

## PREDICTING THE OCCURRENCE OF RARE MOLLUSKS IN NORTHERN CALIFORNIA FORESTS

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**Abstract.** Terrestrial mollusks are important components of forest ecosystems, yet we know very little about the distribution and habitat of many of these species. We sampled for terrestrial mollusks in northern California with the goal of estimating the geographic ranges and developing predictive habitat models for five species that were assumed to be sensitive to land management activities. The species of interest were *Ancotrema voyanum*, *Helminthoglypta talmadgei*, *Monadenia churchi*, *Monadenia fidelis klamathica*, and *M. f. ochromphalus*. We randomly selected 308 plots for sampling from a grid of points across a 2.2 million-ha study area. We used Generalized Additive Models to estimate each mollusk's geographic range and to develop predictive habitat models within their ranges. Models were developed at one microscale (1 ha) and six mesoscales (ranging from 12.5 to 1250 ha) using vegetation, physical, climatic, and spatial location covariates. Estimated geographic ranges varied from 4770 to 15 795 km<sup>2</sup>. Predictive habitat models explained from 40.8% to 94.5% of the deviance in models describing the species' occurrences. Models at the 1-ha scale were generally better than models at larger spatial scales. Of the six mesoscales evaluated, the "best" models were often at very large scales. Spatial location and climatic variables contributed significantly to the predictions of occurrence for most species. Models for species with small geographic ranges generally appeared to be better than models for species with larger geographic ranges, possibly reflecting more restricted environmental conditions. Cross-validation results, however, showed that models for species with more locations were more stable. *A. voyanum* was more frequently associated with late-successional forests and *M. churchi* was found to be a habitat generalist. The remaining three species were not detected enough for us to make strong conclusions about their habitat associations. Our results provide important guidance to land managers who are responsible for determining the necessity for surveys and protective measures for these and other terrestrial mollusk species prior to land management activities.

**Key words:** *Ancotrema*; California; forest; generalized additive model; geographic range; habitat association; *Helminthoglypta*; mollusk; *Monadenia*; Northwest Forest Plan; predictive model.

### INTRODUCTION

The conservation of biological diversity in human-altered landscapes must initially involve an inventory of species, their distributions, and ecological associations. Unlike many charismatic taxa in temperate regions of North America, this basic information does not exist for many non-vascular plants and invertebrate animals. Ehrlich (1996) noted that the distributions of species diversity are almost totally unexplored in temperate forests. Beyond the relatively direct impacts of timber harvesting, road building, or grazing in forested ecosystems, indirect effects of global climate change are unlikely to be predicted or mediated without an understanding of species' tolerances to climate and their associated dispersal abilities (see Kappelle et al. 1999).

The ecology of terrestrial mollusks in the Pacific Northwest of North America is little known, but of interest to federal land managers (USDA and USDI 2001a). Terrestrial mollusks have important ecosystem functions. They influence litter decomposition (Mason 1970) and nutrient cycling (Richter 1979), affect forest vegetation through their foraging (e.g., Nystrand and Granström 1997), are prey for birds and small mammals (South 1980, Churchfield 1984), and are intermediate hosts of parasites (e.g., Ball et al. 2001). Hawkins et al. (1997) estimated that terrestrial mollusks that were active on the boreal forest floor accounted for up to 6% of the energy in those forests. From a global conservation perspective, mollusks represent 20% of all threatened animals, and 37% of known animal extinctions since 1600 A.D. (Seddon 1998). Many mollusks listed by the IUCN are within the "data deficient" category (IUCN 2001); information is absent on the current geographic ranges, rates of population decline, degree of threat, and current habitat.

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Recent studies of terrestrial mollusks have primarily focused on patterns of diversity (Barker and Mayhill 1999, Welter-Schultes and Williams 1999, Tattersfield et al. 2001), decline (e.g., Cowie 2001), and anthropogenic impacts (Prezio et al. 1999). Studies of individual species have generally been at small spatial scales and involved common native or pest species (Gervais et al. 1998, Prezio et al. 1999, Bezemer and Knight 2001, Grimm and Paill 2001). Large-scale inventories and subsequent development of models to predict terrestrial mollusk species distributions and habitat associations were, to our knowledge, nonexistent prior to our study. Such analyses are relatively common for vertebrates (e.g., Carroll et al. 1999, Dettmers and Bart 1999, Knapp and Preisler 1999, Mladenoff et al. 1999, Carroll et al. 2001, Mitchell et al. 2001), plants (e.g., Austin and Meyers 1996, Wisser et al. 1998, McKenzie and Halpern 1999) and selected invertebrates such as butterflies (e.g., Fleishman et al. 2001).

Much of what is known about terrestrial forest mollusks is derived from studies outside the Pacific Northwest of the United States. The need to know more about these species and the effect of forest management on them was recognized during a bioregional assessment referred to as the Northwest Forest Plan (NFP; USDA and USDI 1994). The NFP has the goal of ecosystem management throughout ~10 million ha of federal land in portions of Washington, Oregon, and California, USA, and our work was conducted in close coordination with forest managers and planners responsible for executing the provisions of this plan. Included within the NFP was the identification by taxa experts of >400 species that were thought to be associated with late-successional forests, but for which little-to-no basic ecological information existed. These species were referred to as "Survey and Manage" (hereafter SM) species, because habitat-disturbing management activities (e.g., timber harvest, fuels treatments) could not occur without first surveying to determine their occurrence. Our study focused on five species of terrestrial mollusks: hooded lancetooth (*Ancotrema voyanum*), Klamath shoulderband (*Helminthoglypta talmadgei*), Church's sideband (*Monadenia churchi*), Klamath sideband (*Monadenia fidelis klamathica*; see Plate 1), and yellow-based sideband (*M. f. ochromphalus*).

Published information on the ecology of these species was either nonexistent or restricted to identifying new locations where they were found, with brief site descriptions. Only the study by Roth and Pressley (1986) contained information relevant to any of our species of interest. Dunk et al. (2002) evaluated whether these mollusks were found disproportionately in reserved vs. non-reserved federal lands and found that they were more likely to occur in protected areas near watercourses, but otherwise the mollusks were found to occur proportionate to the areal extent of reserved



PLATE 1. Klamath sideband (*Monadenia fidelis klamathica*). Photo credit: Barry Roth.

and non-reserved lands. To our knowledge, no published range maps existed for any of the target species.

The paucity of information available on the biogeography and ecology of terrestrial mollusks in the Pacific Northwest has led to a precautionary approach to forest management under the NFP. Information on the geographic ranges and the habitat of the five species would potentially enable land managers to make more informed decisions about the necessity of conducting surveys prior to activities that may disturb the species' habitat (i.e., conduct them only when the activity was planned within a species' geographic range) and could also contribute information to regional habitat conservation plans. We sought information that could both add to the basic ecological understanding of the target species and be of value to land management and planning. Herein we present our estimates of each of five mollusks' geographic range, and exploratory associative models that predict the occurrence of each species on the basis of vegetation, physical, climatic, and spatial location covariates.

## METHODS

### *Study area*

The study area included >2.2 million ha of primarily forested land in the Klamath, Six Rivers, Shasta-Trinity, and Mendocino National Forests in northern California (Fig. 1). In general, climatic conditions change from wetter, more moderate temperatures, to dryer more variable (summer highs and winter lows) from northwest to southeast. The study area was almost entirely within the North Coast Floristic Region (Barbour and Major 1988) and included the Klamath Mountains, northern California Coast Range, southern Cascades, and sections of the Sierra forest ecological subregions (Bailey 1995). The northern portion of the study area represents the southern extent of the "Pacific Northwest" and may receive annual precipitation of >350 cm (Schoenherr 1992). Vegetation in the Klamath Mountains is dominated by Douglas-fir (*Pseudotsuga menziesii*)/mixed evergreen-hardwood forests. At

