



Old-Growth Redwood Forest Canopy Arthropod Prey Base for Arboreal Wandering Salamanders: A Report Prepared for the Save-the-Redwoods League.

Michael A. Camann, Karen L. Lamoncha, and Clinton B. Jones

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Researcher Clint Jones inspecting arthropod traps on an old-growth redwood canopy humus mat. The white spot near the base of the trunk his hand is resting on is a pitfall trap. Another pitfall trap and a cluster of litter bags are obscured by *Polypodium scouleri* fronds. This is a medium sized humus mat that extends outside the photo frame at the lower middle right.

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Abstract

Forest canopy arthropods comprise greater than 80 percent of the biological diversity in temperate forests and are vital elements of healthy forest ecosystems, yet we know very little about the canopy arthropods that are part of our remaining redwood forests. Old-growth redwood forests have structurally unique canopies resulting from the great size, age, and architectural complexity of mature redwood crowns, especially in the relatively mesic coastal environment that we studied. This architectural complexity permits retention of significant amounts of litter and organic debris within the forest canopy, creating unique "habitat islands" of arboreal humus. These canopy humus accumulations support a diverse assemblage of epiphytic plants and animals, including a rich assemblage of arthropods normally associated with forest soils. Arboreal populations of the wandering salamander use these mats and their invertebrate fauna as habitat and food resources.

We investigated the biodiversity and assemblage organization of canopy humus associated arthropods in fifteen mats from five old-growth redwood trees at Prairie Creek Redwoods State Park. The mats we studied ranged in area from approximately 6,597 cm² to 450,819 cm² and occurred from 27 m above the forest floor to nearly 84 m. We sampled arthropods regularly for almost two years using flight intercept traps, pitfall traps, humus cores, and litter bags filled with redwood foliage. We compared our results to similar samples obtained on the forest floor.

The laboratory phase of this project was incomplete at the time of this report, so only a portion of the samples were processed and only coarse taxonomic determinations made, but nonetheless several patterns of assemblage structure were evident. Collembola

¹ Address correspondence to M. A. Camann, Associate Professor of Zoology, Institute for Forest Canopy Research, Department of Biological Sciences, Humboldt State University, Arcata, CA. E-mail to: mac24@humboldt.edu.

dominated canopy humus mat arthropod communities, with decreased numbers of sub-dominant Acari as height above the forest floor increased. Biodiversity also decreased with height. Total arthropod abundance in the redwood canopy was lower than on the ground, but within-canopy abundance responded only weakly to increased height.

Canopy arthropod assemblage organization appeared most strongly influenced by dispersal limitations and life-history characteristics of canopy-dwelling arthropods. Our preliminary results suggested that old-growth redwood crowns and humus mat arthropod assemblages were an ideal model system for exploring the ecological effects of island-biogeographic parameters upon arthropod community structure and ecosystem roles. Old-growth redwood forest canopies offer a unique opportunity to study ecological interactions paralleling those structuring communities at global scales.

Finally, we provided the first report of the infrequent, but apparently ubiquitous occurrence of a semi-aquatic crustacean at PCRSP, both in forest floor litter and in canopy humus to 84 m height.

Acknowledgments

We gratefully acknowledge the support and assistance of the Save-the-Redwoods League, Global Forest, Inc., the Humboldt State University Institute for Forest Canopy Research, and Dr. Stephen Sillett.

Introduction

Redwood (*Sequoia sempervirens*) forest canopy ecology is poorly understood at present. There are no data regarding arthropod assemblages in old-growth redwood forest canopies despite the known abundance and importance of arthropods in other forest canopy ecosystems, including other old-growth forest canopies in the temperate Pacific Northwest. Arthropods typically comprise over 80 percent of the biological diversity in such forests.

Redwood forests are confined to northwestern California and southwestern Oregon. Redwood was once the dominant conifer throughout the north coastal fog belt, where the summer dry season is moderated by persistent maritime fog, and it remains dominant in remnant refugia, the most extensive of which are now public lands. Mature

redwoods have massive limbs, branch junctions, and complex crown architecture that retains deep arboreal litter and humus accumulations and provides abundant colonization sites for epiphytes.

Such humus accumulations (hereafter "mats") occur on branch surfaces and at the bases of trunk reiterations within redwood crowns. They are important habitat and nutritional resources for "soil associated" forest canopy arthropods. Litter mats include fresh redwood litter and woody debris, humus accumulations, a characteristic epiphyte flora, and a unique community of canopy fauna. Detritus mats in redwood crowns range from small accumulations comprising a few cubic centimeters to large mats containing many cubic meters of suspended organic debris. Leather fern (*Polypodium scouleri*) and mosses usually dominate epiphyte mats. Ericaceous shrubs also occur as arboreal epiphytes in redwood canopies, as do other conifers and deciduous trees and shrubs.

