

Woodland salamanders as metrics of forest ecosystem recovery: a case study from California's redwoods

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Abstract. Woodland (Plethodontid) salamanders occur in huge numbers in healthy forests in North America where the abundances of many species vary along successional gradients. Their high numbers and trophic role as predators on shredder and decomposer arthropods influence nutrient and carbon pathways at the leaf litter/soil interface. Their extreme niche conservatism and low vagility offer further advantages to the use of these salamanders as metrics of forest ecosystem condition. Mill Creek is a 103 km² commercially logged redwood forest watershed acquired as parkland where original primary forest is being restored. This study evaluated woodland salamanders as metrics of seral recovery at Mill Creek. Surface counts and body condition were examined in four sets of stands, two early seral, one mature, and one of primary forest (never harvested old-growth). Later seral sites were closer to the coast where fog increased available moisture; younger sites were further inland at higher elevations where fog was reduced. We distinguished the effects of geography and succession using ANCOVA with a PCA-derived landscape covariate. Both geography and succession increased counts of California Slender Salamanders (*Batrachoseps attenuatus*); advancing succession alone indicated increased counts of *Ensatina* (*Ensatina eschscholtzii*). Means and variances in body condition of these two species were lower in older stands; for the Del Norte salamander (*Plethodon elongatus*) only the means were lower. Coastal proximity increased mean body condition in *E. eschscholtzii*, but with *P. elongatus* it was the opposite. We modeled surface counts and body condition along environmental gradients associated with succession. The counts and body condition in two of three species when taken together suggested that the increased structural complexity in late-seral forest stands supported larger populations that appeared to be competing for limited resources and, thus, likely have greater population fitness than those in younger forests. *B. attenuatus* and *E. eschscholtzii* proved to be viable metrics of advancing succession with their numbers and body condition providing readily quantifiable measures of ecosystem recovery at Mill Creek.

Key words: *Batrachoseps attenuatus*; biometrics; body condition; *Ensatina eschscholtzii*; *Plethodon elongatus*; redwood forest; seral recovery; succession; surface counts; woodland salamanders.

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INTRODUCTION

Primary, old-growth, or late-seral forests are unique and rapidly diminishing ecosystems that provide critical ecological services such as accu-

mulating and storing carbon in living and dead trees (Mackey et al. 2008, Sillett et al. 2010) and soils (Zhou et al. 2006). These forests contain the greatest terrestrial carbon stocks on the planet and possess the greatest potential as future

carbon sinks (Luyssaert et al. 2008, Hudiburg et al. 2009, Keith et al. 2009). The recovery of late-seral forest does not result from advanced tree stand age alone (see Franklin et al. 2000). While large old trees are the most obvious component of these forests, their development depends upon healthy soils and diverse biota (Likens and Franklin 2009), with intact healthy ecosystems consisting of numerous abiotic and biotic interactions (e.g., Redford 1992, Lindenmayer, 2009), the absence of which can have profound negative effects on ecosystem functions (Terbough and Estes 2010). Tracking the re-establishment of fully functional late-seral forest ecosystems requires finding cost-effective indicators that can monitor and track progress (Nichols and Williams 2006). These indicators need to document meaningful thresholds along environmental gradients leading to recovery (With and Crist 1995, Huggert 2005, Groffman et al. 2006), and ideally have a demonstrable link to specific aspects of ecosystem resistance and resilience. The two primary concerns with indicator species are that their numbers be readily assessed and that changes in these numbers track directly with changes along relevant environmental gradients (Lambeck 1997, Huggert 2005, Lindenmayer et al. 2006). The most pragmatic approach would be to select species whose relative abundances are amenable to accurate and cost-effective monitoring, and that simultaneously provide information on ecological processes of high relevance (Fleishman and Murphy 2009).

The high abundances, ease of sampling, trophic role, and increasing species richness and greater numbers associated with seral advancement (Davic and Welsh 2004) make woodland (Plethodontid) salamanders uniquely suited among North American forest vertebrates as candidates for monitoring the recovery of these ecosystems. Their extremely conservative ecological niches (Wiens and Graham 2005, Kozak and Wiens 2010) render them highly sensitive to altered environmental conditions. For example, they respond to changing moisture and temperature regimes (Spotila 1972, Grover, 2000), important abiotic attributes whose extremes are ameliorated with advancing succession (Chen et al. 1999), and that are known to influence other species dependent on late-seral environments (e.g., Barrows 1981). Woodland salamanders

respond to many additional changes in forest conditions that are altered by the resetting of the seral state such as canopy removal, declines in tree densities, loss of leaf litter, and loss of downed wood (e.g., Ford et al. 2002, Crawford and Semlitsch 2008, Rittenhouse et al. 2008). Compared with other less tractable vertebrates that are typically more difficult and expensive to sample, and more challenging to connect directly with site-specific conditions, the low vagility of woodland salamanders ties them directly with conditions of place. And their often huge numbers (e.g., 2950 to 18,000/hectare, Burton and Likens 1975a, Welsh and Lind 1992, Petranksa and Murray 2001, Peterman et al. 2008) make them readily and inexpensively sampled. Furthermore, their high abundances and enormous biomass in temperate forests evidence an important role in forest trophic dynamics where they function as apex predators transforming invertebrate to vertebrate biomass (Davic and Welsh 2004). Their high assimilation efficiencies (Pough 1983) translate directly into a major protein-rich food resource in forest food webs (Burton and Likens 1975b). However, perhaps their most important and little recognized ecological service is the facilitation of nutrient capture by increasing the amount of leaf litter converted into humus (see Prescott 2010) by preying on shredder and decomposer arthropods (Wyman 1998, Walton and Steckler 2005, Best 2012), invertebrate fauna that would otherwise disarticulate this litter and release much of its content back into the atmosphere. Higher salamander abundances in primary forest evidence a significant role in the processes that promote soil-building, plant nutrient cycling and carbon capture (processes described by Bardgett and Wardle 2010); roles of high conservation concern that contribute to resilience-resistance in these forests.

The intended future for the Mill Creek redwood forest landscape in Northwest California, USA is to return logged-over areas to primary forest (Lorimer et al. 2009, O'Hara et al. 2010), with the intent that it again supports its full complement of native biota and ecological processes (see Noss 2000). The restoration of this property, recently acquired by the state park system, is particularly desirable because it is in the geographically limited coastal redwood forest bioregion, and could provide migration

corridors for currently rare or absent fauna between interior and coast and north and south latitudes (Poiani et al. 2000, Lindenmayer et al. 2006).

The objective of this study was to test the hypothesis that plethodontid salamanders are advantageous metrics of seral recovery in this historically disturbed redwood forest (Welsh and Droege 2001), by testing their ability to indicate advanced succession and the concomitant development of structural complexity with its associated abiotic and biotic processes (see details in Lindenmayer et al. [2006] on attributes of primary forest recovery). Past research supports the use of salamander abundances and body condition as indicators of seral advancement. Their numbers increase along advancing seral continua in multiple temperate forest types in North America (e.g., Welsh and Lind 1991, Cooperrider et al. 2000, Ford et al. 2002, Homyack and Haas 2009), and body condition has been shown to differ with varying forest management (e.g., Karraker and Welsh 2006, Welsh et al. 2008).

Four genera of plethodontid salamanders are present at Mill Creek (Cooperrider et al. 2000), with three species common. Our approach was to determine surface abundances and body condition of these three common species along the seral continuum, comparing their responses at four seral stages along this gradient. Furthermore, assuming we found the predicted differences, we sought to relate variations in their numbers to changes associated with specific attributes of seral advancement that co-vary with the development of older tree stands and are consistent with stands recovering old-growth characteristics and related ecological processes. Specifically our objectives were to test: (1) if salamander surface counts increased, and body condition differed, with successional advancement, and (2) if the increasing numbers and changing body condition corresponded with changes along environmental gradients that are directly linked to advancing forest succession (e.g., greater canopy closure, larger tree diameter, increased leaf litter). Our logic was that increases in numbers and changes in body condition along the seral gradient would be evidence of the usefulness of woodland salamanders as indicators of the recovery of late-seral or old-growth

forest ecosystem conditions (i.e., Odum 1969).

METHODS

Study location

The Mill Creek property (hereafter MC) consists of 103 km² of forest composed primarily of coastal redwood (*Sequoia sempervirens*), with lesser amounts of Douglas-fir (*Pseudotsuga menziesii*), in Del Norte County, California, situated between the native temperate old-growth forests of Jedediah Smith Redwoods State Park to the north, and Del Norte Coast Redwoods State Park to the west (Fig. 1). The MC, situated within 2 km of the Pacific Ocean, historically supported old-growth redwood forest, one of the planet's oldest extant forest types. However, this landscape underwent extensive logging for more than 100 years up until the 1990s, and is now dominated by early seral stages of second-growth redwood forest. Tracts of primary old-growth redwood forest in state parks adjacent to the MC provided appropriate reference stands to compare with recovering stands (Foster et al. 2003, Willis and Birks 2006).