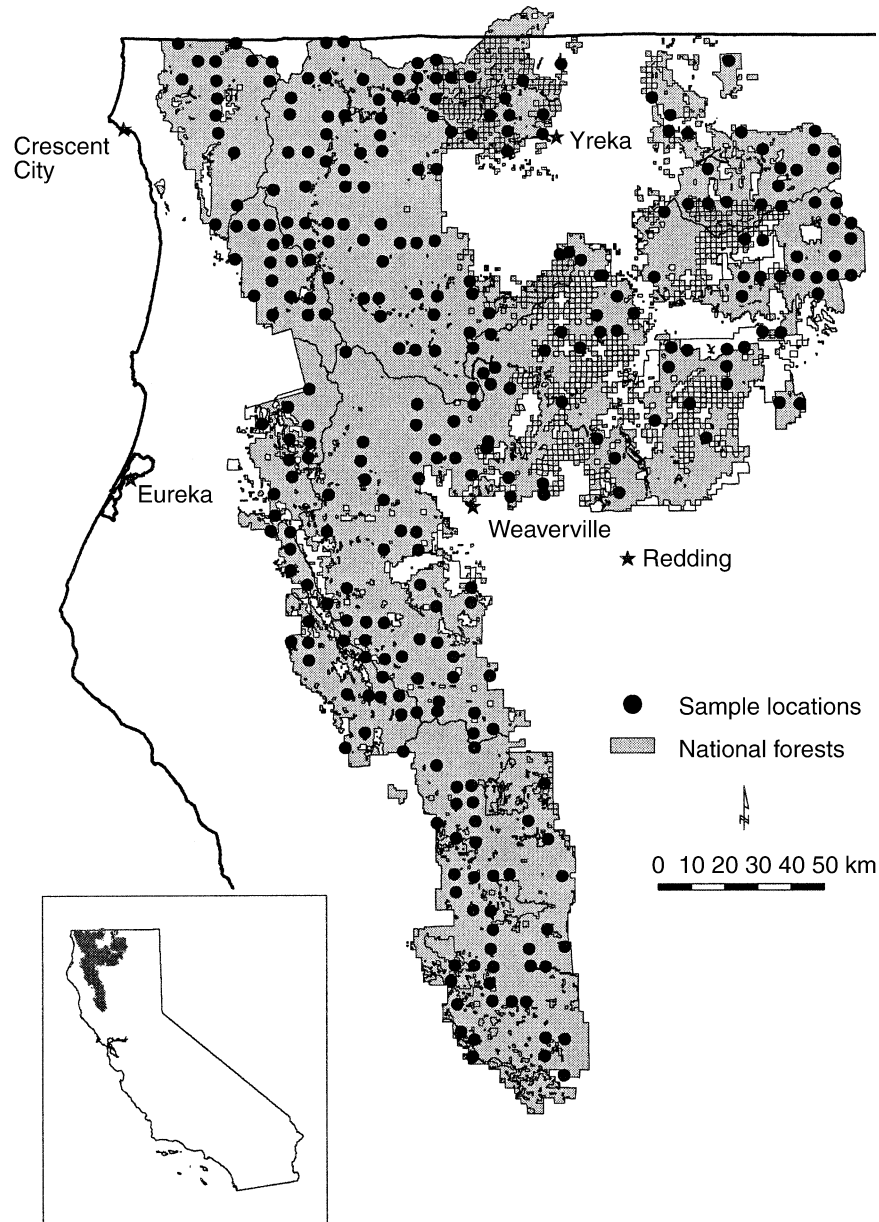


FIG. 1. Map of study area and locations where terrestrial mollusks were sampled in northern California, USA.

higher elevations, white fir (*Abies concolor*) and red fir (*Abies magnifica*) dominate. To the east, the study area becomes more xeric and contains portions of the volcanic Cascade Mountains where vegetation changes from more conifer-dominated to conifer-hardwood, dominated by pine (*Pinus ponderosa* and *P. sabiniana*) and deciduous oaks (*Quercus garryana* and *Q. kelloggii*). There are also north-south transitions with northern portions of the study area generally receiving more rain and having lower summer high temperatures than southern areas. Southern portions of the study area are more mixed-conifer/hardwood (with low conifer abun-

dance) or pure hardwood than northern areas, as well as having more brush-dominated areas. Elevation in the study area ranged from ~100 to 3000 m.

#### Mollusk data

We selected sample locations from the grid of points included in the nationwide Forest Inventory and Analysis program (FIA; Roesch and Reams 1999, USDA 2000). The grid is comprised of points that are ~5.5 km apart and standard vegetation data are regularly collected by the FIA program at 1-ha plots centered on each point that falls on land managed by the federal

government. A stratified-random sampling design (each of the four National Forests as strata) was used to select 308 plots to sample on federal land. Because 10 sample plots were in dangerous (e.g., cliff) locations, those were replaced by FIA plots that were adjacent to watercourses (riparian reserves, see Dunk et al. 2002) so that they too were sampled in proportion to their occurrence.

Locating our mollusk sampling at FIA plots meant that we had access to the vegetation data collected previously at each location and that we could easily apply habitat models developed using these data to all FIA plots throughout the study area. Fieldwork took place from March 1999 to September 2000 on the Klamath National Forest and from April to July 2000 on the other forests. Most plots were sampled during spring, but plots at higher elevations were often sampled during summer after they became accessible.

Each FIA plot was sampled for mollusks twice, with a minimum of 10 days between surveys. All mollusk sampling took place within the 1-ha plot, though much less than the entire plot was thoroughly searched. Surveys were conducted only if the daytime temperature was  $>5^{\circ}\text{C}$  and soil was moist as determined by touch. Surveys began with crews walking through the 1-ha plot and identifying structural features that were likely to provide mollusk habitat (e.g., downed wood), after which two types of focused searches were conducted: (1) Area searches targeted the most likely mollusk habitat by thoroughly inspecting a feature (e.g., downed wood, rocks, ferns) and the area likely to contain mollusks within a 5 m radius (80 m<sup>2</sup>) surrounding that feature. One 20-min time-constrained area search was conducted (all times represent person-minutes; one person for 20 min = two people for 10 min each). (2) Point searches were 40-min time-constrained searches in which surveyors visited many locations within the plot, spending a maximum of 3 min at any location before moving on. Thus, each plot was sampled twice, for 1 h each time. This method was based on the protocol developed by federal land managers to survey prior to land-disturbing activities (Furnish et al. 1997).

Because of the difficulty of distinguishing mollusk species in the field, a single specimen of each putative species (live if available, and shell if that was all that was found) was collected from each plot for laboratory identification. These were given to staff experienced in mollusk identification at the Klamath, Mendocino, and Six Rivers National Forests, and one independent contractor. If these individuals could not confidently identify a specimen as an SM species, the specimen was forwarded to Dr. Barry Roth (Barry Roth Consultants, San Francisco, California, USA), an expert in mollusk taxonomy, for identification.

#### *Vegetation data*

*Microscale.*—The FIA program sampled vegetation in 1997 and 1998 (see USDA 2000 for details on FIA

sampling). Five 0.1-ha subplots were sampled within each 1-ha FIA plot. Within these subplots, trees and shrubs were identified to species and a comprehensive list of vegetation structure and composition variables were either measured or estimated (see Appendix A). In addition, the quantity of downed wood (measured in various size classes), rock, and other physical features were estimated. Due to the interest and importance in determining whether any of the target species should be considered to be associated with old-growth forest, we used a subset of the microscale vegetation data to input into a slightly modified version of the model developed by Bingham and Sawyer (1991) to classify each plot as being either young, mature, or old-growth forest.

*Mesoscale.*—Mesoscale variables were estimated at each of six spatial scales: 12.5, 50, 200, 450, 800, and 1250 ha; all circular with the FIA plot at the circle's center. We characterized the vegetation composition within each circle using the timber strata data from the four National Forests (e.g., USDA 1993). These were estimates of the: (1) dominant tree species, (2) mean tree size, and (3) mean canopy coverage for polygons derived from aerial photographic interpretation. We reduced the original "raw" classes to seven vegetation types that represented distinctly different forest structures and ages (e.g., plantation vs. late-seral forest) and types (conifer dominated vs. hardwood dominated; see Appendix A). We evaluated the percentage of each circle that was of a known vegetation type; unknown types generally occurred on private lands. We excluded those circles where  $>5\%$  was composed of unknown vegetation types. This reduced the total sample size to 296 for the mesoscale analysis. We also calculated the linear distance of streams and roads within the circle using GIS based on the individual national forests' master coverages.

*Physical and spatial.*—We obtained estimates of climatic conditions around each sample location from Parameter-elevation Regressions on Independent Slopes Model (PRISM; Daly et al. 1994), a national climate mapping program (see Appendix A) with  $\sim 2$  km resolution. Slope, aspect, and elevation were estimated at each plot in the field. UTM coordinates of each plot were estimated with Global Positioning System units.