Redwood debris mats are unique resources supporting complex assemblages of invertebrate and vertebrate fauna many meters above the forest floor. The invertebrate community is overwhelmingly dominated by arthropods. The abundance and diversity of insects and other arthropods in humus mats are influenced by a variety of habitat parameters, some of which are unique to redwood canopy ecosystems. Arthropod taxa are often habitat specialists that partition shared resources according to their nutritional and physical habitat requirements. Evidence from other forest systems suggests that arthropod assemblages in forest canopies differ significantly from those inhabiting the forest floor and sub-canopy strata. Arthropod assemblages occupying arboreal humus mats also differ from those using other forest canopy resources, i.e. live foliage. The spatial distribution of arthropods within forest canopy ecosystems is often highly aggregated. For detritus-associated arthropods, humus mat size and within-crown position influence assemblage organization. Large mats offer greater habitat volume for colonization than do smaller mats, provide richer food webs, offer a greater variety of refugia, and retain more water, which buffers microclimate extremes. Mats near the edge of the crown are likely to experience greater microclimate variation than those near the center, for example being more prone to desiccation during dry weather, and to wind disturbance during storms.

Canopy arthropod assemblages also respond to changing seasons and ambient temperature/moisture regimes, although it is likely that maritime conditions prevailing in coastal redwood forests moderate this to some degree. Humus mats themselves can also moderate microclimate variation to produce habitat conditions substantially different from those occurring even short distances away, i.e. by prolonging water release and enhancing thermal mass.

Finally, some arthropod taxa spend only a portion of their life-cycles associated with arboreal humus mats or in other portions of forest canopies. These temporal and spatial influences upon arboreal arthropod assemblage structure create a diverse and dynamic redwood forest canopy community.

Mites (Acari), small spiders (Aranae), pseudoscorpions (Pseudoscorpiones), millipedes (Diplopoda), springtails (Collembola), and other arthropods are abundant in arboreal humus mats and within epiphyte assemblages. Canopy arthropod community organization is likely influenced by the dispersal capabilities of individual taxa and by the specific adaptations predisposing some arthropods to succeed under the habitat extremes of forest canopies.

Structural variation within canopy arthropod communities likely affects prey selection and habitat utilization by arboreal populations of the wandering salamander (*Aneides vagrans*), a heretofore unknown vertebrate occupant of the Earth's tallest forest canopy ecosystem. The wandering salamander inhabits moist coniferous forests in northern California, western Oregon, and Vancouver Island, British Columbia. It lives under loose bark, in rooting logs, and within organic debris. Wandering salamanders consume a variety of small to medium-size arthropods depending upon prey availability, salamander size, and season. Prey are typically partitioned by size, with larger salamanders selecting bigger prey. Wandering salamanders have recently been reported inhabiting arboreal humus mats, decaying wood, and bark crevices in old-growth redwood crowns with relatively high annual rainfall or seasonal fog interception. We have found all life-history stages of *A. vagrans* within the redwood forest canopy suggesting permanent residence rather than temporary or migratory habitat exploitation.

Prey selection by arboreal wandering salamanders might depend upon relative prey abundance or it might reflect intrinsic feeding preferences superimposed upon the

available prey base of arboreal arthropods. Ground-dwelling *A. vagrens* are generalist feeders, so arboreal individuals might simply select the most abundant arthropod prey. Arthropod community variation might produce dietary differences between arboreal populations and ground-dwelling conspecifics in the same forest. This might influence arboreal habitat suitability for wandering salamander populations. There is much to be learned about the trophic preferences of *A. vagrens* and the influence of resource quality on arboreal habitat suitability.

We wished to address this need by meeting three primary research objectives. First, we hoped to determine the dominant arthropod taxa and the composition of arthropod assemblages inhabiting humus mats in old-growth redwood forest canopies. At the time this study was undertaken it appeared that large humus mats were the primary habitat for arboreal wandering salamanders. Although salamanders have subsequently been found in diverse locations throughout old-growth redwood crowns, large humus mats remain an important resource, and perhaps a vital one. We also quantified the effects of humus mat habitat parameters upon the organization of arthropod communities inhabiting them. Finally, we hoped to determine which arthropods actually comprise the primary prey base of arboreal wandering salamander populations in redwood forest canopies.