Study design

Our study design employed space-for-time substitution (Pickett 1989) as a means to study seral advancement where manipulation experiments are not feasible given the length of time required to study forest succession. To test the hypothesis of a positive relationship between salamander surface counts and body condition, and environmental gradients reflecting advancing succession, we measured or estimated variables representing attributes linked with their increasing numbers and seral advancement in previous studies (see *Spatial and environmental gradients*). We identified as sample units forest stands surrounding headwater or first-order channels (Sheridan and Olson 2003). We randomly selected 1st-order sub-basins within the stand age categories available across the MC and adjacent parklands. This process resulted in sets of sites in four seral categories that reflected the anthropogenic disturbance history of the Mill Creek drainage; 11 stands were logged between 16 and 32 years ago, 14 were logged between 33 and 60 years ago, four stands were harvested 61–120 years ago and have regrown to mature forest,

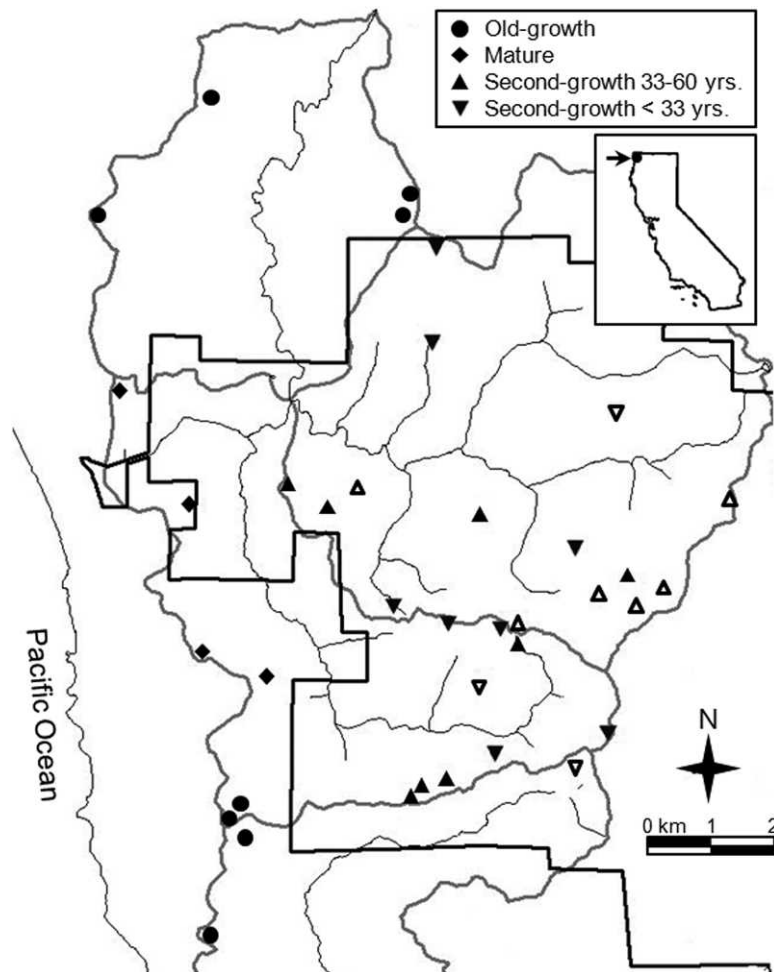


Fig. 1. Locations of 37 study sites on the Mill Creek property (MC) and adjacent state parklands. Thick solid black lines are property boundaries and grey lines are major drainage basins and main tributaries of Mill Creek. The open symbols are the nine sites added in 2007.

and eight were never logged, primary old-growth, reference stands on adjacent parkland (200+ years old) (Fig. 1). Estimates of stand ages were based on harvest histories, with the first age breakpoint coincided with the implementation of California's Z'Berg Nejedly Forest Practice Act of 1973. Age estimates for the reference sites are conservative minima as old-growth redwood trees are typically much older than 200 years of age (Lorimer et al. 2009). Based on their close proximity, we assumed that sites on MC had forest structure and amphibian abundances similar to stands on adjacent parkland prior to being logged. The mean size of the sample basins was 5.67 ha (range 1.24 to 16.8 ha), areas

sufficiently large to encompass multiple territories of individual woodland salamanders (Stebbins and Cohen 1995).

Spatial and environmental gradients

We measured four landscape variables: 'easting' (to quantify distance from the nearby Pacific Ocean; a surrogate for fog-derived moisture), slope, aspect, and elevation. We established the variable 'easting' using GIS (measured in UTM; ArcMap 2004) reasoning that greater proximity of a site to the Pacific Ocean could affect salamander distributions given the significance of moisture in their physiology (Feder 1983), and stand re-growth given the pronounced moisture

gradient of coastal fog essential to the redwood biome (Dawson 1998, Johnstone and Dawson 2010). Percent slope was measured with a handheld clinometer at a single location selected to represent the average slope. Aspect was determined using a hand compass. For the analysis we converted aspect using the formula:

$$\text{Asp} = \cos(\pi \times (\text{Aspect} - 45)/180) + 1$$

where northeast had a value of two, southwest a value of zero, and both northwest and southeast a value of one (adapted from Beers et al. 1966). In the northern hemisphere southwest aspects tend to be the warmest and driest and northwest aspects tend to be the coolest and wettest.

We measured environmental attributes known to correlate with increasing salamander numbers and seral advancement from previous studies (e.g., Welsh and Lind 1991, 1995, Cooperrider et al. 2000, Welsh et al. 2006): tree diameter at breast height (DBH; a measure of tree growth representing forest age and used to replace the categorical stand age group variable derived from harvest history with a more precise and continuous representation of succession in the modeling exercise [see *Salamanders and successional gradients*]), percent canopy closure (overall and by tree species), litter depth, percent downed wood, percent rock cover, and a 10 cm deep soil temperature taken at the time of the animal sampling (Table 1). DBH was determined by taking the average diameter of five randomly selected trees in the dominant size class at each site. We determined the percent of open canopy of the search area at three locations (selected to best represent the site and distributed across the area) with a spherical densitometer which required four measurements per location (sub-samples) taken during two years of sampling equating to the average of 6 measurements per site; for the analysis percent open canopy was converted to percent closed. The amount of canopy (%) provided by the common tree species at each site were visually estimated, as were the percent large downed wood (>10 cm diameter, >1 m long) and rock in the amphibian search area. Litter depth was measured (in millimeters) at three random locations following site reconnoitering, which allowed us to determine representative areas for these measurements. Downed wood is important for terrestrial amphibians as

cover on the forest floor to evade predators and maintain themselves in stable, cool, moist environments (e.g., Rittenhouse et al. 2008). Logs can remain wet inside throughout the summer months. The Del Norte salamander (*Plethodon elongatus*) is associated with rocky substrates throughout its range (Jones et al. 2005), however, at coastal redwood sites this species will also use cover such as wood and leaf litter (Diller and Wallace 1994).

Amphibian sampling

Concern has been expressed about the accuracy of surface abundances of woodland salamanders to estimate population sizes due to their extensive use of subterranean habitats (e.g., Bailey et al. 2004a, b, Kroll et al. 2009). Many studies have determined that total (super) population sizes far exceed the numbers found at any given time on the surface, with surface dwelling individuals comprising as few as 10–15% of a super population (e.g., Taub 1961, Welsh and Lind 1992). However, addressing our hypotheses did not require comparing super population sizes. Neither was our focus on site occupancy (i.e., presence-not detected). By applying identical sampling efforts using both active and passive sampling methods to determine surface counts, we collected relative abundance data at each site that, with multiple sites per seral category and multiple years of sampling, provided estimates (with variance) by stand age category of the relative numbers of surface active target species. Knowledge of salamander behavior as it relates to diel and seasonal cycles, along with appropriate sampling strategies and the use of reference sites (e.g., Olson et al. 1996, Hyde and Simons 2001, Clayton et al. 2009) can address concerns about timing and the appropriateness of a particular sampling strategy. Depending on the questions being addressed, relative counts (i.e., indices) derived using appropriate protocols can generate accurate and comparable data (Smith and Petranksa 2000, Johnson 2008). Where false negatives (failing to detect individuals when present) are a concern and it is not logistically feasible to conduct the near time multiple samplings of closed populations required to accurately estimate and correct for detection probabilities, the validity of raw count data can be verified by simultaneously employing active

Table 1. Landscape, stand, and site scale attributes (means with SD in parentheses) for the four seral groups sampled for woodland salamanders at Mill Creek. Significant differences between groups in selected variables (ANOVA) are indicated by differences in alphabetical superscripts.

Attribute	Group 1 16–32 yr n = 10	Group 2 33–60 yr n = 15	Group 3 34–120 yr n = 4	Group 4 >200 yr n = 8
Basin area (ha)†	6.4 (5.05)	5.2 (3.21)	8.9 (4.90)	4.1 (2.15)
Easting (UTM)	412.1k ^A (1.33k)	412.0k ^A (2.13k)	407.0k ^B (0.99k)	408.0k ^B (1.70k)
Elevation (m)	396 ^A (105.6)	420 ^A (132.2)	259 ^B (13.4)	252 ^B (78.6)
Slope (%)	66.0 ^A (24.13)	66.0 ^A (14.78)	53.7 ^A (17.02)	49.4 ^A (11.16)
Aspect (Asp)	0.83 ^A (0.68)	1.30 ^B (0.70)	1.36 ^B (0.89)	1.64 ^B (0.37)
Total canopy (%)‡	98.02 (4.99)	97.76 (2.32)	96.95 (1.53)	93.16 (4.27)
Redwood canopy (%)‡	22.9 (25.92)	27.4 (23.15)	66.3 (17.02)	81.2 (14.33)
Hardwood canopy (%)‡	43.0 (30.11)	38.7 (22.87)	1.5 (2.38)	0.0 (0.00)
Tanoak canopy (%)‡	23.0 (21.90)	25.27 (19.63)	0.2 (0.50)	0.0 (0.00)
DBH (cm)§	25.8 (6.16)	44.6 (8.53)	78.0 (22.64)	241.5 (54.18)
Log cover (%)¶	16.0 (8.43)	20.0 (8.24)	15.5 (10.21)	16.9 (7.53)
Litter depth (mm)#	34.9 (12.93)	41.2 (15.98)	63.7 (27.88)	48.8 (10.88)
Rock cover (%)	14.8 (15.46)	14.9 (13.39)	9.2 (17.17)	3.1 (6.85)
Soil temperature (°C)	11.2 ^B (0.98)	10.3 ^A (0.99)	11.8 ^B (0.43)	11.4 ^B (0.42)

† Basin area is the ridgeline to ridgeline size of the entire first-order basin.

‡ Canopy estimates are percent closed.

§ Diameter at breast height of five of the dominant size class of trees.

¶ Estimate of percent of VES search area covered by downed wood >15 cm dia. and 1 m long.

Mean of three measurements per site.

|| 10 cm deep soil temperature taken at the time of VES (see text).