#### *Analyses*

##### *Model development.*—

1. *Estimating geographic ranges.*—We quantified each species' geographic range for two reasons: (1) to provide such estimates to land managers, and (2) to restrict our predictive modeling of each species' presence-absence to areas within their geographic range. For our study, presence-absence is technically "detected-not detected" in that we are not certain that a species did not occur at plots where we did not find it. However, the combination of two search methods applied on two separate occasions should achieve a rea-

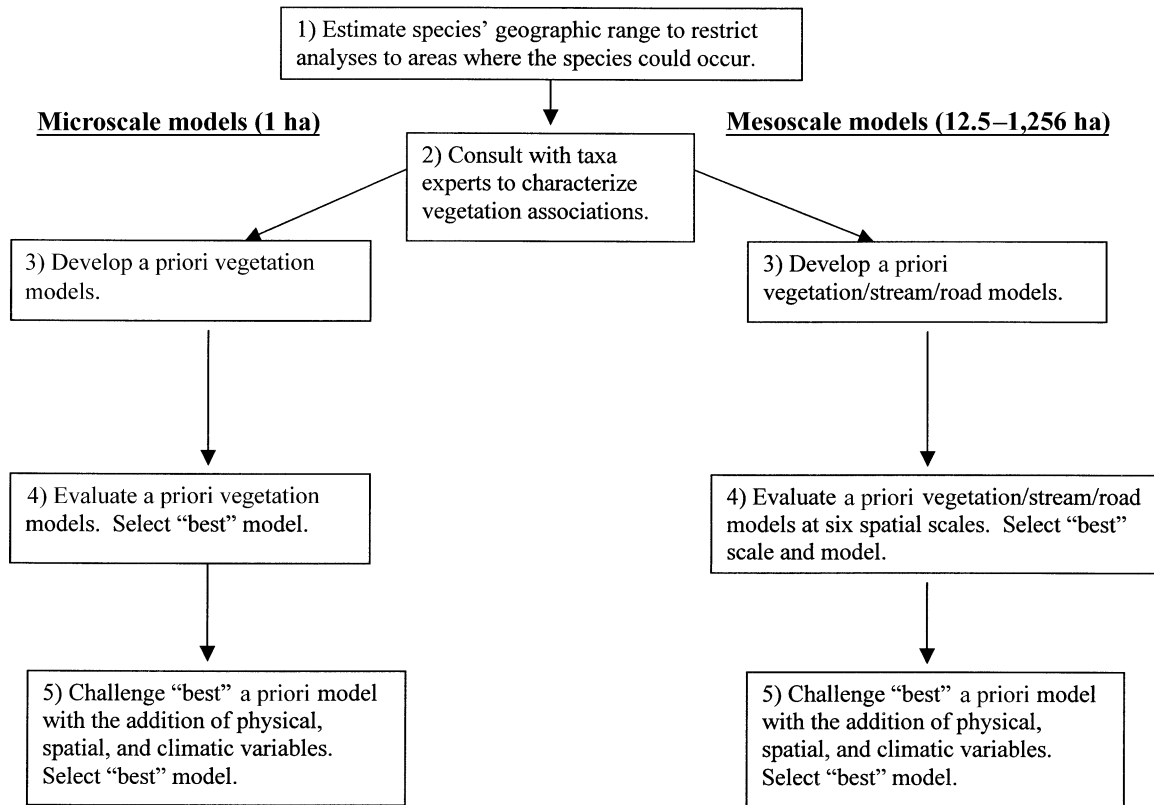


FIG. 2. Flow chart of model-building process.

sonably high probability of detection, especially for sessile organisms. We used non-parametric logistic regression, a subset of Generalized Additive Models (GAMs), with loess smoothing functions (Cleveland 1985) to estimate detection probability surfaces for each species. Spatial (UTM) coordinates were the only covariates entered into these models. We used Akaike's Information Criterion (AIC; Akaike 1973) to evaluate different span values (smoothing parameters; Chambers and Hastie 1997) ranging from 0.2 to 0.75, in increments of 0.05, and chose the span that resulted in the smallest AIC value. Probabilities of presence were then estimated on a 1-km grid for all locations within the range of the sampled points using the spatial model with the smallest AIC value for each species. Next, we defined the species "range" as all locations inside the contour of a threshold probability. We sought threshold levels that would include the vast majority of locations where a species occurred. Regions outside this threshold contour were considered outside of the species' range. Austin and Meyers (1996) discussed regression models where observations extend beyond the feasible range of a species and zero values are included for those locations. The inclusion of such locations could distort the shape of a response function and the explanatory power of a model (Austin and Meyers 1996). We chose the 0.05 probability contour as the boundary

of each species' geographic range (Fig. 2). Theoretically, ~5% of the locations where a species occurs will be outside of this region given a systematic or random sampling of the species within our study area.

2. *Predicting occurrence within geographic ranges.*—We also used GAMs to evaluate the relationship of each species' occurrence to vegetation, climatic, physical, and spatial location covariates at the two scales. The benefits of using GAMs, as opposed to linear regression models, are that: (1) distributional assumptions about the dependent variable may be relaxed, and (2) relationships between dependent and independent variables need not be linear (see Yee and Mitchell 1991). Furthermore, Pearce and Ferrier (2000) reported that species distribution models fitted with GAMs were more accurate than generalized linear models.

3. *Predictions based on microscale vegetation, topographic, and climatic variables.*—Due to the paucity of published information on our target species, we solicited the opinions of knowledgeable biologists on habitat features that they felt were associated with mollusk occurrence. Based on this input, we chose to include 29 of the FIA vegetation variables for our analyses (Appendix A). The presumed association of several species with late-successional/old-growth forests led us to evaluate several metrics related to such forests

(e.g., older age, large-diameter and taller trees, greater basal area, and greater amount of downed wood; see Bingham and Sawyer 1991). Based on these inputs, we first developed 191 a priori microscale vegetation models (sensu Burnham and Anderson 1998) using only the vegetation variables available from the FIA plots (Fig. 2). We did not include highly correlated variables ( $r > 0.8$ ) in the same a priori models. For each mollusk species, each a priori model was evaluated, and the model with the smallest AIC was recorded. This “best” vegetation model was then challenged by individually adding spatial location, climatic, and physical covariates (Appendix A). If none of these models resulted in a lower AIC, the modeling process ended. If, however, the addition of one of the spatial location, climatic, or physical covariates reduced the AIC value, we then challenged the new model by individually adding the remaining spatial location, climatic, and physical covariates. This process was repeated until AIC did not decrease with the addition of more covariates. Because AIC is a combination of the model deviance and the number of estimated parameters in the model, it reduces the over-fitting of models which may result in reduced predictive power (Pearce and Ferrier 2000). Hereafter, we use the term “overall” models to refer to models that included a combination of the covariates in a priori vegetation models and spatial location, physical, and/or climatic covariates.

The result of this stage of modeling was either: (1) a model that only included the vegetation characteristics existing on the 1-ha FIA plot (the best a priori microscale vegetation model) or (2) a model that included both the vegetation characteristics on the FIA plot plus some other physical (elevation, slope), spatial location, or climatic (precipitation, temperature) features (the best overall model). For the latter, it is possible that a best overall model represents vegetation on 1-ha scale and climate over a much larger scale (Fig. 2). It is important to note that we tested for spatial structure *within* each species’ geographic range by allowing UTM coordinates to enter the models after the best a priori vegetation model was determined (Fig. 2).

**4. Predictions based on mesoscale vegetation, topographic, and climatic variables.**—Because the vegetation data collected at FIA plots existed only at these plot locations, microscale models can only be tested or applied to locations where data on these same variables exist. The mesoscale variables, on the contrary, exist as a seamless coverage over the entire study area, so they are amenable to evaluating how models with identical variables perform at various spatial scales. Furthermore, we reasoned that some FIA plots might contain suitable habitat for a species, but the species may not occur there because the larger landscape is unsuitable. If good models can be developed with the mesoscale variables, they can be applied at any location within the study area. Therefore, we evaluated 22 a priori mesoscale models at each of six spatial scales

( $n = 132$  models total). We did not include highly correlated variables ( $r > 0.8$ ) in the same a priori models. These a priori models were an attempt to represent general forest characteristics as well as stream and road lengths (associated with riparian conditions and anthropogenic disturbance, respectively). For each species, we selected the best model and scale based on AIC, and then challenged it with physical, climatic, and spatial covariates, identical to the process we used for challenging the a priori microscale vegetation models (Fig. 2).

**Model evaluation.**—We used two diagnostics to evaluate models:  $D^2$  and modified chi-square statistics. We calculated an adjusted  $D^2$  for each “best” model (see Guisan and Zimmermann 2000) as follows:

$$D^2 = 1 - [(n - 1)/(n - p)] \cdot (1 - D^{2*}) \cdot 100,$$

where  $D^2$  is the percentage of the deviance explained (analogous to  $R^2$  in linear regression [Yee and Mitchell 1991]),  $n$  = the number of observations,  $p$  = the number of parameters in the model ( $p = df_{\text{null model}} - df_{\text{best model}}$ ), and  $D^{2*}$  = the unadjusted  $D^2 = (\text{Null deviance} - \text{Residual deviance})/\text{Null deviance}$ . The Pearson chi-square statistic is usually compared to a  $\chi^2$  distribution with degrees of freedom equal to the number of groups minus the number of parameters in the model. However, because of the small numbers of total occurrences, the number of groups needed to be small in order to have groups with more than one occurrence. Consequently, the  $\chi^2$ -distribution approximation was not appropriate, and we had to use bootstrap simulations to calculate  $P$  values for the observed Pearson chi-square statistic. Values of  $P$  lower than 0.10 suggest poorer fit than larger  $P$  values.

