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Developing landscape habitat models for rare amphibians with small geographic ranges: a case study of Siskiyou Mountains salamanders in the western USA

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Abstract To advance the development of conservation planning for rare species with small geographic ranges, we determined habitat associations of Siskiyou Mountains salamanders (*Plethodon stormi*) and developed habitat suitability models at fine (10 ha), medium (40 ha), and broad (202 ha) spatial scales using available Geographic Information Systems data and logistic regression analysis with an information theoretic approach. Across spatial scales, there was very little support for models with structural habitat features, such as tree canopy cover and conifer diameter. Model-averaged 95% confidence intervals for regression coefficients and associated odds ratios indicated that the occurrence of Siskiyou Mountains salamanders was positively associated with rocky soils and Pacific madrone (*Abutus menziesii*) and negatively associated with elevation and white fir (*Abies concolor*); these associations were consistent across 3 spatial scales. The occurrence of this species also was positively associated with hardwood density at the medium spatial scale. Odds ratios projected that a 10% decrease in white fir abundance would increase the odds of salamander occurrence 3.02–4.47 times, depending on spatial scale. We selected the model with rocky soils, white fir, and Oregon white oak (*Quercus garryana*) as the best model across 3 spatial scales and created habitat suitability maps for Siskiyou Mountains salamanders by projecting habitat suitability scores across the landscape. Our habitat suitability models and maps are applicable to selection of priority conservation areas for Siskiyou Mountains salamanders, and our approach can be easily adapted to conservation of other rare species in any geographical location.

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Abbreviations

AICc	Akaike's information criterion corrected for small sample size
DBH	quadratic mean diameter at breast height
DEM	Digital Elevation Model
GeoBOB	Geographic Biotic Observation
HS	Habitat Suitability
ISMS	the U.S. federal Interagency Species Management System
NRIS	Natural Resource Information System
PRISM	Parameter-elevation Regressions on Independent Slopes Model
TM	Thematic Mapper
TPH	number of trees per hectare
USDA	United States Department of Agriculture
USDI	United States Department of Interior
BLM	Bureau of Land Management

Introduction

With changing landscapes, conservation of rare species requires a clear understanding of species' habitat associations to prevent loss of suitable habitat through human activities and natural events. Conservation of rare endemic species with small geographic ranges is particularly critical in the Klamath–Siskiyou region of the Pacific Northwestern USA because of its exceptional concentration of rare endemic species among global temperate coniferous forest ecosystems and the accelerated rate of habitat loss in this biodiversity hotspot (DellaSala et al. 1999; Myers et al. 2000).

The Siskiyou Mountains salamander (*Plethodon stormi*) is 1 of 3 closely-related rare salamander species endemic to the Klamath–Siskiyou region that straddles the Oregon–California border (Bury and Bury 2005). Because of the potential association of the Siskiyou Mountains salamander with late-successional forests, there is a concern that land management activities in forests, including timber harvesting, road building and rock quarrying, may adversely impact populations and habitats of this salamander (Thomas et al. 1993; Blaustein et al. 1995; Clayton and Nauman 2005; Clayton et al. 2005). Despite this presumed threat of land management activities, very little is known about the ecology or biology of the Siskiyou Mountains salamander. More importantly, to our knowledge, no study previously has demonstrated an effective way to integrate locally available resource or habitat inventory information, Geographic Information Systems (GIS) technology, and species-habitat relationships into conservation strategies across landscapes for this or other rare endemic species in the region.

Previously, habitat relationship models for rare *Plethodon* salamanders in the Klamath–Siskiyou region were developed primarily from field-measured micro- and macro-habitat data at site to forest stand scales (Diller and Wallace 1994; Welsh and Lind 1995; Ollivier et al. 2001). However, these habitat models generally are limited in their applicability to the conservation of species at broad landscape scales for a couple of reasons. First, field surveys to compile these types of data often are too labor intensive and costly to be conducted over a broad landscape. Second, use of existing landscape habitat data, typically available in the form of GIS layers, as surrogates for field-collected data is problematic. Landscape data may not match variables used in these field-derived models. For example, landscape variables may differ from field-measured data in accuracy, precision, and spatial scale. Therefore, these field-derived models may not produce reliable predictions when existing landscape habitat data are applied.