(e.g., timed searches) and passive (e.g., coverboards) sampling strategies and comparing results (Tilghman et al. 2012). Because it is more difficult to find salamanders in old-growth redwood forest compared with young stands due to the greater structural complexity and the amount and size of potential surface cover (old-growth redwood logs cannot be readily moved) (H. Welsh, *personal observation*), the numbers of salamanders sampled in old-growth likely under-represents true numbers when compared with young forests, so differences between old-growth and younger seral stages are conservative estimates.

Two experienced observers conducted timed (one-hour) visual encounter surveys (VES; Crump and Scott 1994) during daylight hours under similar good weather conditions at 28 sites in 2006 (sampled 12 April to 17 May); in 2007 nine additional sites in young forest (logged ~33 years ago) were added to increase the total number of stands to 37 (sampled 17 May to 3 July). VES consisted of sampling upland areas above the headwall and the first-order channel (Fig. 2), staying within 60 m of the channel at each site for a one hour time period. A nearby site known to support *P. elongatus* was checked for salamander surface activity, and prior to

initiating VES air temperature and humidity were determined to not exceed established thresholds (Olson et al. 1996). Four-prong rakes were used to lift cover objects and rake through forest litter. Cover types were sampled in proportion to occurrence. Areas not likely to support amphibians were avoided (i.e., bare soil and sparse leaf cover). Only actual search time counted with timers stopped for processing.

Salamanders were also sampled continuously over the entire study period with passive coverboards (Fellers and Drost 1994). Coverboards consisted of two redwood shakes (each 1.5 × 15 × 40 cm) stacked with a 0.8-cm spacer between, held together with removable metal clips for inspecting between shakes. Coverboards were placed one at the channel head and six (three per side) parallel to the channel's banks within 3 m of the channel and spaced 3 m apart (Fig. 2). Coverboard arrays were first deployed at 28 sites in 2006, with nine more added in 2007; 28 sites were first checked for salamanders between 17 May and 3 July in 2007, with the larger set of 37 arrays checked between 17 March and 21 March 2008. Coverboards in 2008 yielded more detections as a result of longer deployment, but for four sites inaccessible in 2008 (two each in seral groups 1 and 4), we substituted the more

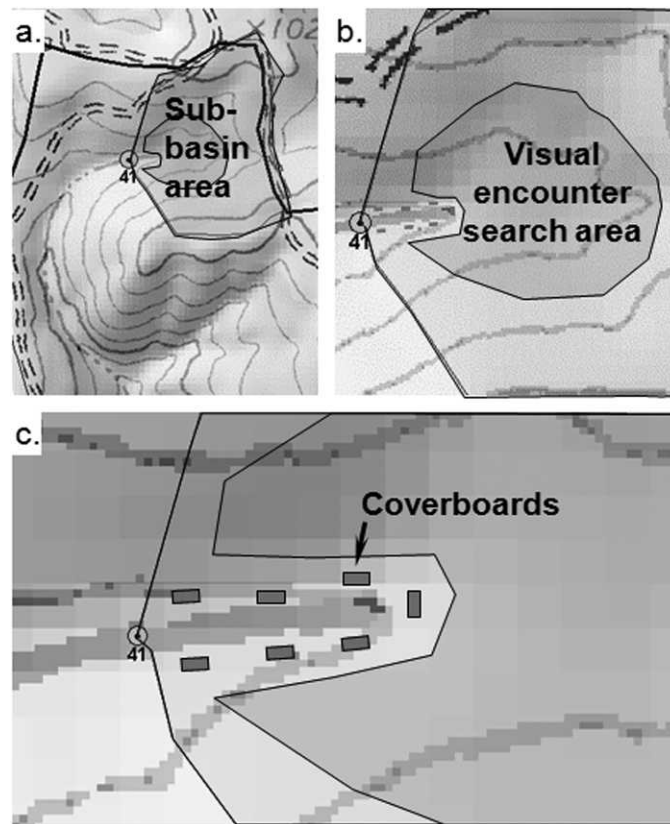


Fig. 2. Three views at increasingly finer spatial scales showing: (a) sub-basin area, (b) visual encounter survey (VES) area within sub-basins, and (c) coverboard deployment around first order tributaries.

conservative 2007 data in the analyses.

All salamanders were weighed (to within 0.10 g), measured (total and snout-vent length to within 0.1 cm), sexed and released. We made notes on gravid females and injuries such as missing or re-grown tails. This information was used to calculate body condition.

Statistical analyses

Analyses were conducted on two response (dependent) variables, surface counts and body condition of the three common species, California slender salamander (*Batrachoseps attenuatus*), *Ensatina* (*Ensatina eschscholtzii*), and the Del Norte salamander (*Plethodon elongatus*). In analyses of surface counts we used the combined data from the 2007 VES data and 2008 coverboards from each site (Table 2), which provided the most data from all 37 sites using the combined sampling methods. In the analyses of body condition we combined all VES (2006 and 2007) and all

coverboard (2007 and 2008) data for these same species (Table 2); gravid females and salamanders with missing body parts were eliminated because of their potential to bias the regression equations.

Accounting for the influence of geography.—Testing the null hypothesis of no differences in surface counts or body condition of the three common species among seral stages was confounded by the geography at Mill Creek because mature and old-growth sites were closer to the coast than younger sites. This prompted us to examine differences in the independent landscape variables among the seral groups with ANOVA (Table 1) so they could be accounted for when investigating salamander responses using analyses of covariance (ANCOVA). We found that older stands were significantly closer to the coast (Easting, $F = 17.08$, $df = 3, 36$, $p < 0.0001$), young stands more inland and at higher elevations (Elevation, $F = 2.10$, $df = 3, 36$, $p = 0.003$),

Table 2. Numbers of each amphibian species found by sampling method and year. Visual encounter surveys (VES) in 2006 sampled 28 sites, all other data are from all 37 sites. VES 2007 data and coverboard (CB) 2008 data were used in the ANCOVA of surface counts by seral stage and the exploratory modeling (AIC_c) analysis. Analyses of body condition used all of the data combined.

Response	2006 VES	2007 VES	2007 CB	2008 CB	Total
California slender salamander (<i>Batrachoseps attenuatus</i>)	171	135	38	71	415
Ensatina (<i>Ensatina eschscholtzii</i>)	33	42	6	13	94
Del Norte salamander (<i>Plethodon elongatus</i>)	19	40	12	9	80
Wandering salamander (<i>Aneides vagrans</i>)†	3	4	0	1	8
Coastal giant salamander (<i>Dicamptodon tenebrosus</i>)†	3	4	0	0	7

†Data not included in statistical analysis.

and there were differences in aspect among the four groups (Aspect, $F = 2.35$, $df = 3, 36$, $p = 0.091$) (Table 1). To account for geographic differences while testing for the effects of changes in seral stage on salamanders we used PCA (McCune and Grace 2002) to construct a composite variable from the three landscape attributes that differed among seral group to employ in the ANCOVAs. The composite variable (hereafter composite landscape variable or CLV) was determined by the first PCA axis (which explained 67% of the total variation); the CLV was highly negatively correlated with Easting ($r = -0.934$) and Elevation ($r = -0.907$), and less so and positively with Aspect ($r = 0.567$). We examined surface counts and body condition of the three common salamander species among seral groups with ANCOVAs employing the CLV as a covariate using SAS 9.3; Tukey-Kramer tests were used for pairwise comparisons. In the case of those species that had unequal variances in body condition we used “repeated/group = means” in SAS to allow for differences in variances in each seral group.

Salamander body condition.—To examine body conditions of the three salamander species among the four seral groups we compared residuals from least squared regressions of weight to total length as an index of body condition (Schulte-Hostedde et al. 2005) using the equation:

$$\log(\text{body mass}) = \beta_0 + \beta_1 \log(\text{body length}) + \delta$$

where β_0 and β_1 are constants representing the intercept and slope of the regression line and δ

(the index of body condition) is the residual with median equal to zero (see Welsh et al. 2008); positive residuals represent better body condition than negative residuals (Jakob et al. 1996).

Salamanders and successional gradients.—To better understand the relationships with seral processes revealed by the ANCOVAs of surface counts and body condition, we conducted exploratory analyses using modeling to examine relationships with environmental gradients that vary with advancing succession. Exploratory analyses of poorly known species are essential to provide the basic information needed to maintain a complete complement of native biota. The relationships of most environmental variables to forest succession are straightforward and well documented (e.g., Lindenmayer et al. 2006, Lorimer et al. 2009); however, how variables might interact to influence counts or body condition of these salamander species at Mill Creek was a key question of this research. We built models to predict changes in surface counts or body condition of *B. attenuatus*, *E. eschscholtzii* and *P. elongatus* with variables from three descending spatial scales: landscape, forest stand, and site (Table 1), and included the CLV (described above); counts (*B. attenuatus* and *E. eschscholtzii*), or presence/absence (*P. elongatus*), and the body conditions of co-existing salamander species (potential competitors or predators). We also examined interactions among these variables. As such, a priori candidate models for each response variable (counts or body condition) were composed of independent variables we selected to measure at the initiation of the study (Table 1),

along with salamander counts and body conditions determined during the study. We used the information-theoretic approach (Burnham and Anderson 2002) to evaluate relationships with counts or body condition and candidate models. Because we did not assume these relationships to be linear we used generalized additive models (GAMs), which are non-linear regression models that describe relationships between predictor and response variables (Cleveland and Devlin 1988, Hastie and Tibshirani 1990). Selection of best candidate models was determined based on differences in bias corrected Akaike information criterion (AIC_c) and model weights (w) (Burnham and Anderson 2002). Models with the lowest AIC_c and those within 2 AIC units were considered competitive. Model weights represent the probability that a model is the best of those being considered given the dataset (Burnham and Anderson 2002). Models were evaluated at the three spatial scales and across scales (multi-scale) (e.g., Welsh et al. 2007), using adjusted D^2 (sensu Guisan and Zimmermann 2000). The importance of significant variables in the top models was assessed by examining whether the 95% confidence interval (CI; mean $\pm$ 2 SE) overlapped zero. We calculated single variance inflation factors (c) for the global model of each independent variable (Burnham and Anderson 2002). Model structure was acceptable and data not over-dispersed ($c \leq 1.5$); analyses were in SPLUS 6.1. Alpha level for all tests was set at $p \leq 0.10$, appropriate for ecological studies (Schrader-Frechette and McCoy 1993).