**1. Geographic range models.**—Additional data on the presence of each of the target species was available from the Interagency Species Management System (ISMS) database (see USDA and USDI 2000). The ISMS data were from surveys conducted by the Forest Service and Bureau of Land Management between 1994 and 2001 at sites where habitat-disturbing activities were planned. Thus, they were a nonrandom sample of the study area. These surveys were similar to ours; however, surveyors searched  $\sim 4$  ha in the same amount of time that we searched 1 ha. In addition, specimen identification for ISMS records was not as stringent as for our study. Because every mollusk identified was entered into the ISMS database, there was the potential for  $>1$  sighting at the same location. In order to avoid multiple detections of a species from similar locations, we sorted these samples such that no two samples of a species were within 250 m of each other. To test the accuracy of our geographic range models, we evaluated the percentage of the ISMS locations that fell within the estimated 0.05, 0.025, and 0.01 contours.

**2. Micro- and mesoscale predictive models.**—We evaluated how well our models fit data not used in their

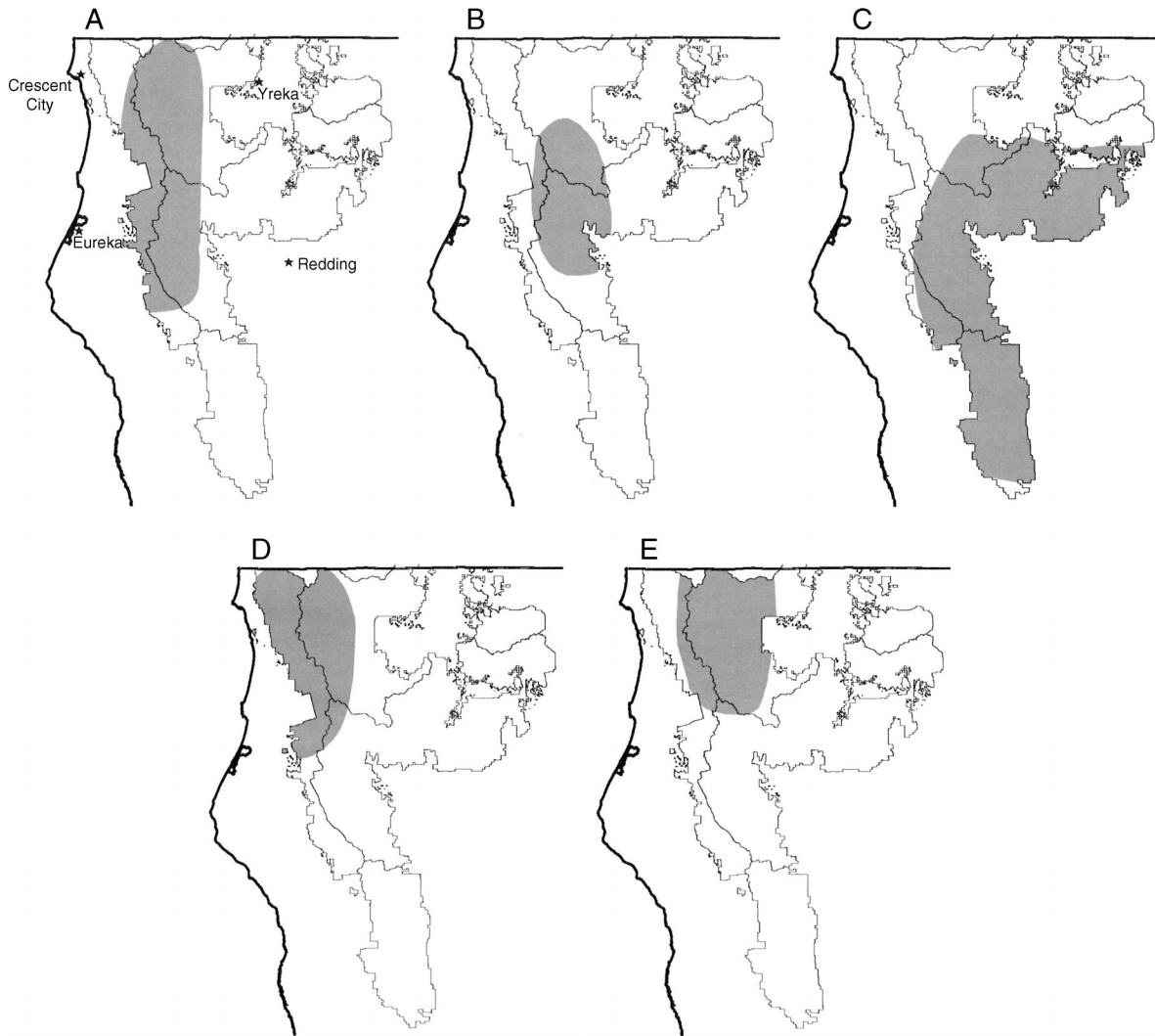


FIG. 3. Estimated geographic ranges, as defined by the 5% probability contours, of (A) *Ancotrema voyanum*, (B) *Helminthoglypta talmadgei*, (C) *Monadenia churchi*, (D) *M. fidelis klamathica*, and (E) *M. f. ochromphalus* within the boundaries of the study area.

development using a jackknife cross-validation procedure followed by graphical evaluations of model fit. We were looking for differences in fitted functions between those from the cross-validation and those from the entire data set for each species. Large differences would indicate models that were not stable and, therefore, not as useful for prediction in new areas.

## RESULTS

### Geographic ranges

Of the 308 sampled plots, *M. churchi*, *A. voyanum*, *M. f. klamathica*, *M. f. ochromphalus*, and *H. talmadgei* were detected at total of 55, 24, 9, 8, and 8 plots, respectively. For every species, 100% of the locations at which it was detected fell within its estimated geographic range (0.05 probability contour). Within esti-

mated geographic ranges, 10.1, 11.7, 16.3, 22.2, and 35.0% of the FIA plots sampled detected *M. f. ochromphalus*, *M. f. klamathica*, *H. talmadgei*, *A. voyanum*, and *M. churchi*, respectively. Estimated geographic range sizes within our study area varied from 4770 km<sup>2</sup> (*H. talmadgei*) to 15 795 km<sup>2</sup> (*M. churchi*; Fig. 3A–E).

### Testing geographic range models

The number of independent (ISMS) sites at which a species was detected ranged from 10 for *M. f. klamathica* to 1718 for *M. churchi* (Table 1). For all species combined, the mean percentage of independent sites that fell within estimated geographic ranges (0.05 contour) was 85.6%, ranging from 72.6 to 99.8% (Table 1). A greater percentage of independent locations occurred within the 0.025 (range 87.2–99.9%) and 0.01 (range 94.1–99.9%) bounds (Table 1).

TABLE 1. Percentage of independent locations of each mollusk species falling within the estimated geographic ranges at various probability contours.

Species	<i>n</i>	0.05 contour (% inside)	0.025 contour (% inside)	0.01 contour (% inside)
<i>Monadenia churchi</i>	1718	99.8	99.9	99.9
<i>Helminthoglypta talmadgei</i>	188	82.5	87.2	94.1
<i>Ancotrema voyanum</i>	53	93.2	93.2	95.5
<i>Monadenia fidelis ochromphalus</i>	50	72.0	98.0	100
<i>M. f. klamathica</i>	10	90.0	90.0	100

#### Microscale univariate comparisons

Univariate comparisons revealed some features of the physical environment that differed between locations where each species was detected and where it was not, as well as some similarities (Appendix B). For all species except *A. voyanum*, plots where individual mollusks were detected were at significantly ( $P < 0.10$ ) lower elevations than plots where they were not detected. *H. talmadgei* and *M. f. klamathica* were both detected at plots with less mean annual precipitation than plots where they were not detected. Nonetheless, relative to the other species, plots at which *H. talmadgei* was detected had the lowest mean annual precipitation, whereas plots at which *M. f. klamathica* was detected had the highest mean annual precipitation (Appendix B). All species except *H. talmadgei* were detected at plots with significantly ( $P < 0.05$ ) higher mean summer temperatures and August maximum temperatures relative to plots where they were not detected.

*A. voyanum* was detected in plots with older trees, more conifer basal area, larger diameter conifers, less grass cover, and more downed woody debris than plots where it was not detected. *M. f. ochromphalus* was detected in plots containing a more dominant hardwood component (greater hardwood canopy cover, tree diameters, and tree heights) than plots where it was not detected. *M. f. klamathica* was detected at plots with more conifer and hardwood canopy cover, more hardwood basal area, larger diameter and taller hardwoods, but less large downed woody debris.