Recent advances in remote sensing and GIS technologies not only make it possible to examine habitat relationships of organisms across broad landscapes, but they also allow for flexibility in developing conservation assessments at multiple spatial scales (Torgersen et al. 1999; Fleishman et al. 2001; Fuhlendorf et al. 2002; Luoto et al. 2002). Researchers have successfully incorporated GIS information into habitat relationship models for many vertebrate species (Murkin et al. 1997; Cox et al. 2001; Maehr and Cox 1995; Gros and Rejmánek 1999), including amphibians (Gustafson et al. 2001; Ray et al. 2002). However, there is no GIS-based habitat association model for Siskiyou Mountains salamanders for use in conservation planning across the landscape. We propose that GIS layers of habitat features across landscapes can be effectively used to determine habitat associations and to develop habitat suitability models that can be readily used for regional conservation planning.

The Siskiyou Mountains salamander occupies one of the most xeric portions of the range of the western *Plethodon* species (Blaustein et al. 1995; Bury and Pearl 1999). The local availability of cool and moist habitat is considered essential for the survival of this species during the hot and dry summers of the Klamath–Siskiyou region (Bury and Pearl 1999). Physiological constraints may explain why Siskiyou Mountains salamanders are documented to reach their highest abundance on north-facing, dense forest stands with talus slopes (Nussbaum et al. 1983; Leonard et al. 1993). Talus slopes and rocky substrates appear to provide these salamanders with a stable microclimate as well as reliable cover in a region where down wood often is not available (Bury and Pearl 1999). These observations have led some to suggest a close association of Siskiyou Mountains salamanders with late-successional forests (Thomas et al. 1993; Blaustein et al. 1995; Clayton and Nauman 2005; Clayton et al. 2005).

Our first research objective was to determine associations of Siskiyou Mountains salamander with abiotic factors, forest stand structure, and tree-species abundance by quantifying GIS information at 3 spatial scales. To guide our analyses, we formulated the following hypotheses about species-habitat associations from current knowledge of the Siskiyou Mountains salamander's range, life history, and patterns of habitat use as summarized below. Because salamanders avoid extreme heat and dry conditions as well as cold areas in high elevations, we hypothesized that Siskiyou Mountains salamanders are positively associated with rocky substrates and negatively associated with elevation and solar illumination. Solar illumination is an estimate of solar radiation inputs in GIS (see methods). Furthermore, we hypothesized that Siskiyou Mountains salamanders are positively associated with closed canopy conditions and large-diameter conifers. Cool and moist microclimates are maintained on the forest floor under closed canopies, and large conifers are an indicator of late-successional forest. Finally we used the abundance of 4 common tree species in the Klamath–Siskiyou region as indicators of microclimate conditions because each species occupies a different microclimate regime. We hypothesized that Siskiyou Mountains salamanders are negatively associated with white fir (*Abies concolor*), a species found in cold high-elevation habitats (Laacke 1990), Oregon white oak (*Quercus garryana*), a species found in hot and dry low-elevation habitats (Stein 1990), and Pacific madrone (*Abutus menziesii*), a species frequently associated with dry sites (McDonald and Tappeiner 1990), and positively associated with Douglas-fir (*Pseudotsuga menziesii*), an abundant species in mesic habitats (Herman and Lavender 1990). We additionally tested the relationship of Siskiyou Mountains salamanders with hardwood density based on a previous observation of a positive association (Ollivier et al. 2001). Our second research objective was to develop habitat suitability models based on the findings under our first research objective and map habitat suitability for Siskiyou Mountains salamanders across the landscape at 3 spatial scales.

Materials and methods

Study area

The Applegate River Watershed is located at the Oregon–California border in the Klamath–Siskiyou ecoregion of the western USA (Fig. 1). For model development, we used available habitat and species data from a 121,406-ha area in the Applegate River Watershed within the range of the Siskiyou Mountains salamander. Elevations in the area range from 364 to 2067 m. Over 90% of the study area was in Jackson County, Oregon; the remaining <10% was in eastern Josephine County, Oregon, and northern Siskiyou County, California. The climate across this area is generally cold and wet in winter, and hot and dry in summer. Mean annual temperatures range from 8.3 to 10.5°C, and precipitation ranges from 60 to 170 cm at mid elevations (Franklin and Dyrness 1988). Mid-elevation vegetation falls within the Mixed-Evergreen zone in the western Siskiyou Mountains and the Mixed-Conifer zone in the eastern Siskiyou Mountains; the Interior Valley zone is found at lower elevations (<~700 m) and the White-fir zone occurs at upper elevations (~1400–1800 m; Franklin and Dyrness 1988).