RESULTS

A total of 604 individual plethodontid salamanders were found using the combined techniques of VES and coverboard arrays on the 37 sites over three years (2006–2008) (Table 2).

The influences of geography and forest succession on surface counts

ANCOVAs of the four seral groups, using the composite landscape variable (CLV) to account for differences in geography, were applied to a conservative sample of 318 plethodontids (2007 VES + 2008 coverboards) that represented an equal sampling effort across the 37 sites (Table 2). The ANCOVA of the counts of *B. attenuatus*

revealed a significant effect of geography (CLV) ($F = 3.92$, $p = 0.056$); and with geography accounted for, also indicated a significant effect of seral stage ($F = 2.95$, $p = 0.048$) (Table 3). *B. attenuatus* counts were higher closer to the coast and on the two sets of old stands compared with the older of the two sets of young stands; no differences were found within either of these pairs (Table 3, Fig. 3).

The ANCOVA of counts of *E. eschscholtzii* found no effect of geography ($F = 0.35$, $p = 0.558$), but significant differences by seral stage ($F = 2.96$, $p = 0.047$); the youngest stands had fewer *E. eschscholtzii* than the two sets of old stands, with no differences found within either pair (Table 3, Fig. 3).

The ANCOVA of the counts of *P. elongatus* found no effect of either geography or seral stage (Table 3, Fig. 3).

The influences of geography and forest succession on body condition

The ANCOVA of the mean body condition of *B. attenuatus* among seral groups allowed for potential differences in variance among these groups because the values were unequal (Modified-Levene equal-variances test; $F = 3.30$, $p = 0.037$). The results indicated no effect of CLV on mean body condition ($F = 0.83$; $p = 0.37$), but significant differences between the seral groups ($F = 5.00$; $p = 0.008$); the youngest stands had higher mean body condition than the two sets of old stands (Table 3).

Variance in the body condition data for *E. eschscholtzii* and *P. elongatus* were not unequal, and both showed significant effects of geography (CLV) and seral stage on mean condition (Table 3). The CLV showed a greater effect on *E. eschscholtzii* ($F = 13.0$, $p = 0.0016$) compared to seral stage ($F = 3.59$, $p = 0.03$); with body condition higher closer to the coast, and on the pair of old stands compared with the young stands (Table 3).

The effect of CLV on the body condition of *P. elongatus* ($F = 4.38$, $p = 0.048$) was slightly greater than that of seral stage ($F = 2.97$, $p = 0.054$); however, contrary to *E. eschscholtzii*, the body condition of *P. elongatus* was higher away from the coast and on the older of the two sets of young stands compared to the set of oldest stands (Table 3).

Table 3. ANCOVAs of surface counts and body condition of three species of woodland salamander in four seral groups at Mill Creek using a composite landscape variable (CLV; see text) as a covariate. Effect size (mean and SE [standard error]) in order from youngest to oldest seral groups. Degrees of freedom were 1 (CLV) and 3 (seral group) for all tests. The sample size for surface counts is 37 sites (see Table 1); for condition index sample size is 28 sites for *B. attenuatus*, and 27 sites for *E. eschscholtzii* and *P. elongatus*.

Metric	Observed mean (SE)	Adjusted mean (SE)	F	p	Multiple comparisons
<i>B. attenuatus</i>					
Surface counts†					
Seral groups	3.30 (1.211), 2.73 (0.948), 11.75 (2.954), 10.62 (1.335)	4.29 (1.309), 3.49 (1.059), 9.93 (2.121), 8.87 (1.617)	2.95	0.0476	2 < 3, 2 < 4
CLV			3.92	0.0564	
Condition index‡					
Seral groups	0.22 (0.079), 0.03 (0.074), −0.03 (0.031), −0.06 (0.016)	0.09 (0.028), 0.01 (0.033), −0.02 (0.015), −0.03 (0.010)	5.00	0.008	1 > 3, 1 > 4
CLV			0.83	0.3723	
<i>E. eschscholtzii</i> †					
Surface counts					
Seral groups	0.40 (0.221), 1.067 (0.284), 3.25 (0.854), 2.75 (0.750)	0.29 (0.182), 0.62 (0.147), 1.29 (0.295), 1.10 (0.225)	2.96	0.0470	1 < 3, 1 < 4
CLV			0.35	0.5588	
Condition index					
Seral groups	−0.17 (0.442), 0.05 (0.235), 0.21 (0.164), 0.13 (0.083)	−0.50 (0.250), −0.30 (0.206), 0.68 (0.314), 0.65 (0.259)	3.59	0.0300	1 < 3, 1 < 4, 2 < 4
CLV			13.00	0.0016	
<i>P. elongatus</i> †					
Surface counts					
Seral groups	1.70 (0.615), 1.20 (0.279), 1.00 (0.707), 1.62 (1.923)	0.67 (0.205), 0.58 (0.166), 0.72 (0.333), 0.97 (0.254)	0.50	0.6838	
CLV			1.94	0.1730	
Condition index					
Seral groups	0.00 (0.040), 0.09 (0.040), 0.02 (0.097), −0.05 (0.066)	0.05 (0.055), 0.15 (0.053), −0.06 (0.088), −0.12 (0.059)	2.97	0.0540	2 > 4
CLV			4.38	0.0481	

†Natural log transformed for analysis (means and SEs are not transformed).

‡Did not pass equal variance assumption.

Based on the significant differences revealed in the ANOVAs occurring between the pairs of young and old stands (Table 3), we re-examined the body condition data after combining data from the two young and two older seral groups. At this two group level, variances of *B. attenuatus* and *E. eschscholtzii* (but not *P. elongatus*) were unequal (Modified-Levene equal variance test; *B. attenuatus*, $F = 10.82$, $p = 0.003$; *E. eschscholtzii*, $F = 4.35$, $p = 0.047$); with both much greater on the young compared with the old stands (Fig. 4).

These ANCOVAs and variance tests indicated that the greatest differences in both counts and body condition occurred between the pair of young and the pair of older stands (Table 3; Figs. 3 and 4). Viewing the data from this perspective, the combined counts of the three species on the sets of young stands ($n = 25$) had a mean of 5.4 salamanders/site (SE = 0.8; range 1–15), whereas the mean for the combined mature and old-growth stands ($n = 12$) was 15.8 salamanders/site

(SE = 1.5; range 7–24), equating to an average of 2.93 times more salamanders per site on old stands.

Comparing the two sampling methods, the VES (2007) yielded 104 salamanders or 4.2/hour on the 25 young stands and 122 or 10.2/hour on the 12 mature and old-growth stands; an average of 2.43 times as many salamanders per site on the old stands. The coverboards (2008) produced 30 salamanders on the 25 young stands and 67 on the 12 old stands; means were 1.2 salamanders/site (SE = 0.3; range 0–4) on the young, and 5.6 salamanders/site (SE = 1.7; range 0–22) on old stands, averaging 4.66 times as many salamanders per site on the old stands.

Relationships with environmental gradients

Batrachoseps attenuatus.—The best overall predictor of increased counts of *B. attenuatus* was the landscape scale model consisting of the interaction of easting and elevation; this model explain-

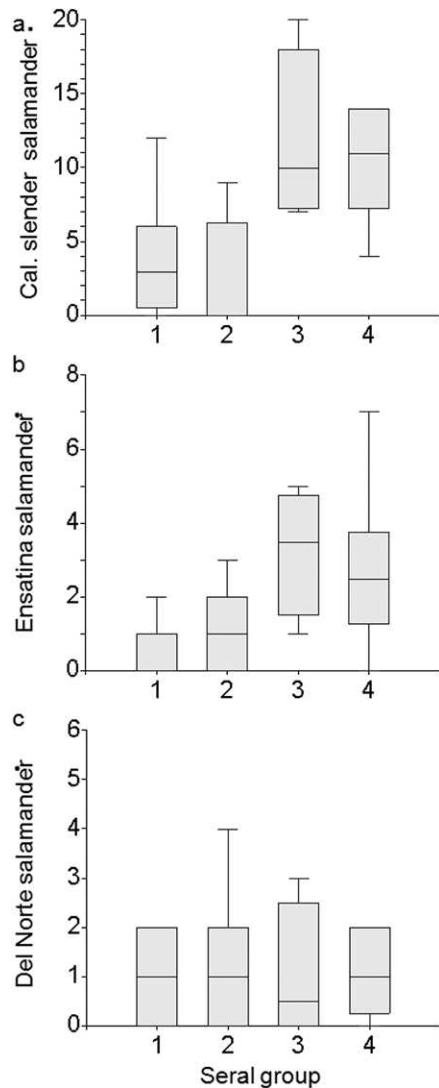


Fig. 3. Surface count of the three common plethodontid salamanders (2007 VES and 2008 coverboard data combined) in the four seral groups (see Table 1 for stand ages and the number of stands in each group). Boxes represent the mid 50% of the data, inside lines are the median, the whiskers are data 1.5 times past the mid 50%.

ing 73.8% of deviance in these data and indicated more salamanders closer to the coast and at lower elevations (Fig. 5a) (Table 4). The best models at the other scales, while not competitive with the top model (Table 4) were informative at their respective scales. The best of these was a multi-scale model explaining 59.8% of the deviance and indicating that counts of *B. attenuatus*