Sites where *H. talmadgei* and *M. churchi* were detected did not often have features generally associated with late-successional forests. *H. talmadgei* was detected at plots with more grass cover and taller hardwoods than plots where it was not detected. Though not significantly different, plots where *H. talmadgei* was detected had, on average, less conifer and hardwood basal area, less conifer canopy cover, and younger trees than plots where it was not detected. This was not true for any other species. *M. churchi* was on average detected at plots with more hardwood canopy cover and basal area, and more *Quercus* basal area. Only *A. voyanum* was found to occur more often than expected by chance in plots classified as old-growth by the modified Bingham and Sawyer (1991) model (Appendix B).

#### Microscale vegetation: multivariate predictive models

Among the five mollusks, the best a priori vegetation models contained from two to five variables. The best a priori vegetation model was better (lower AIC) than the best overall model for only *M. f. klamathica* (Appendix C). Thus, for only one of five species was the best microscale model not improved when spatial location, physical, or climatic variables were added. For each species, predicted probabilities at plot locations were readily separated, with the majority of non-detection sites having low predicted probabilities and detections sites having high predicted probabilities (Fig. 4A–E).

The best model for *A. voyanum* included mean diameter of conifers, percent hardwood cover, *Quercus* basal area, coefficient of variation of December and July precipitation, and mean annual precipitation. The best model for *H. talmadgei* included hardwood basal area, *Quercus* basal area, total downed woody debris, and mean summer precipitation. The best model for *M. churchi* included mean diameter of conifers, percent hardwood cover, UTM coordinates, summer temperature/summer precipitation, and coefficient of variation of December and July precipitation. The best model for *M. f. klamathica* included percent conifer canopy cover, percent hardwood canopy cover, mean tree age, mean standard deviation of tree age, and volume of downed woody debris. The best model for *M. f. ochromphalus* included hardwood basal area, *Acer* basal area, volume of downed large woody debris, and mean summer precipitation.

The  $D^2$  values for each species' best microscale model were 56.6, 94.5, 42.3, 81.6, and 83.3 for *A. voyanum*, *H. talmadgei*, *M. churchi*, *M. f. klamathica*, and *M. f. ochromphalus*, respectively. For each species, the overall difference between observed and predicted frequencies suggested that the data fit the model well (all  $P$  values were  $>0.1$ , range 0.163–0.663).

#### Mesoscale univariate comparisons

The best scale for each species varied from 50 ha for *M. f. ochromphalus* to 1250 ha for *H. talmadgei* and *M. churchi*. *A. voyanum* was detected at plots where the surrounding 450 ha had significantly ( $P < 0.10$ )



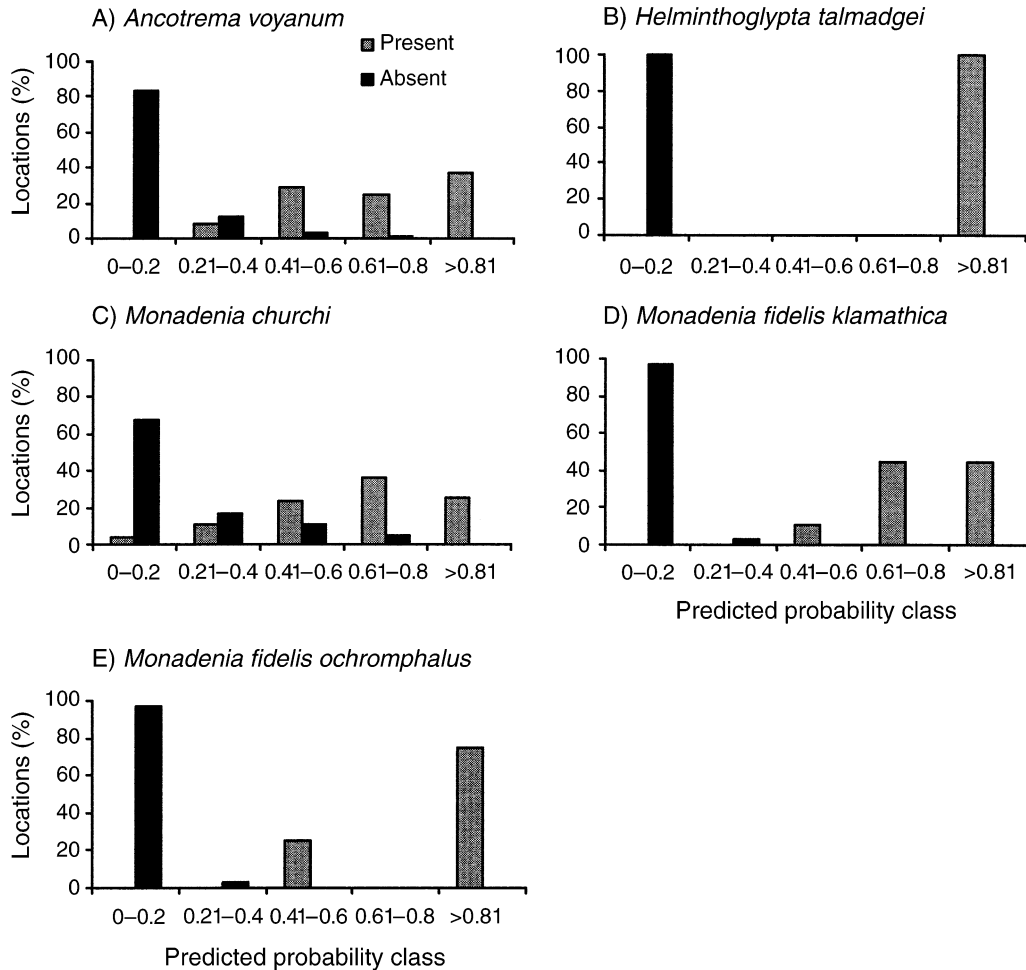


FIG. 4. Histograms displaying the distribution of predicted probabilities of occurrence classes by each of five mollusk species' actual presence and absence.

more plantations and late-seral conifer forest, but less low-density, young conifer forest than around plots where it was not detected (Appendix D). *H. talmadgei* was detected at plots where the surrounding 1250 ha had a significantly greater area of plantations; lesser area of hardwoods, low-density late-seral conifer forest, and late-seral hardwood dominated forest than around plots where it was not detected (Appendix D). *M. churchi* was detected at plots where the surrounding 1250 ha had significantly smaller areas of young conifer forest and hardwood forest, and a greater length of stream than area surrounding plots where it was not detected (Appendix D). *M. f. klamathica* was detected at plots where the surrounding 200 ha had a significantly smaller area of low-density young conifer forest, but greater area of late-seral hardwood dominated forest and length of road than areas surrounding plots where it was not detected (Appendix D). *M. f. ochromphalus* was detected at plots where the surrounding 50 ha had a significantly greater area of plantations and

length of road, but a smaller area of late-seral conifer forest than areas surrounding plots where it was not found (Appendix D).

#### *Mesoscale predictive models*

Among the five mollusks, the best a priori mesoscale models contained from two to nine variables (Appendix E). Climate, physical, and spatial variables improved models for three of five species; not for *M. f. klamathica* or *M. f. ochromphalus* (Appendix E). For each species, predicted probabilities at plot locations were readily separated, with the vast majority of non-detection sites having low predicted probabilities and detection sites having high predicted probabilities. The worst case of separation was for *A. voyanum* with >90% of non-detection locations having probabilities of occupancy ( $P_o$ )  $\leq 0.4$  and ~67% of the locations where it was detected having  $P_o > 0.4$ .