Salamander location data and survey methods

We obtained 260 localities of Siskiyou Mountains salamanders from an existing spatial database, the U.S. federal Interagency Species Management System (ISMS; Molina et al. 2003) compiled by the U.S. Department of Interior, Bureau of Land Management (USDI BLM), and the U.S. Department of Agriculture, Forest Service (USDA Forest Service). Distinct localities of Siskiyou Mountains salamanders referred to as "known sites" had been archived in the spatial database as part of the U.S. federal Protection Buffer and Survey & Manage provisions of the federal Northwest Forest Plan (Molina et al. 2003). ISMS data have been subsequently migrated to the Geographic Biotic Observation (GeoBOB) and Natural Resource Information System (NRIS) databases, and these have been maintained by USDI BLM and USDA Forest Service, respectively (Pres. Comm. Kelli Van Norman, BLM Oregon State Office, Portland). The 260 known sites of Siskiyou Mountains salamanders included all the localities of Siskiyou Mountains salamanders ever recorded in our study area up to the end of 2003, thus representing the most comprehensive distribution of this species at the initiation of this study. Of the 260 known sites, 213 (82%) were identified after 1993 based on surveys conducted by the USDI BLM and USDA Forest Service, and 47 sites (18%) were identified prior to 1993, largely from museum records archived by natural historians and field researchers (Nauman and Olson 1999). Of the 213 federally identified sites, 130 sites (50% of all 260 known sites) were identified as a result of surveys required under the U.S. federal Northwest Forest Plan when proposed land management activities were considered potentially disturbing to Siskiyou Mountains salamanders and their habitat (referred to as pre-disturbance survey); these potentially disturbing land management activities included timber harvesting, mining, road and trail development, and recreational development (Olson 1999; Nauman and Olson 1999). Other USDA Forest