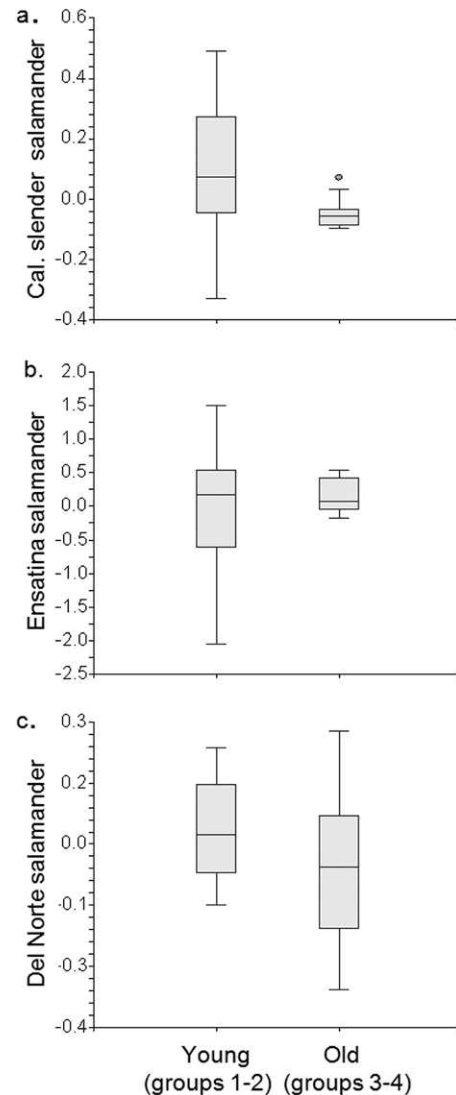


Fig. 4. Body condition indices (residuals) of: (a) *Batrachoseps attenuatus* (groups 1 and 2, $n = 134$; groups 3 and 4, $n = 245$); (b) *Ensatina eschscholtzii* (groups 1 and 2, $n = 13$; groups 3 and 4, $n = 50$); and (c) *Plethodon elongatus* (groups 1 and 2, $n = 38$; groups 3 and 4, $n = 24$); in the paired young and paired old seral groups. See Table 1 for stand age ranges. See Fig. 3 for explanation of box plots.

declined with increasing tanoak canopy (–), increased closer to the coast (easting [+]), and with greater tree size (DBH [+]) (Table 4). The best model at the site scale, explaining 50.2% of the deviance, indicated *B. attenuatus* counts decreased with greater litter depth (–), more

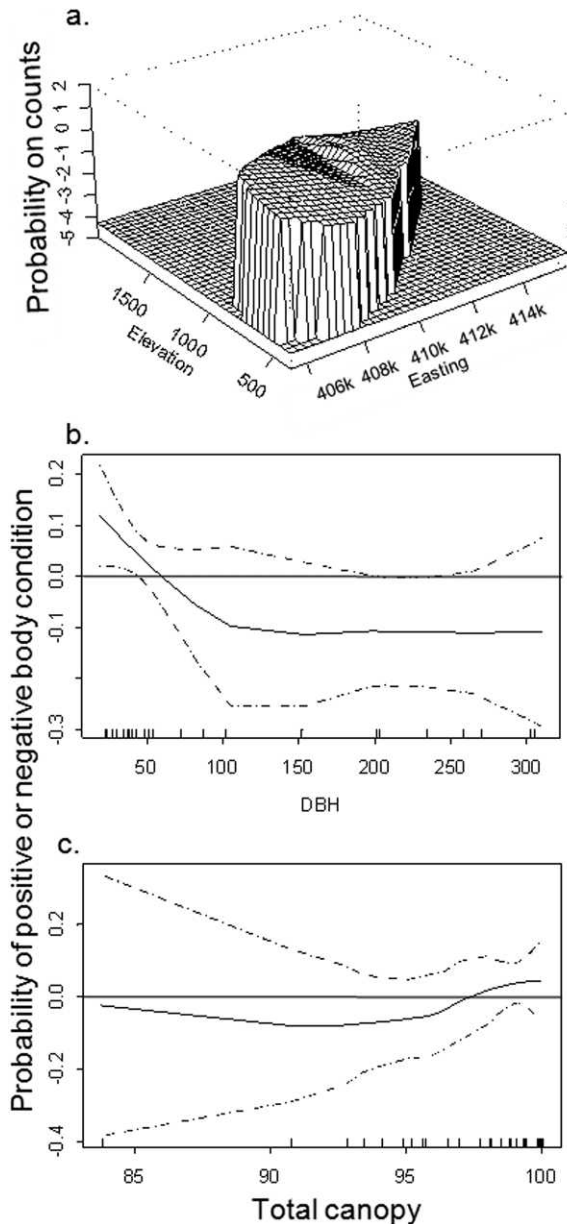


Fig. 5. The best GAM models of the estimated effects of environmental variables on probability of *Batrachoseps attenuatus* surface counts: (a) the interaction of easting and elevation (+); and on *B. attenuatus* body condition: (b) DBH (+), and (c) total canopy (+), at Mill Creek and adjacent parklands. Dotted lines on each plot are approximate 95% confidence intervals (CI). Hatch marks at the bottom represent data points. Significance is indicated when CIs fall completely above or below the no-effect line at zero (the dark horizontal line).

rock cover (–), and the presence of *P. elongatus* (–), and increased with higher soil temperature (+), and higher counts of *E. eschscholtzii* (+) (Table 4). The best model at the stand scale explained 40.1% of the deviance and indicated higher counts of *B. attenuatus* with greater redwood canopy (+) and greater tree size (DBH [+]) (Table 4).

Based on the deviance explained, the best body condition models for *B. attenuatus* were not as good as the count models, likely due to high variance in these data (Fig. 4). Regardless, the diagnostic metrics indicated they were informative with regard to environmental relationships (Table 4). Two competitive stand scale models were the best; the first indicating that body condition declined with greater tree size (DBH [–]) (Fig. 5b), and the second indicating that body condition improved with higher amounts of total canopy (Fig. 5c) (Table 4). The best site scale model indicated negative relationships between body condition and greater log cover (–), higher counts of *B. attenuatus* (–), and greater body condition of *E. eschscholtzii* (–) (Table 4); this model suggested both intra- and inter-specific competition. The best landscape scale model indicated a decline in mean body condition of *B. attenuatus* away from the coast, at higher elevations (CLV [–]), and toward the northeast (aspect [–]); and a positive effect of greater slope (+) (Table 4). Several multi-scale models were competitive with one another but poor predictors of *B. attenuatus* body condition (Table 4).

Ensatina eschscholtzii.—The best predictor of *E. eschscholtzii* counts was a multi-scale model indicating declining numbers eastward (easting [–]), and increasing numbers with greater litter depth (+) (Fig. 6a) (Table 5). A competitive site scale model indicated counts increased with greater litter depth (+) and higher *B. attenuatus* counts (+) (Fig. 6b) (Table 5). The best landscape model indicated lower counts eastward (–); the best site scale models indicated higher counts with greater litter depth (+), and higher counts of *B. attenuatus* (+), and lower counts with greater rock cover (–) (Table 5). The two best stand scale models, redwood canopy (hump-shaped) and DBH (+), and hardwood canopy (–) and DBH (+), were poor and competitive only within that scale (Table 5).

The best models for body condition of *E.*

Table 4. Best models (AIC_c) by spatial scale for surface counts and body condition of *Batrachoseps attenuatus* at Mill Creek. See Table 1 for details on individual variables. Deviance (adjD²) is comparable to R² in regression; model weights are the probability the model represents the best of those being considered for the dataset.

Scale	Model variables	n	Within-scale ΔAIC _c	Overall ΔAIC _c	Overall W _i	adjD ²
Surface count						
Landscape	Easting × Elevation	37	0.00	0.00	0.693	0.738
Stand	Redwood canopy + DBH	37	0.00	62.26	<0.000	0.401
Site	Litter + Rock + Soil temp + ENES + PLEL	37	0.00	47.08	<0.000	0.502
Multi-scale	Tanoak canopy + Easting × DBH	37	0.00	27.07	<0.000	0.598
Body condition						
Landscape	CLV + Slope + Aspect	28	0.00	4.73	0.029	0.205
Stand	DBH	28	0.00	0.00	0.315	0.153
Stand	Total canopy	28	0.12	0.12	0.297	0.034
Site	Logs + BAAT + ENES condition	23	0.00	4.54	0.033	0.241
Multi-scale	Redwood canopy + Easting × DBH	28	0.00	12.48	0.001	0.335
Multi-scale	Total canopy + Easting × DBH	28	0.13	12.61	0.001	0.180
Multi-scale	Tanoak canopy + Easting × DBH	28	0.14	12.63	0.001	0.163
Multi-scale	Hardwood canopy + Easting × DBH	28	0.15	12.63	0.001	0.159
Multi-scale	CLV + Slope + Redwood canopy + DBH + Soil temp + ENES	28	0.16	13.65	<0.000	0.202

Note: Species abbreviations are: ENES = *Ensatina eschscholtzii*; PLEL = *Plethodon elongatus*; BAAT = *Batrachoseps attenuatus*.

eschscholtzii were three competitive at the site scale: the first, *B. attenuatus* body condition, indicated the body condition of *E. eschscholtzii* declined as that of *B. attenuatus* improved (–) (Fig. 6c) (Table 5). The second model included *B. attenuatus* body condition (–) and log cover (–) (Fig. 6d); and the third model was simply log cover (–) (Fig. 6e) (Table 5). Two of these three models suggested competition between these two most common species. The two best landscape models, easting (+), and CLV (+) and slope (–), were competitive only within that scale (Table 5), and indicated improving body condition eastward and on gentler slopes. The best multi-scale model, easting (+) and DBH (+), and two stand scale models, hardwood canopy (+) and DBH (+), and redwood canopy (–) and DBH (+), were competitive only within scale (Table 5). These models indicated improved *E. eschscholtzii* body condition eastward and in older forest with a greater hardwood component, with the reverse effect in redwood-dominated coastal stands.

Plethodon elongatus.—The best predictors of counts of *P. elongatus* were three competitive multi-scale models: CLV (+), slope (u-shape), redwood canopy (+), and rock cover (+) (Fig. 7a); slope (–), redwood canopy (+), rock cover (+), and *B. attenuatus* count (–), and CLV (–), slope (–), redwood canopy (+), rock cover (+) and *B. attenuatus* count (–) (Table 6). The best site scale model, while not competitive with the top

models, was positive with more rock (+) and negative with *B. attenuatus* counts (–) (Table 6). Three landscape scale models were competitive only at that scale: easting (+) and slope (–), CLV (humped-shape) and slope (–), and elevation (+) and slope (–) (Table 6), and indicated higher counts eastward, at higher elevations, and on gentler slopes. The best stand model, also not competitive with the top models, indicated a positive relationship with greater tanoak canopy (+) and trees up to 200 cm (DBH [humped-shape]) (Table 6).