The best mesoscale model for *A. voyanum* was at the 450-ha scale and included area of plantations, coeffi-

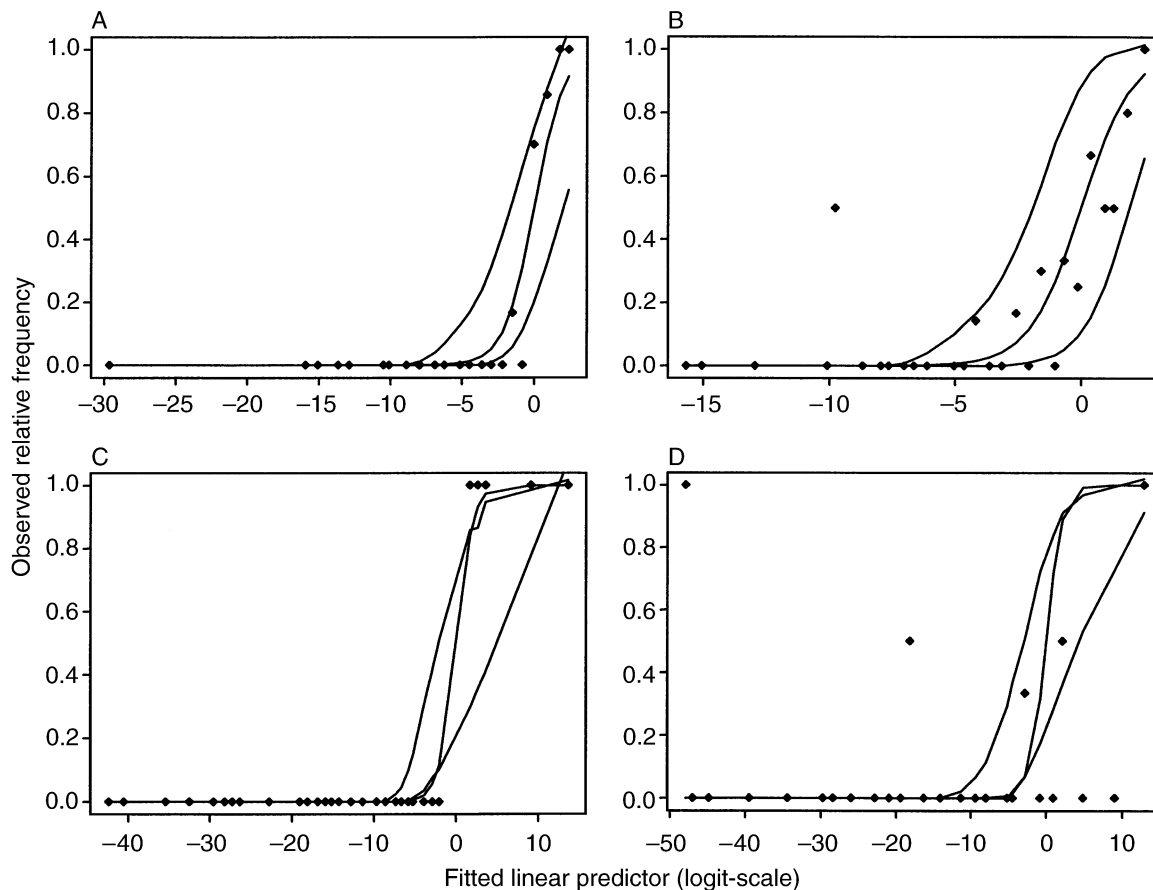


FIG. 5. Examples of model fit using the entire data set vs. cross-validation for *Ancotrema voyanum* (microscale model) in which both the model using (A) the entire data set and (B) cross-validated data showed a relatively stable model; and for a *Helminthoglypta talmadgei*, where models (microscale) developed from (C) the entire data set and (D) cross-validated data revealed an unstable model.

cient of variation of December and July precipitation, and UTM coordinates. The best mesoscale model for *H. talmadgei* was at the 1250-ha scale and included area of plantations and coefficient of variation of December and July precipitation. The best mesoscale model for *M. churchi* was at the 1250-ha scale; it included meters of blue-lined streams, area of vegetation dominated by late-seral hardwood, percentage of slope, mean December minimum temperature, mean summer temperature, coefficient of variation of December and July precipitation, elevation, and UTM coordinates. The best mesoscale model for *M. f. klamathica* was at the 200-ha scale and included areas of young early mature conifers, young early mature low-density conifers, and plantations, as well as length of road. The best mesoscale model for *M. f. ochromphalus* was at the 50-ha scale and included the same variables as the model for *M. f. klamathica*.

The  $D^2$  values for each species' best mesoscale model were 40.8, 76.4, 52.4, 75.8, and 83.3 for *A. voyanum*, *H. talmadgei*, *M. churchi*, *M. f. klamathica*, and *M. f.*

*ochromphalus*, respectively. For each species, the overall difference between observed and predicted frequencies suggested that the data fit the model well (all  $P$  values were  $>0.10$ , range 0.250–0.614).

#### Evaluation of predictive models

Models were considered stable if the full data set and cross-validated data had similar distributions of predicted probabilities (evaluated on the logit scale). Cross-validation of the best models at both the micro- and mesoscales showed that models developed for species with more detections were more stable than those developed for species with fewer locations (Fig. 5). The microscale model for *A. voyanum* ( $n = 24$  detections), however, was more stable than the microscale model for *M. churchi* ( $n = 55$  detections), whereas the mesoscale model for *M. churchi* was more stable than that for *A. voyanum*. Of the species with eight or nine detections, only the models for *M. f. klamathica* appeared to be relatively stable.

## DISCUSSION

The mollusks we evaluated included species that occurred at many locations over a large region (e.g., *M. churchi*) and those that occurred at <10 locations over an area <5000 km<sup>2</sup> (e.g., *H. talmadgei*). Individual species were detected at as few as 10.1% to as many as 35% of the sampled plots within their geographic ranges in the study area. Although the selected species were considered to be among a group of “rare” species (USDA and USDI 1994) before this study was undertaken, they include species with widely varying characteristics of abundance, distribution, and habitat associations. Prior to this study, each of the species was also presumed to be either associated with late-successional forest conditions or sensitive to the effects of grazing. Our study was not designed to address the effect of grazing, but the species of interest demonstrated markedly different associations with late-successional forest conditions.

*Geographic ranges*

Our choice of  $P_o = 0.05$  as a threshold for geographic range models appeared to be satisfactory in that very few of a set of independent observations for each species fell outside the predicted range. However, more conservative thresholds of 0.025 and 0.01 may be warranted for some of the species (Table 1). For example, our use of the 0.05 contour was warranted for the objectives of our study. For rare species conservation planning, however, the more conservative threshold values would be less likely to exclude occupied portions of a species range. Our findings support the idea that relatively few detections of a species are necessary to adequately characterize its geographic range, if samples are selected at random.

Estimates of geographic ranges have direct relevance for identifying species at greater risk of decline or extinction and for prioritizing species for conservation efforts. Rare species are usually the focus of conservation efforts, and information on geographic range is often used as an indicator of rarity. Gaston (1991) defined rarity as “the first quartile of the frequency distribution of species abundances or range sizes.” If we accept this rarity definition as a working definition, then it is crucial to have accurate and defensible estimates of geographic ranges. Relative to all mollusks detected and identified during our study, 57 species or subspecies were detected at two or more locations. The target species and subspecies all fall within the third or fourth quartile of estimated geographic range sizes (*M. churchi* had the second largest estimated geographic range; J. R. Dunk and W. J. Zielinski, unpublished data). Thus, using geographic range as an index to rarity, the target SM species were not particularly rare. Nonetheless, relative to IUCN (2001) standards, all species except for *M. churchi* could be considered globally rare based on range size, but such a determination would consist

of additional data on each species’ habitat and/or population trend.

*Associations with late-successional forest conditions*

Prior to the analyses, we expected all of the mollusks to exhibit strong positive relationships to late-successional forest conditions measured at the microscale (i.e., older trees, more basal area, uneven distribution of tree diameter at breast height, large quantities of large woody debris) and to moist, cool climates. Within the same study area, Dunk et al. (2002) reported that SM mollusks as a group showed no significant association to Late Successional Reserves, a land allocation developed under the NWP. The results of our current analyses suggest that not all of the target species are associated with late-successional forest conditions.

All species were found in some plots with late-successional forest characteristics. However, two of the species (*H. talmadgei* and *M. churchi*) were not primarily found in plots with such characteristics. Tree age by itself does not signify late-successional characteristics, but is often considered a proxy for such characteristics (USDA and USDI 2001b). USDA and USDI (2001b) stated that late-successional forests typically begin to develop at 80 to 130 years. Nonetheless, we believe it would be a mistake to use either of those ages as a threshold for defining late-successional characteristics. Spies (1997) noted that the “early transition old-growth phase” in Douglas-fir–western hemlock (*Tsuga heterophylla*) forests requires 100 to >500 years to develop. Although the durations may vary for forests in our study area, the 80- to 130-year mark is more likely to represent the time at which standing trees begin to assume late-successional characteristics. A more thorough evaluation of the relationship of tree age to species presence is to use age as a continuous variable and compare plots where each species was detected to those where it was not detected within its geographic range. For example, the mean tree age at plots where *H. talmadgei* was detected was 94.9 years as compared to 140.9 years, where it was not. Using 80 years as the late-successional threshold might lead us to conclude it was associated with such forests.