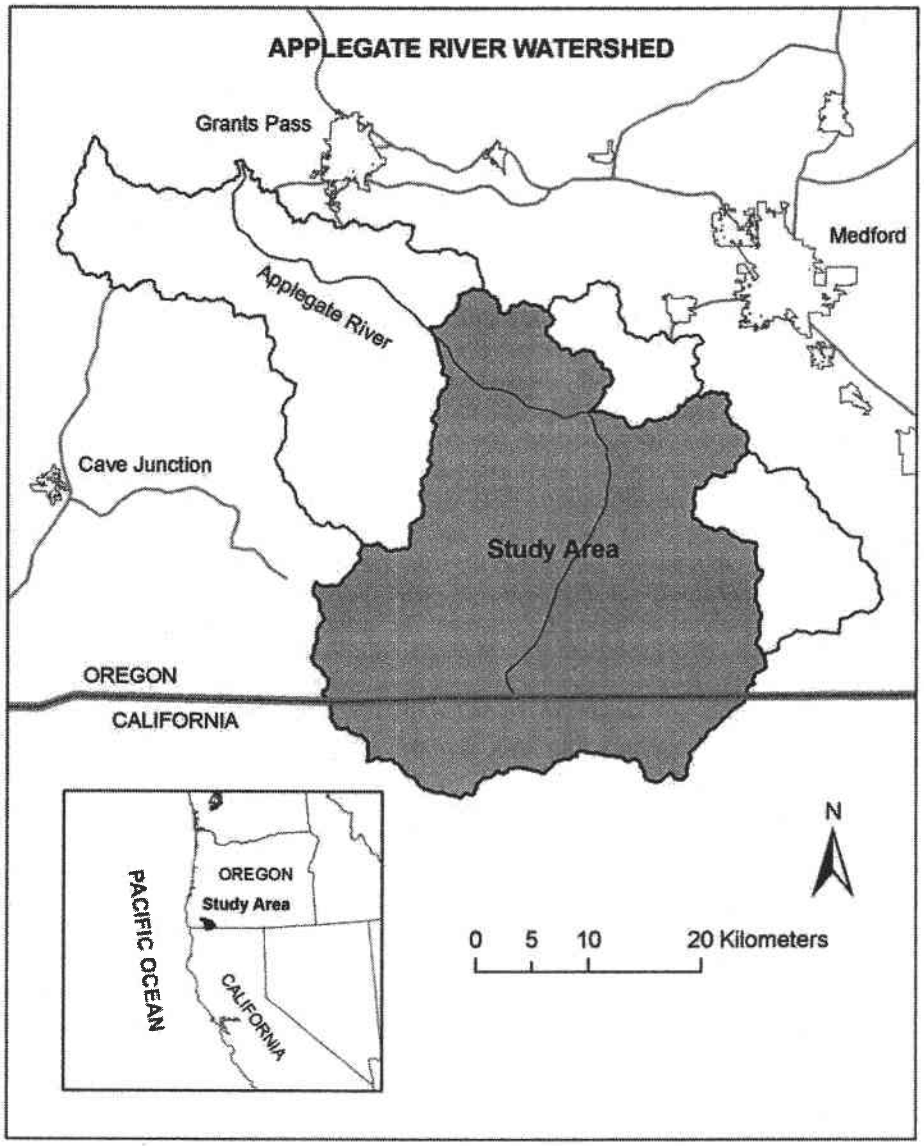

Fig. 1 Map of the study area in the Applegate River Watershed of the Klamath–Siskiyou region, Oregon–California border, USA

Service projects identified 49 sites (19%) using a stratified random sampling during a field study (Ollivier et al. 2001) and 34 sites (13%) during surveys to fill the gaps in the species distribution (Nauman and Olson 2004).

Spatial habitat sampling with GIS Layers

From the GIS layer of 260 known Siskiyou Mountains salamander sites, we randomly selected 2 sets of 53 known salamander sites (hereafter, salamander sites) and 133 sites that were not known to have salamanders (hereafter, unoccupied sites) within 10-ha square areas. Because of the rarity of the Siskiyou Mountains salamander, we assumed that the chances of these salamanders being present at randomly selected locations in the landscape were low. The 10-ha area approximates the typical size of a forest stand that is being considered for Siskiyou Mountains salamander conservation areas as well as for many proposed forest management projects. To our knowledge, there is no relevant biological or ecological information, such as home range size or movement pattern, to determine a spatial scale for the analyses of habitat associations of this species. Sample sizes for salamander (53) and unoccupied sites (133) were based on the observed ratio of salamander to unoccupied sites (approximately 2:5) from a previous field study of Siskiyou Mountains salamanders (Ollivier et al. 2001). We used the first 186 sites (53 + 133) to analyze habitat associations and to develop habitat suitability models; we used the second set to validate the habitat suitability models. The distance between any 2 selected sites was >1425 m to avoid redundant sampling, and we sampled no more than 1 site per 202 ha area. On average, this resulted in 1 site per 650 ha across the study area.

For each sample site, we quantified habitat features using GIS layers at fine (10 ha [25 acres]), medium (40 ha [100 acres]), and broad (202 ha [500 acres]) spatial scales, and we used a square as the sample shape to make our results compatible with pixel-shaped GIS grid layers. Fine and medium spatial scales approximated the sizes of common and large forest stands that are typically considered for land management and species conservation areas, and the broad spatial scale represented a small landscape. We quantified 10 habitat variables for the analyses of habitat associations. These habitat variables included 3 abiotic factors (abundance of rocky soils [%], elevation [m], solar illumination [index value between 0 and 254]), 3 stand structural features (tree canopy cover [%], conifer diameter [quadratic mean diameter at breast height in cm, DBH], and hardwood density [no. trees/hectare, TPH]), and abundance (%) of 4 common tree species (Douglas-fir, white fir, Oregon white oak, and Pacific madrone).

The abundance of rocky soils was determined from digital soil survey maps from Jackson (1993) and Josephine Counties (1983), Oregon (USDA Natural Resources Conservation, available at http://www.or.nrcs.usda.gov/pnw_soil/or_data.html) and from USDA Forest Service Level 2 Soil Resource Inventory maps (Badura and Jahn 1977). Soil types associated with rocky deposits known to have interstitial spaces and those with ≥50% gravel or cobble content were classified as rocky soils (D. Clayton, personal communication). At each site, we estimated the proportion of 25-m pixels classified as rocky soils among all 25-m pixels in 10 ha (fine scale), 40 ha (medium scale), and 202 ha (broad scale).