The best predictors of body condition of *P. elongatus* were three competitive stand scale models: redwood canopy (–) (Fig. 7b), tanoak canopy (hump-shape) (Fig. 7c), and DBH (u-shaped) (Fig. 7d) (Table 6); the latter model indicating body condition was lowest in stands with the mid-size range of trees. A site scale model and three at the landscape scale, while competitive only at their respective scales, were informative with regard to *P. elongatus* body condition (Table 6). The site scale model indicated higher body condition with more rock cover (+), with the opposite effect with higher counts of *B. attenuatus* (–), suggesting inter-specific competition. The best landscape scale models, elevation (u-shape) and slope (+), easting (u-shape) and slope (+), and CLV (u-shape) and slope (Table 6), indicated *P. elongatus* with the higher mean body condition occurred at mid elevation

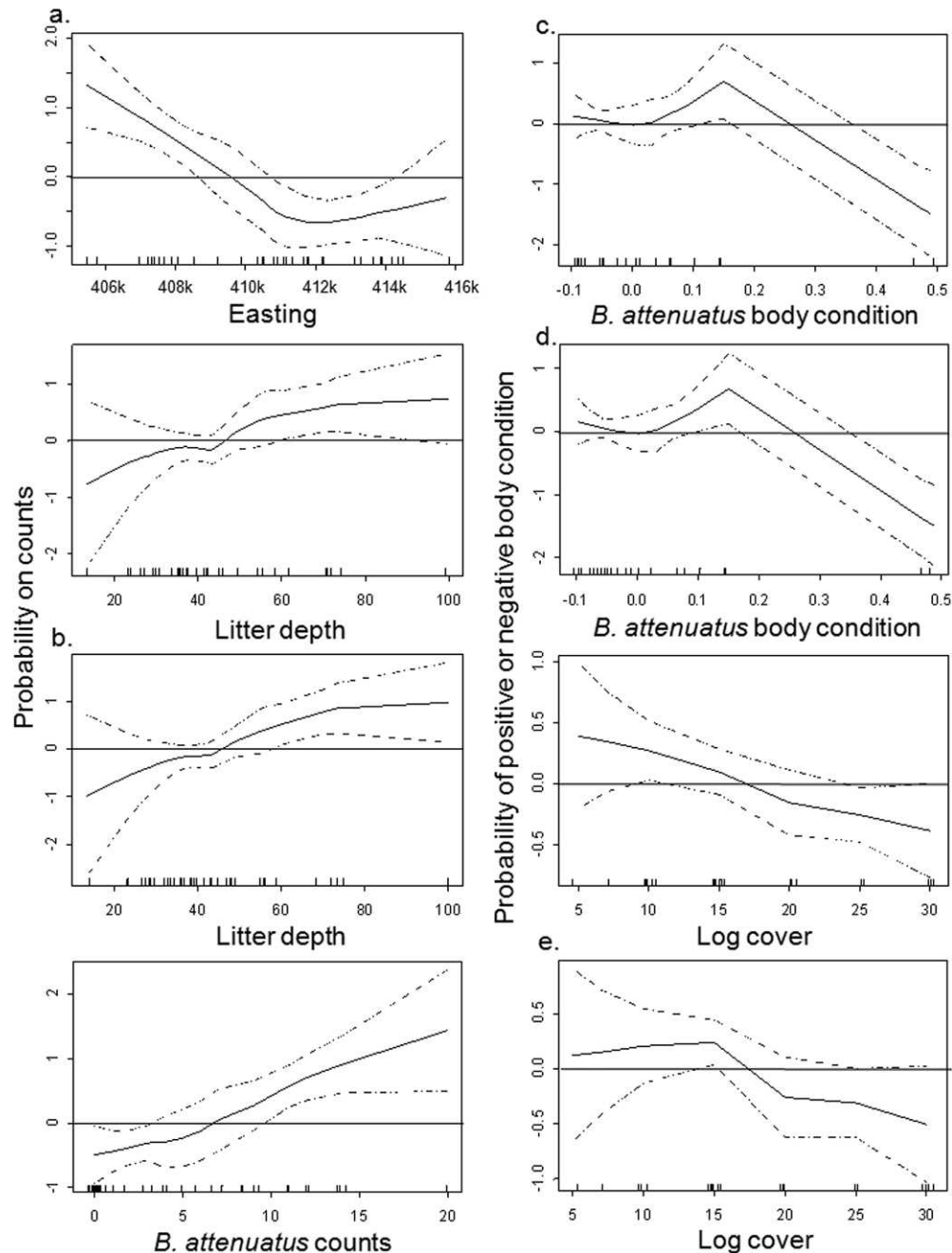


Fig. 6. The best GAM models of the estimated effects of environmental variables on probability of *Ensatina eschscholtzii* surface counts: (a) easting (–) and litter depth (+), and (b) litter depth (+) and *Batrachoseps attenuatus* counts (+), and on *E. eschscholtzii* body condition: (c) *B. attenuatus* body condition (–); (d) logs (–) and *B. attenuatus* body condition (–); and, (e) logs (–), at Mill Creek and adjacent parklands. See Fig. 5 for an explanation of figure details.

Table 5. Best models (AIC_c) by spatial scale for surface counts and body condition of *Ensatina eschscholtzii* at Mill Creek. See Table 1 for details on individual variables. Deviance (adjD²) is comparable to R² in regression; model weights are the probability the model represents the best of those being considered for the dataset.

Scale	Model variables	N	Within-scale Δ AIC _c	Overall Δ AIC _c	Overall W_i	adjD ²
Surface count						
Landscape	Easting	37	0.00	2.64	0.104	0.511
Stand	Redwood canopy + DBH	37	0.00	12.58	<0.000	0.326
Stand	Hardwood canopy + DBH	37	0.22	12.80	<0.000	0.301
Site	Litter depth + BAAT	37	0.00	1.19	0.215	0.452
Site	Litter depth + Rock + BAAT	37	1.94	3.13	0.082	0.443
Multi-scale	Easting + Litter depth	37	0.00	0.00	0.391	0.495
Body condition						
Landscape	Easting	27	0.00	2.95	0.079	0.034
Landscape	CLV + Slope	27	0.16	3.11	0.073	0.186
Stand	Hardwood canopy + DBH	27	0.00	8.00	0.006	0.000
Stand	Redwood canopy + DBH	27	0.20	8.19	0.006	0.263
Site	BAAT condition	23	0.00	0.00	0.347	0.232
Site	Logs + BAAT condition	23	0.87	0.87	0.225	0.341
Site	Logs	27	1.58	1.58	0.158	0.144
Multi-scale	Easting + DBH	27	0.00	6.82	0.011	0.086

Note: BAAT = *Batrachoseps attenuatus*.

at Mill Creek, and mid-distance from the coast on steeper slopes. The best multi-scale model, also not competitive with the top models, consisted of redwood canopy (–), *B. attenuatus* body condition (–), and *E. eschscholtzii* body condition (–) (Table 6). This model suggested competition between *P. elongatus* and both of the other common species, and an avoidance of redwood dominated stands, possibly because these other species have a competitive advantage in redwood forest.

DISCUSSION

During the initial analyses it was apparent that our primary question regarding salamanders and seral relationships was confounded by the fact that mature and old-growth sites were in closer proximity to the Pacific Ocean than the young forest sites. This spatial juxtaposition, the higher and more dependable humidity nearer the coast, and the critical role of moisture in the physiology of plethodontid salamanders and its link with their ecology (Feder 1983), made it imperative that we account for the effects of marine moisture (i.e., fog and higher relative humidity) in our investigation of relationships with forest succession. Consequently, we used ANCOVA to test the relative effects of coastal proximity (a moisture surrogate) and succession on the three most common salamander species. We found significant differences in the counts of *B. attenuatus* and

E. eschscholtzii, but not *P. elongatus*, between young and old seral stages; however, only *B. attenuatus* showed significant influences of coastal proximity on their counts. Finding higher counts for two of three species on older stands was not unexpected, as this result is consistent with numerous retrospective studies of forest succession and forest dependent amphibians (reviewed by deMaynadier and Hunter 1995); and with several recent experiments (Homyack and Haas 2009, Semlitsch et al. 2009). The negative influence of easting (i.e., less ambient moisture inland) on *B. attenuatus* distributions has also been noted before (Welsh and Lind 1991).

Of the three species, *B. attenuatus* showed the strongest responses along both the spatial and successional gradients, with both the ANCOVA and the modeling exercise indicating coastal proximity and succession positively influenced surface counts; with the interaction of easting and elevation the best predictor of those independent variables we tested (Table 4). Given the characteristic development of cooler, moister, and more stable microclimates with advancing forest succession (Chen et al. 1999), and the close relationship between redwood forest and the coastal fog regime (Dawson 1998, Johnstone and Dawson 2010), the relative influences of these two phenomena are a particular challenge to discern in the redwood biome. Evidence of the abiotic/biotic interrelationship with fog is appar-