*A. voyanum* and *M. f. ochromphalus* were associated with many late-successional forest characteristics, while *M. f. klamathica* was associated with some late-successional forest features, but did not occur in areas with large amounts of large downed woody debris. In contrast, *H. talmadgei* was detected in areas with less conifer canopy cover and basal area, more grass cover, younger trees, and on drier aspects; characteristics not usually associated with late-successional forests. Agee (2001) evaluated the association of mollusks to evidence of fire and found that *H. talmadgei* was the only mollusk that was found more frequently on more recently burned plots. *M. churchi* occurred in areas with more hardwood cover and basal area, and “medium sized” conifers; also not characteristic of late-succes-

sional forests. The modified Bingham and Sawyer (1991) model applied to our data supports the conclusion, based on the univariate habitat associations, that *A. voyanum* is associated with late-successional/old-growth forests and *M. churchi* is not. We believe it is premature to draw conclusions about late-seral associations for *M. f. klamathica*, *M. f. ochromphalus*, and *H. talmadgei* due to the small number of plots where they were detected during this study. Prior to this study, grazing was perceived as a threat to *A. voyanum*, *M. f. klamathica*, and *M. f. ochromphalus*, and harvest of late-successional forests was perceived as a threat to *H. talmadgei* and *M. churchi* (USDA and USDI 1994, 2001a). Our findings suggest instead that *A. voyanum* may be sensitive to loss of late-successional forests and that *M. churchi* may be less vulnerable to this threat than previously expected.

Previous assumptions also led us to expect areas with less late-successional forest to be negatively associated with each species when evaluated at the mesoscale. This expectation was based on two assumptions: (1) mollusk species that require late-successional conditions and that inhabit small isolated fragments would have a higher likelihood of having gone locally extinct due to stochastic events, and (2) smaller forest patches of late-successional forest would be more likely to experience deleterious edge-effects than larger patches (cf. Chen et al. 1995). Contrary to this expectation, for *A. voyanum*, *H. talmadgei*, and *M. f. ochromphalus* there was a larger ( $P < 0.10$ ) area of tree plantations (i.e., areas of recent timber harvest) around plots where they were detected than where they were not detected (Appendix D). Paradoxically, two of these species (*A. voyanum* and *M. f. ochromphalus*) were associated at the microscale with the *oldest* stands and with a number of late-successional forest features, so the positive association with plantations at the mesoscale was not expected. However, detections of these two species were also centered on areas with *more* late-successional forest (conifer for *A. voyanum* and hardwood-dominated for *M. f. klamathica*). It may also be that area of plantation is positively correlated with the amount of lower elevation productive forest, and thus areas that were first targeted for timber harvesting. Areas around plots where *H. talmadgei* was detected, on the contrary, had no late-successional hardwood-dominated forests, whereas areas around plots where it was not detected averaged 107 ha of late-successional hardwood-dominated forests. This result is consistent with the microscale analysis that suggested *H. talmadgei* was not associated with late-successional forest features. Areas around plots where *M. f. ochromphalus* was detected had less late-successional conifer forest than sites where it was not detected (Appendix D).

Although our mesoscale expectations were not met for each species, the two hypothesized mechanisms that might be responsible for an association with late-successional forests cannot be definitively addressed by

our study. For example, for a small forest patch, time since isolation may be more important than isolation per se. Similarly, the time-scale at which edge-related microclimate effects might manifest themselves may be a function of both time and frequency of extreme, larger scale climate events, especially droughts. Further, we do not know the scale at which such effects might influence these mollusks. Our findings suggest, however, that neither *H. talmadgei* nor *M. churchi* have a strong association with late-successional forest conditions, at the micro- or meso-habitat scale. We recommend that additional data be collected for each of the species with <10 detections, so that more robust predictive models can be developed.

We view the results of our predictive habitat modeling as “first generation” predictions because we had no prior quantitative information to work with. Unlike the geographic range models, we did not have available an independent set of vegetation data with which to evaluate the habitat models. We understand the value of accuracy assessment (Fielding 2002), and we are embarking on such a test that we hope will help us understand the magnitude of classification errors.

For low vagility species, such as terrestrial mollusks, the area immediately surrounding them should ultimately be a better predictor of survival and reproduction than more distant (larger scale) areas. All appropriate habitat conditions must exist within a very small area. Terrestrial mollusks may not be able to emigrate more than 50 m if conditions deteriorate (van der Laan 1971, Roth and Pressley 1986). Our microscale (1 ha) measurements are probably large enough to contain entire populations, whereas our mesoscale measurements (12.5–1250 ha) probably characterize the environment for meta-populations. Unlike multiscale evaluations of vertebrate habitat relations (e.g., Mitchell et al. 2001) where authors often infer that various species select habitat at various scales, individual mollusks do not have the ability to choose amongst sites within large (landscape-scale) areas. Thus, we believe that our microscale associations are more indicative of specific mollusk–habitat relationships.

For mollusks, unlike more vagile species such as birds and mammals (see Tyre et al. 2001), models based on presence–absence data may in fact be indicative of survival and reproduction rather than simply predicting occurrence. Due to their limited ability to emigrate from sites, their presence is likely to represent their tolerance to both contemporary and historic site conditions, and thus their ability to both survive and reproduce at the site.

#### *Association with stream courses*

*H. talmadgei*, *M. f. ochromphalus*, and *M. churchi* were detected in areas exceeding an average of 2 km of stream/km<sup>2</sup>. For *H. talmadgei* and *M. f. ochromphalus*, the density of streams did not differ between sites where they were and were not detected, but for

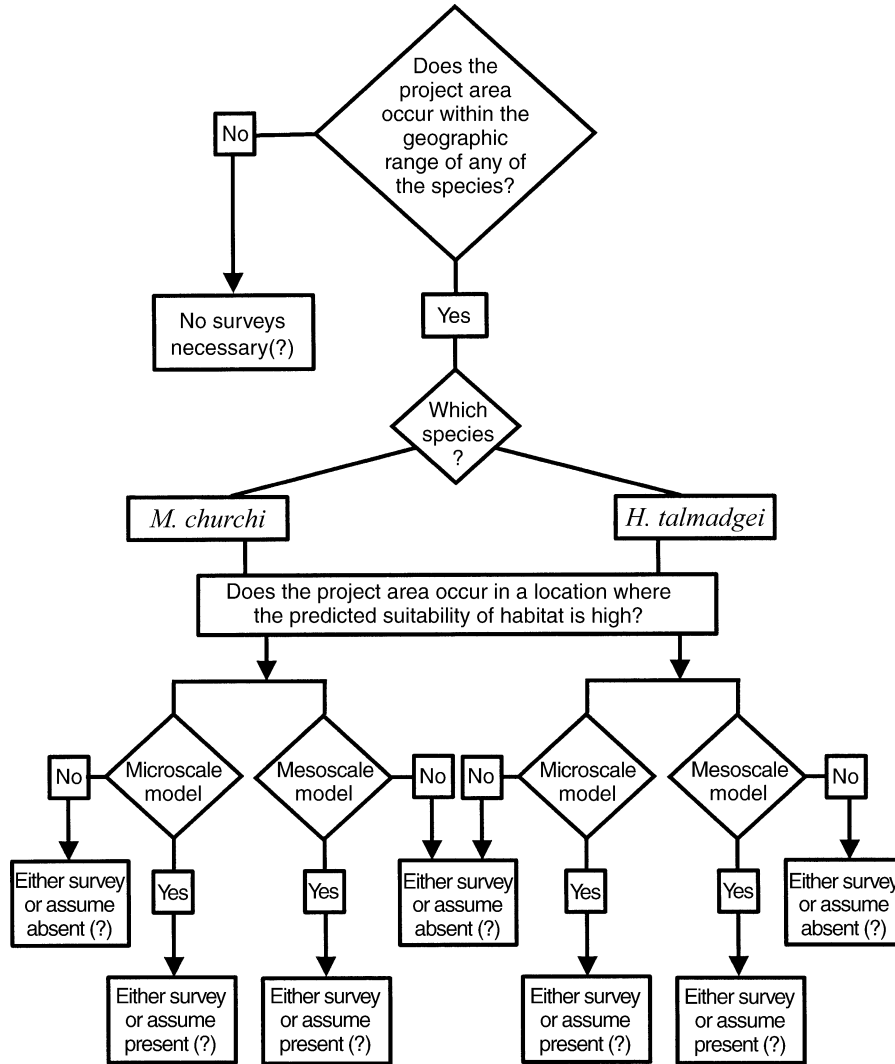


FIG. 6. An example of a proposed decision process for a forest manager who must consider surveys for “Survey and Manage” mollusks under the Northwest Forest Plan.