Elevation and solar illumination at sites were taken from a 10-m resolution U.S. Geological Survey Digital Elevation Model (DEM; Gesch et al. 2002). Solar illumination is an index that represents the amount and extent of solar radiation reaching the ground surface, and it accounts for various topographic features that might cast shade over a given point. The solar illumination model was developed using the hillshade command in ArcView (Environmental Systems Research Institute 1996). The position of the sun at noon on June 21, 2003 for the specific longitude and latitude of each site was used to calculate solar illumination values. June 21 is the day each year that the sun is at its highest position. Solar illumination values ranged from 0 to 254, where smaller values indicated lower solar radiation inputs.

Three features of stand structure and abundance of 4 tree species were estimated from 25-m GIS grid layers of a remote sensing vegetation classification map based on the image analysis of Landsat Thematic Mapper (TM) data conducted by Geographic Resource Solutions in Arcata, California, in 1993 (Hill 1996). We calculated the average value of 25-m pixels in 10 ha (fine scale), 40 ha (medium scale), and 202 ha (broad scale) at each sample site for percent tree canopy cover, conifer DBH, and hardwood density. To quantify the abundance of the 4 most common tree species in the region (Douglas-fir, Oregon white oak, white fir, and Pacific madrone), we estimated the proportion of 25-m pixels for which each tree species was classified as most abundant among all 25-m pixels in 10 ha, 40 ha, and 202 ha at each sample site. We used ArcGIS 9.0 to estimate all variables except solar illumination, which was estimated in ArcView (Environmental Systems Research Institute 2004).

In the image analysis of Landsat TM data, field data and Landsat imagery were compared to develop spectral classes of habitat variables referred to as supervised training sets, and the supervised classification method (Howard 1991) was used to initially produce habitat values for areas where field data were available (Hill 1996). Following the initial supervised classification, a maximum likelihood classification based on the supervised training sets was performed at a 90% probability threshold to estimate habitat values across the landscape. After calibrating the discrepancy in value between the supervised training sets and the initial maximum likelihood estimation, 3 additional maximum likelihood classifications were performed, 2 at a 95% probability threshold followed by 1 at a 100% probability threshold to estimate habitat values for the entire 25 m pixels in the Applegate River Watershed (Hill 1996). Ground truthing was conducted, and the accuracy of the image analyses for habitat variables ranged from 86 to 92% at the 2-ha aggregation level (Hill 1996).

The timeframes of our diverse data sets differ, leading to several assumptions in our analyses. Because the Landsat TM image was produced in 1993, our analysis compared habitat conditions in 1993 between the salamander sites and unoccupied sites. Salamander sites identified after 1993 are assumed to have been occupied by Siskiyou Mountains salamanders in 1993 when the Landsat imagery was produced, and sites identified before 1993 are assumed to be occupied in 1993. These assumptions are supported by the following. For the salamander sites identified after 1993 (213 of 260 sites), no land management activity or natural disturbance had significantly altered habitat conditions at these sites between 1993 and the time when these sites were identified. It also is unlikely that a significant number of these sites had been newly established well after 1993 because the Siskiyou Mountains salamander is suspected to be a low mobility species with high site fidelity, and their primary habitat component (i.e., rocky substrate) is patchily distributed across the landscape. For the known sites identified before 1993 (47 of 260 sites), aging of forests from the time when the sites were identified until 1993 is not likely to have adversely impacted habitat conditions for Siskiyou Mountains salamanders because they are known to occur in relatively high abundance in older forests (Nussbaum et al. 1983; Leonard et al. 1993; Blaustein et al. 1995; Clayton and Nauman 2005; Clayton et al. 2005). However, we were unable to determine the history of management activities and natural disturbance at these sites identified before 1993, hence it is possible that habitat conditions had been altered by 1993, potentially affecting species' occupancy of sites.