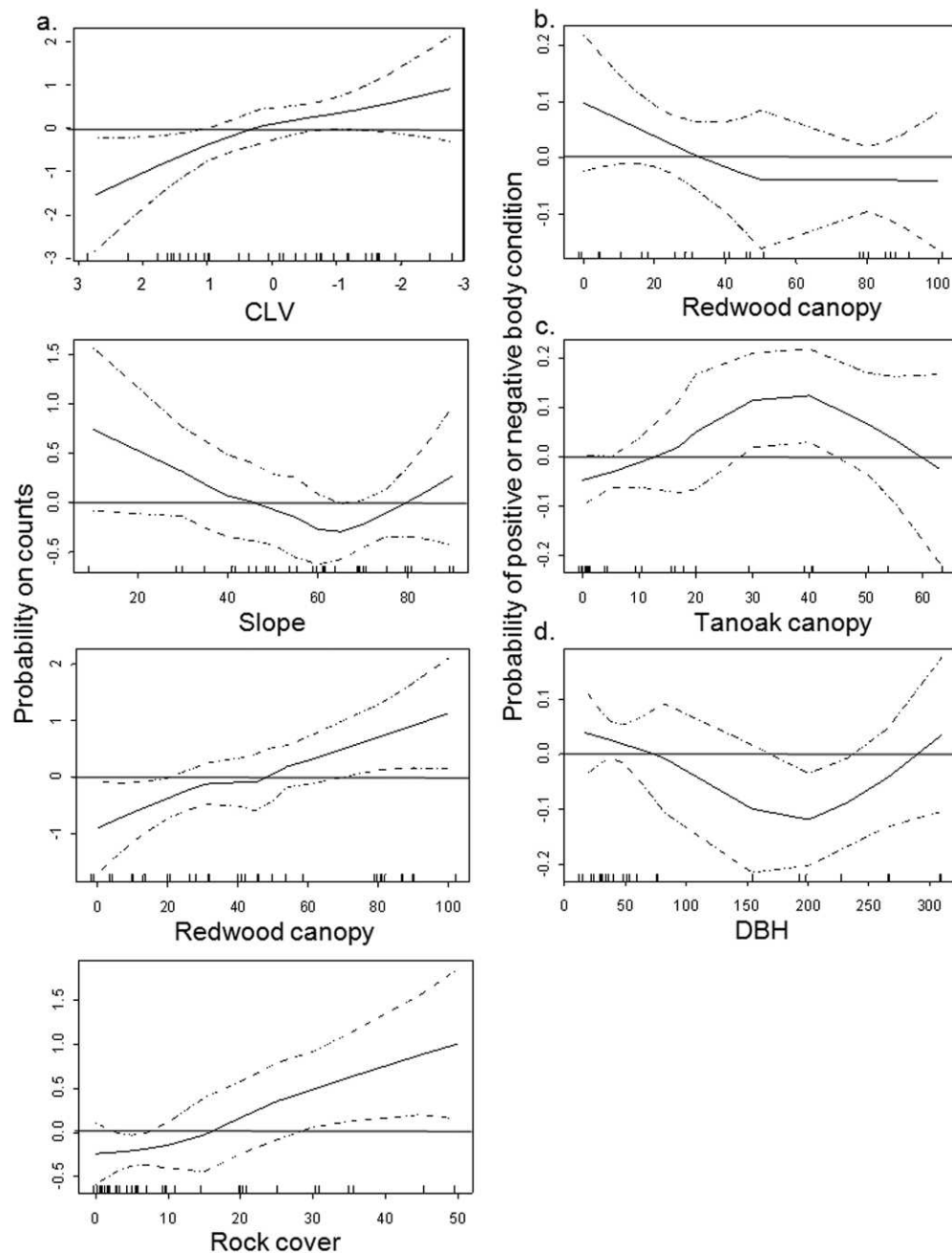


Fig. 7. The best GAM models of the estimated effects of environmental variables on probability of *Plethodon elongatus* counts: (a) CLV (+), slope (–), redwood canopy (+), and rock (+); and on *P. elongatus* body condition: (b) redwood canopy (–); (c) tanoak canopy (hump-shape); and (d) DBH (u-shape), at Mill Creek and adjacent parklands: See Fig. 5 for an explanation of figure details.

ent with much of the redwood forest flora (e.g., Fischer et al. 2008, Limm et al. 2009) where marine-generated fog can comprise on average 34% of the annual hydrologic input in the form of

fog drip from the trees themselves (Dawson 1998). *B. attenuatus* is the most abundant salamander in redwood forests (Cooperrider et al. 2000), and the moisture/fog linkage in these

Table 6. Best models (AIC_c) by spatial scale for surface counts and body condition of *Plethodon elongatus* at Mill Creek. See Table 1 for details on individual variables. Deviance (adjD²) is comparable to R² in regression; model weights are the probability the model represents the best of those being considered for the dataset.

Scale	Model variables	n	Within-scale Δ AIC _c	Overall Δ AIC _c	Overall W_i	adjD ²
Surface count						
Landscape	Easting + Slope	37	0.00	6.50	0.017	0.191
Landscape	CLV + Slope	37	1.08	7.59	0.010	0.147
Landscape	Elevation + Slope	37	1.19	7.70	0.009	0.145
Stand	Tanoak canopy + DBH	37	0.00	11.99	0.001	0.065
Site	Rock + BAAT	37	0.00	5.07	0.034	0.167
Multi-scale	CLV + Slope + Redwood canopy + Rock	37	0.00	0.00	0.435	0.336
Multi-scale	Slope + Redwood canopy + Rock + BAAT	37	0.66	0.66	0.313	0.284
Multi-scale	CLV + Slope + Redwood canopy + Rock + BAAT	37	1.87	1.87	0.171	0.289
Body condition						
Landscape	Elevation + Slope	27	0.00	2.37	0.062	0.000
Landscape	Easting + Slope	27	<0.00	2.37	0.062	0.000
Landscape	CLV + Slope	27	<0.00	2.28	0.062	0.000
Stand	Redwood canopy	27	0.00	0.00	0.204	0.092
Stand	Tanoak canopy	27	<0.00	<0.00	0.204	0.091
Stand	DBH	27	0.03	0.03	0.201	0.037
Site	Rock + BAAT	27	0.00	2.37	0.062	0.000
Multi-scale	Redwood canopy + BAAT condition + ENES condition	18	0.00	5.35	0.014	0.083

Note: Species abbreviations are: BAAT = *Batrachoseps attenuatus*; ENES = *Ensatina eschscholtzii*.

forests may be important for their surface activities because their small size and elongate body form renders them particularly prone to desiccation. A similar interpretation likely explains the negative effect of increased elevation in the best model for *B. attenuatus* counts, as the higher elevation sites are further inland at MC, receive less fog, and are drier compared to sites at lower elevations. This relationship with a moisture continuum is also reflected in the more extensive hardwood components on more interior sites where *B. attenuatus* becomes less common. MC is very near the northern extent of the *B. attenuatus* range, which comprises a narrow coastal distribution that reaches just north of the Oregon border (Stebbins 2003). This range corresponds closely with the northern extent of redwood forest (Noss 2000), with both trees and salamanders likely limited by drier, warmer conditions eastward where the terrain rises rapidly, and north where the forest type changes abruptly.

Increased moisture and lower more stable temperatures are associated with advancing succession in multiple forest ecosystems (Brosofske et al. 1997, Chen et al. 1999, Zheng et al. 2000, Welsh et al. 2005, Brooks and Kyker-Snowman 2008). This commonality in the successional process in multiple forest ecosystems

would suggest that this relationship exemplifies an abiotic and biotic union, derived evolutionarily, linking late-seral forests and much of their unique constituent biota (i.e., coevolution). The complex structure unique to these forests provides the specific range of microclimatic conditions required by late-seral-adapted organisms like plethodontid salamanders with their highly conservative niches (e.g., Kozak and Wiens 2010). Examples of similar relationships with advanced states of forest succession and resident biota are found from the forest floor (e.g., Willett 2001) into the canopy (e.g., Cary et al. 1992, Hamer and Nelson 1995, Spickler et al. 2006). These niche-defining ecological relationships that derive from evolutionary processes (Wiens and Graham 2005) render moisture-late-seral linkages with specific biota, in any practical sense, inseparable. Such interrelationships have been repeatedly demonstrated for amphibians (e.g., Welsh 1990, Karraker and Welsh 2006, Semlitsch et al. 2009), many of whom are inextricably linked to mild, stable temperatures and high ambient moisture by their physiological limits (Wieser 1991, Feder and Burggren 1992). The essential role of moisture in the physiology and ecology of plethodontid salamanders is particularly well established (Spotila 1972, Feder 1983, Grover 2000, Homyack et al. 2011), and is likely the

result of their late Jurassic evolution into a primarily terrestrial clade (Vieites et al. 2007); with most members entirely lacking aquatic life stages (Wake and Hanken 1996).

Body condition has proven highly informative for examining the relative status of amphibian populations in forested habitats (e.g., Todd and Rothermel 2006). Karraker and Welsh (2006) reported higher body condition of *E. eschscholtzii* in un-thinned versus thinned interior Douglas-fir dominated late-seral forest in northern California. Welsh et al. (2008) reported higher body condition in the Siskiyou Mountains salamander (*Plethodon stormi*) in mature compared with young forest. Interestingly, the only species whose counts varied relative to the geography (*B. attenuatus*), showed no changes in body condition along this gradient. However, both of the other target species had significant differences in mean body condition along the geographic gradient (CLV); *E. eschscholtzii* had higher condition toward the coast and at lower elevations, whereas *P. elongatus* showed the opposite effect. Ultimately, all three species had higher mean body condition on young compared with old stands; with both *B. attenuatus* and *E. eschscholtzii* showing significantly greater variance among individuals on young stands (Fig. 4). These body condition results indicated significant differences in physiological states in each population; conditions that are likely the result of differences in the competitive regimes under which they live and that relate directly to their relative fitness. We acknowledge our evidence for competition is correlative, and it is possible that fine-scale niche separation could promote co-existence with variation in relative abundances and body condition without competition. However, we propose that lower means and variances in body condition on older stands, in conjunction with the higher counts (Fig. 8), is best explained as the result of increased competition on these stands. The models that show increased reciprocal intra- and interspecies interactions in both counts and body condition on older stands further support the interpretation of variation in competition among populations along the successional gradient (e.g., Miller and terHorst 2012). Older stands with three times the number of individual salamanders, and low variance in body condition, indicate a more rigorous and more stable

