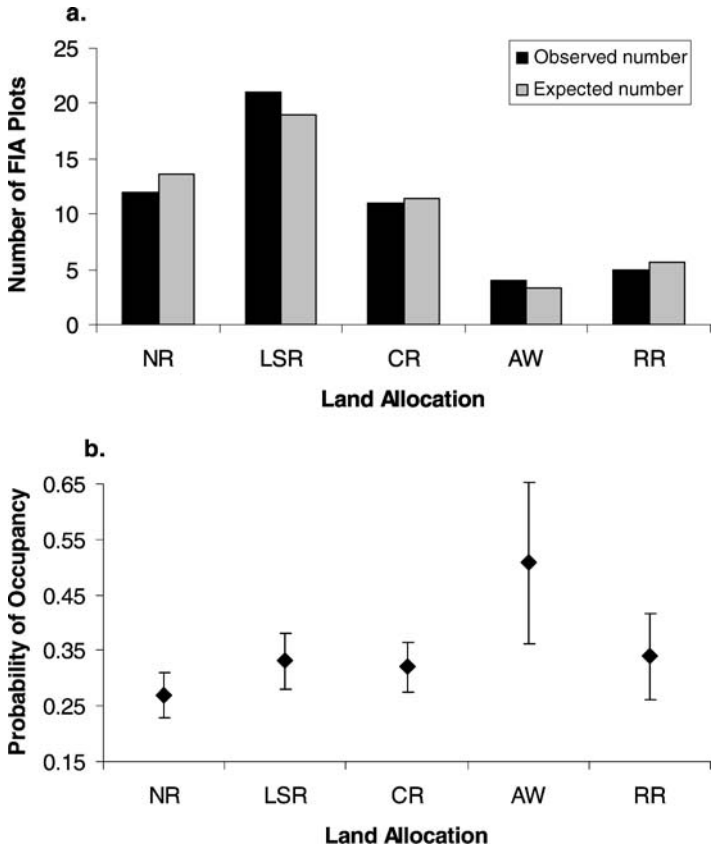

Figure 5. (a) Empirical evaluation of observed versus expected number of plots at which *P. elongatus* was found. NR = nonreserved, LSR = late-successional reserve, CR = congressionally reserved, AW = administratively withdrawn, and RR = riparian reserve (U.S. Forest Service and U.S. Bureau of Land Management 1994). (b) Model-based evaluation of mean probability of occupancy of *P. elongatus* by land allocation (mean ± SE). Salamander detection data were collected from FIA plots within the range of *P. elongatus* on the Six Rivers, Klamath, and Shasta-Trinity national forests of northern Calif., USA (Fig. 1), in 1999, 2000, and 2001.

none of the explanatory variables used were specifically measured with this (or any other) species in mind. For at least this species, the coupling of broad-scale organism sampling at FIA locations with readily available FIA and regional climate data has resulted in a highly accurate model over its entire range within national forests in California. Using the more conservative estimates derived from the cross-validated data, our model predicted *P. elongatus*' presence and absence ~74% (kappa = 0.74) better than would be expected by chance. Such results are encouraging given the large number of species for which much less is known. Dunk et al. (2004) also found that the coupling of FIA vegetation and animal sampling data resulted in good predictive models for some rare terrestrial mollusk species and Zielinski et al. (in press) used FIA variables to predict resting habitat suitability for the fisher (*Martes pennanti*).

Management Implications

Our best model estimates the probability of occupancy of *P. elongatus* at specific locations across its range within national forests in northern California, and thus can be used by researchers and managers (e.g., Welsh and Droege 2001). Such uses could include the evaluation of proposed habitat corridors between populations to sustain migration and gene flow, the identification of mitigation tracts, estimating the effects of land management practices prior to conducting them, prioritizing monitoring and survey efforts, and investigating land allocation allotments relative to newly discovered and unique phylogeographic entities. This later application is particularly important for the conservation of *P. elongatus*' genetic diversity in light of recent genetic data indicating several highly divergent populations in the southern portion of the range (Mahoney 2001, 2004).

Land managers have various opportunities to manipulate variables that our model suggests influence suitability. Although they generally cannot influence percent slope, rock cover, temperatures, or precipitation, they can manipulate canopy cover, hardwood basal area, and tree age distributions, all of which can have profound effects on stand microclimates (Chen et al. 1999). The biotic variables in our top model can provide guidance to land managers in terms of the quantities of each that should be maintained if they wish to increase, or not decrease, P_o of *P. elongatus* within an area.

Models necessarily simplify reality, and therefore will never be a better estimator of change than on-the-ground sampling for organisms. However, in many instances, the use of a predictive model to provide estimates of habitat status may be sufficient for management purposes. The application of this model to the periodically updated FIA plot data could allow land managers to predict the quantity, quality, and spatial distribution of *P. elongatus*' habitat. The model could then be used to predict changes in salamander occupancy rates of FIA points, with implications for the surrounding areas, at a much-reduced cost relative to on-the-ground sampling. For example, given our data, with 2 sampling periods (e.g., our current estimates and estimates applied to the next iteration of resampling these FIA plots) each with a sample size of 224, we estimated that the power of detecting a 25, 15, and 5% decline in the predicted *P. elongatus*' P_o

between those 2 sampling periods would be 0.76, 0.41, and 0.12, respectively. These estimates of power provide land managers with an understanding of the degree of change that they are likely to be able to detect given a similar sample ($n = 224$) of FIA plots.

We encourage researchers and managers to carefully consider how FIA data might be used in their specific geographic regions and to engage in a dialogue with those individuals and entities responsible for the periodic gathering of FIA plot data. It is possible that for a modest increase in funding, relevant, species-specific habitat data could be collected, and the FIA program could be more broadly integrated into ecological studies of species–habitat relationships.

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