*M. churchi*, there was a significant difference with an average of 0.6 km/km<sup>2</sup> more streams around plots where it was detected than where it was not. Dunk et al. (2002) reported that terrestrial SM mollusks as a group were found in riparian reserves more than expected. Further investigation of the relationship of *M. churchi* to riparian areas seems warranted. For *H. talmadgei*, stream densities were nearly equal around plots where it was detected relative to those where it was not detected. Considering all plots sampled within each species’ geographic range, *M. churchi* and *H. talmadgei* occurred in areas with the highest and second highest stream densities, respectively. Perhaps their apparent lack of association with climate-mediating late-successional forests is compensated by an association with areas containing high stream densities.

*Predictive models*

Predictive models fit the data quite well for all species and at both micro- and mesoscales, explaining from 40.8 to 94.5% of the deviance. The somewhat unexpected success of our predictive models may be due to the extent over which we sampled. Because we sampled over a large portion of each species’ geographic range, we were probably able to detect more “signal” in our models than those developed within smaller areas, or from models developed from retrospective data (e.g., museum records, atlas data). That is, we were more likely to achieve the advantage of sampling a broader spectrum of habitat conditions (e.g., Austin and Heyligers 1991) than studies taking place in very small portions of a species geographic range.

### Management implications

Our results provide important guidance to land managers who are responsible for determining the necessity for surveys prior to management activities. Currently, these surveys are generally required at every location where a habitat-disturbing activity (e.g., prescribed fire, timber harvest, recreational activity development) is proposed on federal land within the NFP area (USDA and USDI 2001a, b). However, we expect that if the geographic ranges for the species of interest were known that surveys for individual species may not be necessary outside the estimated perimeter of the ranges. Second, no quantitative descriptions of habitat for the target species were available prior to this study. Thus, land management actions likely to be “habitat disturbing” were based on presumptions of each species’ habitat, not on quantified estimates of habitat metrics. Although we do not claim to have a complete understanding of any of the species’ habitats, we have provided more clarity towards understanding each species’ habitat associations than existed previously. Moreover, we can also envision the predictive habitat models being useful for determining where surveys may or may not be necessary, or what effects a project may have on habitat value in the project area or, cumulatively across the range of a species. Pre-project habitat conditions could be entered into the models and a  $P_o$  value determined. Projected post-project habitat conditions could also be entered into the model (prior to conducting the activity) to estimate the difference between  $P_{opre}$  and  $P_{opost}$ . Some pre-defined “threshold” in this difference, or absolute value of  $P_{opost}$ , could be identified and thus guide the intensity of management.

We anticipate that one of the first questions that our data would help land managers answer was whether a proposed land management project occurred within the geographic range of any of the mollusks of interest (see Fig. 6 for an example of a proposed decision process). A manager could portray the geographic ranges of a set of species at a pre-determined level of confidence (e.g., 0.05, 0.01) and identify the species’ ranges that overlap the project area. If none of the ranges include the project area, a decision to not conduct pre-project surveys may be justified. Alternatively, if the project area is included within the range of one or more species, managers could decide whether the proposed management action was likely to alter the species’ habitat. If so, they could either use a spatially interpolated map of predicted habitat value to estimate the effect of the project on the species of interest (e.g., Fig. 7) or could collect new micro-habitat scale data at the project area to estimate relative habitat value. This information could be used to: (1) determine the necessity of pre-project surveys (costly surveys could be avoided in areas of high and low predicted habitat suitability by simply assuming presence and absence, respectively),

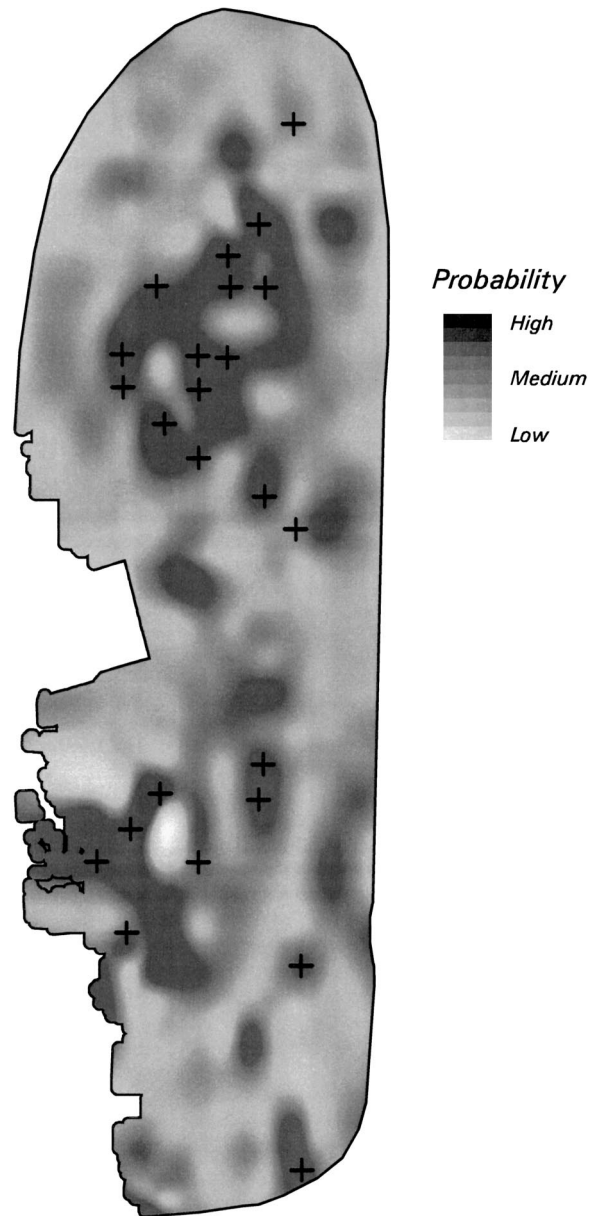


FIG. 7. An example of spatially interpolating probability of occupancy values of *Ancotrema voyanum* between forest inventory and analysis plots (~5.5-km grid). Black crosses depict locations at which *A. voyanum* was detected during this study.

and (2) to evaluate the effects of the project on habitat value at various spatial scales.

We provided micro- and meso-habitat scale models, in part, to provide land managers with options in the face of uncertain funding for information. The micro-scale models include variables that are immediately affected by most land management activities (e.g., mean tree dbh, mean tree age, overstory cover, downed woody debris). We recommend that managers use these models to sample site-specific habitat value in areas

proposed for management. However, collecting new field data is expensive, so we also provide the option of estimating habitat value at a location from either: (1) a model based on spatially interpolated values of habitat from the micro-habitat scale (FIA) model or (2) from the mesoscale model. Either of these options can result in an estimated habitat value for a site of interest without the cost of collecting new field data, but it should be understood that they may also be less accurate and/or less precise.

Although there is precedent and value for developing exploratory models based on few locations (e.g., Pearce and Ferrier 2000), the accuracy of predicting species' distributions generally improves with increasing sample size (Pearce and Ferrier 2000). This observation notwithstanding, our findings suggest that large-scale, probability-based sampling surveys for rare organisms, even those with small ranges, can provide extremely useful information to land managers. We are in agreement with Johnson (2001) who, in reference to models, suggested use of the term *evaluation* as opposed to *validation*: "A model has value if it provides better insight, predictions, or control than would be available without the model" (Johnson 2001). As with much of applied ecology, it is the manager and not the researcher who must choose what level of confidence they desire and the usefulness of model predictions. Among the questions left for managers to answer are: (1) How "good" must internal cross-validation results be to warrant expending more money on gathering independent test data to thoroughly evaluate a model's predictive ability; (2) what predictive ability is sufficient to apply a model; and (3) given limited budgets, when is a model good enough for one species such that further refinement is not necessary and monies can be allocated to equally important species for which little or no information currently exists?

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#### APPENDIX A

A table of candidate explanatory variables used to model mollusk presence–absence in northern California forests, 1999–2000 is available in ESA's Electronic Data Archive: *Ecological Archives* A014-012-A1.

#### APPENDIX B

A table showing means ( $\pm 1$  SD) of microscale variables that entered at least one of the “best” models for any of the five mollusk species with an Akaike weight  $> 0.05$  is available in ESA's Electronic Data Archive: *Ecological Archives* A014-012-A2.

#### APPENDIX C

A table of microscale predictive models rankings based on Akaike's Information Criterion for models with Akaike weights  $> 0.05$  is available in ESA's Electronic Data Archive: *Ecological Archives* A014-012-A3.

#### APPENDIX D

A table showing means ( $\pm 1$  SD) of mesoscale variables at the scale for which we found the best model for each mollusk species is available in ESA's Electronic Data Archive: *Ecological Archives* A014-012-A4.

#### APPENDIX E

Mesoscale predictive models rankings based on Akaike's Information Criterion for models with Akaike weights  $> 0.05$  is available in ESA's Electronic Data Archive: *Ecological Archives* A014-012-A5.