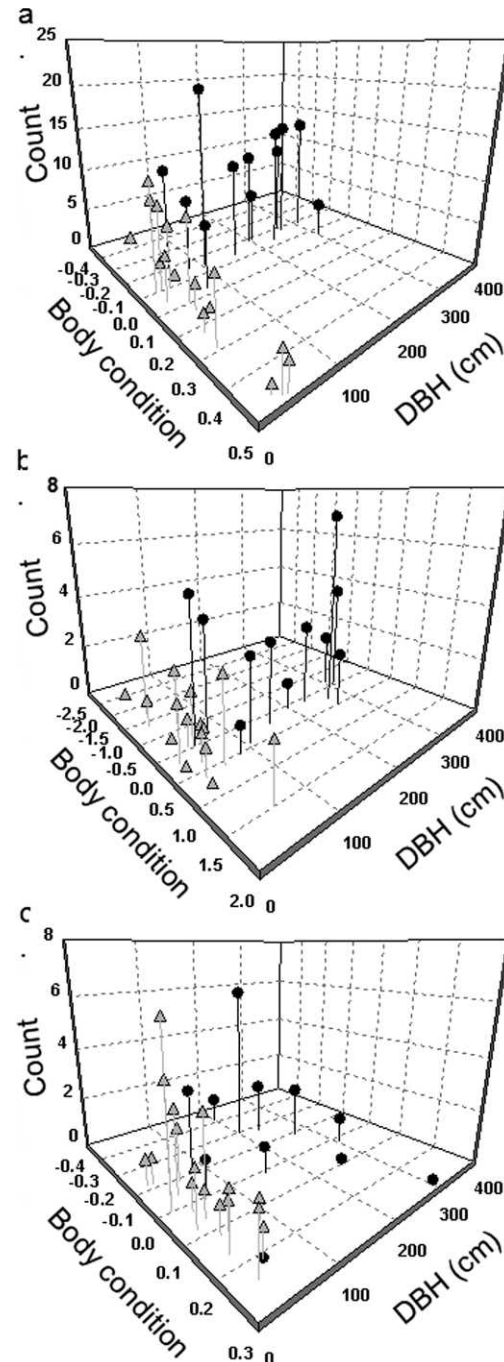


Fig. 8. Comparison of count, body condition index (residuals), and tree diameter at breast height (DBH) on the paired young stands (triangles) and paired old stands (circles) for: (a) the California slender salamander (*Batrachoseps attenuatus*); (b) *Ensatina eschscholtzii*; and (c) the Del Norte salamander *Plethodon elongatus*.

selective regime, where the low individual variability of so many more individuals equates to greater overall fitness in these much larger populations. Primary productivity in older and more stable forest environments, particularly at the ground level with far lower ambient light, is markedly reduced (Perry 1994), resulting in greater competition for fewer invertebrate resources among more individual salamanders, which results in lower mean body condition and narrower variance (Fig. 8). By contrast, the much greater variance among far fewer individuals indicates that fitness is highly variable and with fewer individuals, fitness of the population is far lower on the younger stands.

While the less variable mean body condition we found in *B. attenuatus* and *E. eschscholtzii* in late-seral redwood forest is likely the result of greater competition for more limited resources among more numerous conspecifics, and more individuals of other salamander species in these much larger populations (e.g., Jaeger et al. 1998), the greater variance in body condition among individuals of *B. attenuatus* and *E. eschscholtzii* on young stands indicates different factors are influencing these populations. Depending upon site conditions within particular young stands (and reflective of the more extreme conditions across young sites [e.g., more hardwoods, reduced redwood canopy, less litter; see Table 1]), the more robust (more fit) individuals are likely benefiting from reduced competition from conspecifics (and other species) on young stands where conditions are most amenable for surface foraging. This interpretation is supported by the modeling which indicated that the intensified reciprocal relationships, indicative of competition, in both counts and body condition among these species is occurring on the older seral sites (Tables 4–6). These findings also appear consistent with the intermediate disturbance hypothesis (Connell 1978) where the amount of disturbance on some post-harvest stands has created optimal conditions for the resident salamanders at the time we sampled. In contrast, individuals with poor body condition (less fit) are likely responding to temporal and spatial surface conditions on those young stands less amenable for surface foraging regardless of the lack of competition. This interpretation is also consistent with documented changes along forest

seral continua where young stands show much greater variation in microclimatic variables (e.g., Brosnoff et al. 1997, Chen et al. 1999, Zheng et al. 2000, Brooks and Kyker-Snowman 2008); conditions that often exceed the physiological limits of plethodontid salamanders (Feder 1983, Homyack 2010). Homyack et al. (2011) reported greater variation in body condition for plethodontid salamanders on their most disturbed sites (albeit with a small sample) in the eastern U.S.; where they also found the least variation on unharvested control sites (Homyack et al. 2011: Fig. 5). Similarly, Welsh et al. (2008) reported significantly lower mean body condition for *P. elongatus* on a late-seral Douglas-fir site with the largest population of the 57 sites they studied. Consistent differences in body condition along seral continua in multiple studies showing greater uniformity (lower variance) among individuals in larger populations in older forests suggests that population fitness is more stable overall in late-seral compared with young forest as the result of greater competition (e.g., Miller and terHorst 2012); evidencing how the natural landscape can shape the genetic landscape (sensu Gavrillets 2004).

Plethodon elongatus was fairly common across the landscape of MC, showing a greater dependence on rock substrates than on landscape or other stand attributes. Our data indicate that this species was slightly more common in early seral redwood forest, particularly with a hardwood component (see also Welsh et al. 2006), where it also had higher mean body condition. This species appears little affected by timber harvesting in the redwoods (Diller and Wallace 1994); however, because this is not the case with *P. elongatus* in interior regions (Welsh and Lind 1995, Welsh et al. 2006), it appears that the redwood biome may have a positive effect on relative abundances similar to other redwood associated biota (Fischer et al. 2008, Limm et al. 2009). Based on differences in numbers of the species we found across the MC watershed, and our models, it appears that *P. elongatus* responds negatively to *B. attenuatus* or *E. eschscholtzii*, especially in older stands, while their relationship with the young seral sites (Fig. 3) suggests they have a competitive advantage there, possibly due to a greater physiological tolerance; an advantage that appears to lessen closer to the

coast.

Finding higher abundances of plethodontid salamanders at the upper ends of seral continua is consistent with the majority of studies on succession and forest amphibians (deMaynadier and Hunter 1995, Homyack and Haas 2009, Semlitsch et al. 2009). Views to the contrary (e.g., Kroll et al. 2009) appear to not accept the preponderance of the evidence (Welsh et al. 2009), and are contrary to a recent meta-analysis (Tilghman et al. 2012). The age break that divided our sites at approximately 60 years, while somewhat artificial due to our use of forest age categories pre-determined by disturbance history; nonetheless suggests a recovery time for salamanders populations at or near 60 years of age in redwood forest. Sixty years is at the high end of the recovery time estimated for plethodontid populations from timber harvest in the Appalachians (30–60 years; Petranka 1999, Hyde and Simons 2001, Homyack and Haas 2009), but within the age range reported for recovery in common forest types of the Pacific Northwest (30–100 years; Welsh et al. 2008). Tilghman et al. (2012) reported a continuing decline in negative effect size with year post-harvest, and determined that response ratios still corresponded to declines of 24% and 20% at 40 years and 80 years post-harvest, respectively; suggesting incomplete recovery of populations even at those ages. However, they did acknowledge that viable populations may exist without complete recovery (Tilghman et al. 2012:6).

The ecological roles of salamanders are fairly well known qualitatively (Davic and Welsh 2004); however, their effects on critical forest ecosystem processes of conservation concern such as nutrient cycling (e.g., Burton and Likens 1975b), litter decomposition and soil-building are only now coming to light (e.g., Wyman 1998, Walton et al. 2006, Best 2012). Just how these processes are influenced by salamander richness and relative abundances (Schmidt 2008) are as yet unknown. Nonetheless, the huge numbers of woodland salamanders found across forest ecosystems of North America (see Introduction) suggest an ecological dominance in trophic webs in these forests, (e.g., Terbough and Estes 2010); one that influences leaf litter decomposition and forest-floor carbon pathways (Wyman 1998) and comprises an enormous prey base for other fauna

(e.g., Brodie and Brodie 1980, Ducey and Brodie 1983).

CONCLUSIONS

Using amphibians as indicators of ecosystem status is gaining acceptance as researchers test and verify their usefulness and applicability (e.g., Perkins and Hunter 2006, Welsh and Hodgson 2008, Johnson et al. 2009). Karr (2006) noted "... organisms are integrators of all that is happening in a watershed ..."; while he was referring primarily to aquatic systems, his statement is no less true for terrestrial organisms, especially those closely linked with the landscape (=highly philopatric). Given the ecological dominance of woodland salamanders in North American forests (Davic and Welsh 2004), and their significant top-down effect on shredder and decomposer invertebrates that slows litter decomposition and facilitates greater nutrient cycling and carbon sequestration (Wyman 1998, Best 2012); the suppressed populations in so much of early seral forest likely reduces nutrient cycling and carbon storage potential on these landscapes, reducing the beneficial effects of these critical ecological services.

Likens et al. (1978) reported a recovery time of 65 years for forest floor organic matter in a northern hardwood forest and Michels and Russell (2012) reported recovery of stand density, canopy cover, and understory plant species richness in post-harvest redwood forest approached old-growth conditions within 40 to 80 years. This time frame is very similar to recovery times reported for many terrestrial salamander populations, suggesting that a return to their pre-disturbance levels could serve as a useful index of forest recovery (Tilghman et al. 2012:7). Primary forests sequester the most atmospheric carbon (Luyssaert et al. 2008, Hudiburg et al. 2009; Keith et al. 2009), and support the planet's greatest terrestrial biodiversity (Lindenmayer 2009). The surface abundances of woodland salamanders and their relationship to states of post-harvest seral recovery in temperate forests of North America, along with other useful metrics of their status (Welsh et al. 2008), in conjunction with their important roles in vital ecological processes (Davic and Welsh 2004), are strong arguments for their use as biometrics of

ecosystem integrity and the enhanced ecological services of primary forest (Odum 1969). Regardless of the specific attributes driving their numbers (e.g., moisture, litter depth, canopy closure, or some combination), positive links with multiple attributes of advancing succession and the associated changes in structural features, in conjunction with high abundances, and less variable body condition, indicate that *B. attenuatus* and *E. eschscholtzii* are legitimate metrics of advancing succession, and useful quantitative biometrics of ecosystem recovery at MC (e.g., Odum 1969, Welsh and Droege 2001).

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