These objectives will enhance our understanding of *A. vagrens* life-history and our knowledge of canopy ecology in old-growth redwood forests. Analyses of prey selection by arboreal wandering salamanders might provide insight into the advantages of arboreality for this species and into the role of redwood old-growth in extending or maintaining its habitat range. For example, salamanders that climb plants were shown to be more successful than conspecifics that forage on the forest floor. This might be true for *A. vagrens* as well, since seasonal moisture variability limits salamander mobility and foraging range. Arboreal wandering salamanders likely benefit from high densities of arthropods in redwood canopy humus mats by expending less energy foraging and by avoiding desiccation. Worldwide declines in amphibian populations provide additional urgency for improved understanding of salamander survival strategies in redwood forests.

Preservation and management of the remaining old-growth redwood forests are informed by our understanding of the importance of habitat diversity and integrity,

especially when canopy habitats are utilized by rich taxonomic assemblages including vascular and non-vascular epiphytes, invertebrates, and vertebrates. Although this investigation focuses upon the prey base for arboreal salamanders, it is important to note that these arthropods also serve as trophic resources for other canopy residents and as vital elements of the nutrient processing and mobilization systems in redwood forests.

Very little information is available regarding redwood canopy ecosystems in general and none is available about arboreal soils and their associated fauna, despite the ecological importance of these systems in redwood forest communities. Improved understanding of the ecosystem roles played by canopy humus mats and their fauna will foster management efforts to preserve this important component of habitat heterogeneity in mature redwood forests.

Materials and Methods

Study sites and canopy access. Five old-growth redwood trees were selected on an alluvial flat in Prairie Creek Redwoods State Park (PCRSP) in Humboldt County, CA. Trees were selected on the basis of stand dominance (> 80m height, > 3m DBH) and the presence of at least three suitably large humus mats at approximate lower, middle, and upper crown locations, yielding 15 humus mats sampled at monthly and bimonthly intervals. Although there were no *a priori* limits imposed upon mat size, in practice their selection was constrained by the need for sufficient surface area to deploy the arthropod sampling devices (described below). Tree crowns were accessed using non-destructive single-rope techniques. Canopy access and arthropod sampling were suspended during the nesting season of the marbled murrelet, a federally listed endangered bird that is resident at PCRSP and reproductively dependent upon coastal old-growth forests.

The study grove was located near Boyes Creek and contained the well known Cal-Barrel Tree. The selected trees were designated Prometheus (PR), Pleiades I (PL), Atlas (AT), Ballantine (BA), and Bell (BE) along an approximate north-south transect. Tree heights were measured, wood volume was estimated, and crowns were mapped (crowns were mapped by Dr. Stephen Sillett for another study, so mapping results will not be presented here).

Arthropod sampling. Arthropods associated with humus mats were sampled using mesh litter bags, pitfall traps, and humus cores. Litter bags were constructed from nylon mesh window screen with relatively coarse mesh openings. They were filled with 100g of fresh redwood needles and the smallest foliage bearing branchlets, then dried at 80 °C for seven days to obtain dry weights prior to field deployment. Mean dry mass was 50g. Dried fresh litter was possibly a higher quality resource than senescent litter, but it is not uncommon for large amounts of fresh litter to fall onto humus mats during storms and fresh litter, which we clipped directly from trees, was not affected by prior contact with forest floor soil. Tagged and numbered litter bags were placed directly on the surface of humus mats and secured with a short stick passed through the tag loop.

Two litter bags were collected bimonthly from each mat's surface for extraction of arthropods and estimation of litter decomposition rate. Arthropods were live-extracted into 70 percent ethanol by a high-gradient Tullgren funnel apparatus for a minimum of 48 hours. Following extraction, litter bags were desiccated for several days at 80 °C for measurement of dry mass loss.

Similarly prepared litter bags were also place onto the forest floor in four clusters of twenty litter bags each. Ten were randomly collected bimonthly to provide baseline data regarding assemblage structure and succession of colonizing arthropods and estimates of litter decomposition rate on the forest floor, which was spared the environmental extremes of the arboreal humus mats.

Humus cores were obtained bimonthly using a sharpened 7.6 cm diameter × 11.5 cm tall cylinder pressed directly into the loose detritus on each humus mat surface. Arthropods were live-extracted under high temperature/moisture gradients similarly to the litter bags.

Pitfall traps were constructed from plastic food containers with tight fitting lids. A row of 1.25 cm diameter holes was drilled all the way around each plastic cup just beneath the lid. A strip of one-quarter inch mesh hardware cloth was fitted inside the holes to exclude salamanders. Two pitfall traps were deployed on each mat by removing humus cores and placing the trap directly into the resulting hole, with the entrance holes flush with the mat surface. Approximately one cm of 50 percent propylene glycol with 1

percent detergent added was placed in each trap as a killing and preservation agent and the lid was replaced to exclude rain. Arthropods were collected from each trap monthly.