Data analysis

We used logistic regression analysis (PROC LOGIST, PROC GENMOD; SAS Institute 1999a) with an information theoretic approach (Burnham and Anderson 2002) to assess competing hypotheses about species-habitat associations and to develop Siskiyou Mountains salamander habitat suitability models from these results. We developed 26 a priori models from combinations of 10 habitat variables in 3 categories (abiotic habitat, stand

Table 1 Twenty six a priori models outlining hypotheses about Siskiyou Mountains salamander (*Plethodon stormi*) habitat associations in the Applegate River Watershed of the Klamath–Siskiyou Region along the Oregon–California border in the USA

Models and hypotheses[a]	Model No.
Abiotic models	
+Rocky soils	1
+Rocky soils, −Elevation,	2
+Rocky soils, −Solar illumination	3
+Rocky soils, −Elevation, −Solar illumination	4
−Elevation, −Solar illumination	5
Stand structure or abiotic and stand structure combination models	
+Canopy cover, +Hardwood density	6
+Rocky soils, +Conifer DBH	7
+Rocky soils, +Canopy cover, +Hardwood density	8
+Rocky soils, −Elevation, −Solar illumination, +Canopy cover	9
+Rocky soils, −Elevation, −Solar illumination, +Conifer DBH	10
+Rocky soils, −Elevation, −Solar illumination, +Canopy cover, +Hardwood density	11
−Elevation, −Solar illumination, +Canopy cover, +Hardwood density	12
Tree Species Models	
+Douglas-fir, +Pacific madrone	13
+Douglas-fir, −White fir	14
−White oak, −White fir	15
Tree Species and Abiotic Combination Models	
+Rocky soils, +Douglas-fir	16
+Rocky soils, −White fir	17
+Rocky soils, −White oak	18
+Rocky soils, +Pacific madrone	19
+Rocky soils, +Douglas-fir, +Pacific madrone	20
+Rocky soils, +Douglas-fir, −White fir	21
+Rocky soils, −White oak, −White fir	22
+Rocky soils, +Douglas-fir, +Pacific madrone, −Solar illumination	23
+Rocky soils, +Douglas-fir, −White fir, −Solar illumination	24
+Rocky soils, −White oak, −White fir, −Solar illumination	25
Global Model	26

[a] Positive (+) and negative (−) signs indicate that salamander presence was hypothesized to be positively or negatively associated with each variable

structure, and tree species abundance) underlining our hypotheses (Table 1) that could explain the habitat association of Siskiyou Mountains salamanders. Based on current knowledge of the biology and ecology of Siskiyou Mountains salamanders, we hypothesized positive associations of this species with 5 variables (tree canopy cover, conifer DBH, hardwood density, rocky soils, and Douglas-fir) and negative associations with 5 variables (elevation, solar illumination, white fir, Oregon white oak, and Pacific madrone). To avoid multicollinearity in regression analysis, correlations between variables were screened with Pearson's correlation coefficient using all selected sites ($n = 186$; PROC CORR; SAS Institute 1999b). Variables with a moderate to strong correlation ($r \geq 0.4$) were assessed in separate models in the logistic regression analysis. We tested for spatial autocorrelation in the deviance residuals from logistic regression models by calculating Moran's I statistic in ArcGIS 9.0 (Cliff and Ord 1981). Z-tests were used to examine the significance of Moran's I for the presence of spatial autocorrelation.

We calculated Akaike's Information Criterion corrected for small sample size (AICc) for each model and ranked the 26 a priori models from most- to least-supported given the data based on AICc values. We calculated Δi, the difference between the AICc value of a particular model and the lowest AICc value of all the models, and Akaike weight (ω_i). Akaike weight is the proportional likelihood of each model over the sum of likelihood of all the a priori models. For a given spatial scale, we considered a model with $\Delta i \leq 2$ as having substantial support in making inference, and only reported those models with $\Delta i \leq 7$ as having some level of support (Burnham and Anderson 2002:127–128). We considered any model with $\Delta i > 7$ as having insufficient evidence to support it as the best model.

Best model selection took into account the number of competing models with $\Delta i \leq 2$, Akaike weight, and number of parameters in the model. For example, when more than one model had $\Delta i \leq 2$, the best model was the one with the highest Akaike weight and the fewest parameters. The best a priori model selected for each spatial scale was cross-validated with the second data set of 53 salamander and 133 unoccupied sites (validation data) in logistic regression analyses, and correct classification rates were calculated.

For each spatial scale, we developed a habitat suitability model to estimate relative likelihoods of species occurrence as a measure of habitat suitability using the odds ratio equation for habitat variables in the best a priori model: Habitat Suitability (HS) = $\exp(\beta_1\chi_1 + \beta_2\chi_2 + \ldots\ldots + \beta_{n-1}\chi_{n-1} + \beta_n\chi_n)$, where β is the coefficient and χ is the value for a particular habitat variable (Manly et al. 2002; Pearce and Boyce 2006). We did not use the logistic regression equation as a habitat-suitability model because the retrospective approach in our study limited our ability to estimate the prospective intercept and prospective probability of species occurrence (Ramsey and Schafer 1997, pp. 586–587), and relative likelihoods of occurrence based on the exponential function is an alternative approach suggested for rare species when probabilities of occupancy are low (Keating and Cherry 2004; Manly et al 2002; Pearce and Boyce 2006). We used our habitat suitability models to calculate HS scores of relative likelihoods of species occurrence from GIS layers of habitat variable. These HS scores were projected in pixels across the landscape to develop habitat suitability maps of Siskiyou Mountains salamanders at 3 spatial scales.

We addressed model-selection uncertainty by providing model-averaged coefficients with 95% confidence intervals in logistic regression analysis across the set of a priori models. The model averaged coefficient for a habitat variable was calculated by summing the multiples of normalized Akaike weights and the original coefficient across the a priori models with the variable in common, and the model-averaged 95% confidence interval for the coefficient was from the unconditional standard error (Burnham and Anderson 2002, pp. 118–158). From these model-averaged statistics, we calculated the odds ratio and 95% confidence interval of the odds ratio for each variable. We interpreted a habitat variable as having a significant association with Siskiyou Mountains salamanders when the model-averaged 95% confidence interval for the variable coefficient did not include 0, which indicated the habitat association of the salamanders with the variable was consistent across a priori models regardless of the presence of other habitat variables in these models. The same conclusion could be made by interpreting a habitat variable as having a significant association when the model-averaged 95% confidence interval of odds ratio for the variable did not include 1. We reported odds ratios and associated 95% confidence intervals for each 1- and 10-unit change for habitat variables to describe the strengths of habitat association of Siskiyou Mountains salamanders with each variable. Additional odds ratios and associated 95% confidence intervals for the change in 100-units (100 m) and 400-units (400 m) for elevation and the change in 100-units (100 trees per hectare) for hardwood density were reported because a change in 1 or 10 units generally is not biologically meaningful for these habitat variables.

Results

Correlations among habitat features

There were moderate to strong correlations between stand structure and tree species abundance (Fig. 2). Tree canopy cover increased as Douglas-fir increased (*r* range: 0.850 to 0.899) at all 3 spatial scales and decreased as Oregon white oak increased at medium ($r = -0.422$) and broad ($r = -0.503$) spatial scales. Conifer DBH increased as white fir increased at all spatial scales (*r* range: 0.652 to 0.730). Hence, tree canopy tended to be closed in areas where Douglas-fir was abundant and open in areas where Oregon white oak

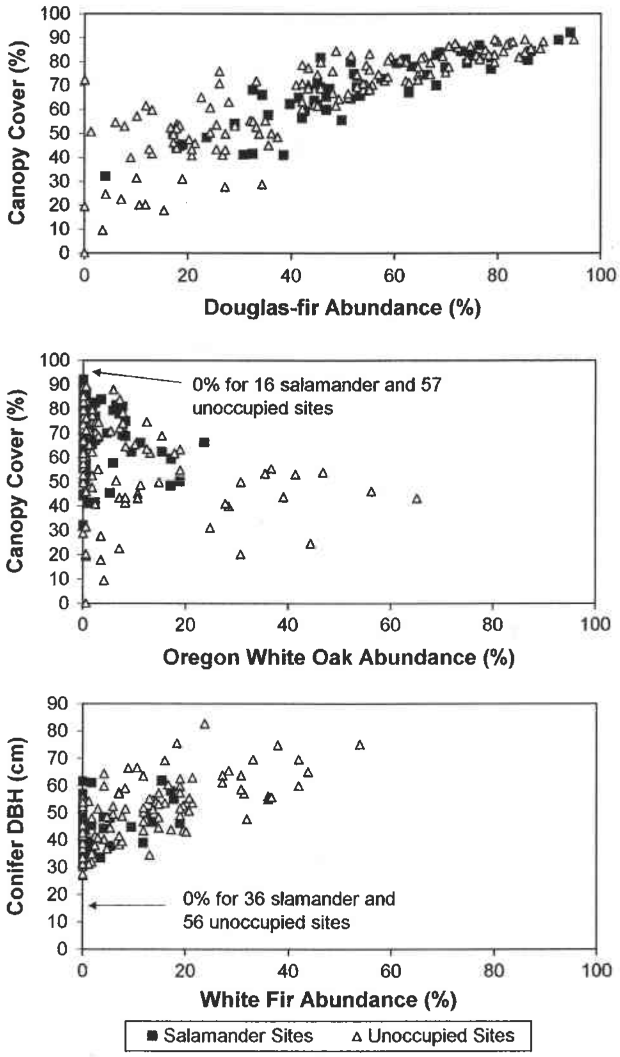

Fig. 2 Relationships between tree species abundance and stand structure in the Applegate River Watershed of the Klamath–Siskiyou region, Oregon–California border, USA

was abundant, and many large-diameter trees tended to be found in areas where white fir was abundant.

Among abiotic habitat factors, elevation showed moderate to strong correlations with the abundance of most tree species (Fig. 3), with the exception of Douglas-fir, which was equally abundant across elevations (r range: −0.083 to −0.138). White fir increased with elevation at all spatial scales (r range: 0.698 to 0.819), whereas Pacific madrone (r range: −0.539 to −0.754) and Oregon white oak (r range: −0.437 to −0.612) decreased with elevation. The decrease in these 2 hardwood species coincided with the decrease in hardwood density with elevation (r range: −0.659 to −0.754).

Correlations between tree species also were apparent. Pacific madrone decreased as white fir increased with elevation, and this pattern was detected at all spatial scales (r range: −0.534 to −0.710). Furthermore, Pacific madrone increased as Oregon white oak increased at the broad spatial scale ($r = 0.507$); however, the correlation between these 2 hardwood species was weak at medium ($r = 0.390$) and fine ($r = 0.319$) spatial scales. Douglas-fir and Oregon white oak showed moderate negative correlations (r range: −0.401 to −0.449) at all spatial scales, indicating that Douglas-fir tended to increase as Oregon white oak decreased.

Species habitat associations

Overall, a priori habitat models of Siskiyou Mountains salamanders that received some support ($\Delta i \leq 7$) were similar across 3 spatial scales (Table 2). Explanatory variables for these models consisted of some combination of tree species abundance and 2 abiotic factors (rocky soils and solar illumination); however, no stand-structural features were present in these models. Two closely-related models (model with rocky soil, Oregon white oak, and white fir; and model with rocky soil, Oregon white oak, white fir, and solar illumination) received substantial support ($\Delta i \leq 2$) with combined Akaike weights of 74% and 67 % at fine and medium spatial scales. Three additional a priori models received substantial support at the broad spatial scale ($\Delta i \leq 2$). Although the same 2 models at the finer spatial scales remained as the top models at the broad spatial scale, the support for these models relative to other models, judged by the combined Akaike weight of 57%, was not nearly as high as that at finer spatial sales. In contrast, the relative support based on Akaike weights for the 3 bottom models (among the 5 top models) at the broad spatial scale was higher than that for the same models at finer spatial scales. Consequently, a total of 5 competing a priori models received substantial support at the broad spatial scale, whereas only 2 a priori models received substantial support at 2 finer spatial scales.

Across 3 spatial scales, model-averaged 95% confidence intervals for the logistic regression coefficients and associated odds ratios did not include 0 and 1, respectively, for elevation and abundance of rocky soils, white fir, and Pacific madrone, indicating that Siskiyou Mountains salamanders were positively associated with rocky soils and Pacific madrone and negatively associated with elevation and white fir across 3 spatial scales (Table 3). Only at the medium spatial scale did the coefficient and odds ratio for hardwood density not include 0 and 1, respectively, indicating that there was an additional positive association with hardwood density at the medium spatial scale.

On average across the models, a 10% increase in rocky soils increased the odds of salamander occurrence by ~1.22–1.27 times across 3 spatial scales (Table 4). In comparison, a 10% decrease in white fir and a 10% increase in Pacific madrone increased the odds of salamander occurrence by ~3.02–4.47 times and by ~1.87–3.12 times, respectively, depending on spatial scales. Considerable changes in elevation are required to affect the odds of salamander occurrence compared to abundance of tree species. A decrease in