Specially designed flight intercept traps were deployed in the upper and lower crowns of each study tree. These were a modified malaise trap design, having two 1.0 m^2 fine mesh intercept panels crossing at right angles with collection funnels and containers above and below the panels. These were suspended within clusters of foliage as near to the top and bottom of each tree crown as was practical. Arthropods were removed from both upper and lower collectors monthly.

All arthropod samples were returned to the Entomology Laboratory at Humboldt State University for extraction or storage immediately after collection. Most samples were stored in 70 percent ethanol prior to taxonomic determination; dry specimens from the flight intercept traps were either mounted on pins or frozen for storage. Arthropod taxa were identified to the lowest possible taxon (at the time of this writing taxonomic determinations were incomplete).

Physical habitat parameters. Humus mat length, width, thickness, shape, height, aspect, and position relative to the trunk and crown edges were measured (most measurements required estimated means since mat shapes were irregular). Epiphyte species composition, size, and relative coverage were recorded for all mats. The number of *P. scouleri* fronds, maximum frond length, and maximum number of pinnae were recorded for all mats save one on which leather fern was absent. These mat parameters were used to estimate mat volume, *P. scouleri* live biomass, and total mass of dead organic material. Humus mat habitat parameters were tested as explanatory variables for arthropod assemblage organization (this effort is also incomplete at the time of this report, since it depends upon the current level of taxonomic resolution).

Data analyses. Arthropod abundance, species richness, assemblage heterogeneity, evenness, and dominance structure were compared at the tree and crown position levels. Heterogeneity comparisons used the Brillouin diversity index, evenness comparisons were made with the Camargo index, and dominance relationships were accessed using rank-abundance plots and the dominance-rank index. In most cases Kruskal rank-sum tests were used for hypothesis testing in these comparisons, followed by pairwise Wilcoxon rank-sum tests. *P*-values reported in the Results section are from the latter

tests unless otherwise noted. Patterns of taxonomic co-occurrence were determined using multiple pair-wise G-test for independent association between all taxon pairs.

Assemblage similarities were compared with dendrograms of Morisita-Horn indices and with group and pair-wise multi-response permutation procedures (MRPP). Ecological distances between mats and relationships between mats in species-space and assemblage organization estimates were explored with Bray-Curtis ordination following Beals' smoothing of the taxon abundance data. Indicator-species analyses were used to determine whether there were significant relationships between individual taxa and humus mat size, height class, and relative crown positions.

Although the results from preliminary analyses were collected for this report, results remain incomplete pending the completion of taxonomic determinations.

Results and Discussion

During the course of field work for this study 210 humus core samples were collected from fifteen humus mats in the five study trees. Additionally, 210 pit fall trap samples were collected, 145 flight intercept trap samples, and 105 litter bag samples. A further 40 litter bag samples were obtained from the forest floor adjacent to the study transect. The flight intercept samples were archived for future examination because they contained far too many insect specimens to process in the context of this project's timeline and because our preliminary data encouraged us to focus attention on the humus mat samples.

Habitat parameters were characterized for all fifteen humus mats (Table 1). Mean mat heights for the lower-crown, mid-crown, and upper-crown mats were 45.5 m, 68.2 m, and 77.1 m, respectively. Estimated mat surface area ranged from 6,597 cm² to 450,819 cm², with mat thickness ranging from 12.3 cm to 88.0 cm. Surface material was typically coarse litter and organic debris, including redwood foliage and branchlets, sticks and broken branches, and epiphyte litter. Interior materials included epiphyte rhizomes and roots, embedded coarse woody debris, and decomposing dead organic matter (DOM). Estimated DOM mass ranged from $2,712 \pm 183$ g to $74,782 \pm 8,474$ g. All but one of the study mats supported luxuriant leather fern populations with the number of fronds ranging from 10 to 2,280 fronds per mat. Mean frond length was 65.9 cm. The largest

Table 1. Humus mat habitat parameters.

Humus mat	Crown position	Height (m)	Length (cm)	Width (cm)	Estimated mat area (cm ²)	Mean depth (cm)
Bell mat 1	upper	80.8	245	45	8659	18.4
Bell mat 2	middle	78.0	200	90	14137	52.5
Bell mat 3	lower	45.0	195	84	12865	32.0
Ballantine mat 1	upper	83.5	110	140	12095	27.5
Ballantine mat 2a [†]	middle	68.5	180	60	8482	27.2
Ballantine mat 2b [†]	middle	66.0	105	80	6597	88.0
Ballantine mat 3	lower	60.0	180	70	9896	21.1
Pleiades I mat 1	upper	77.0	220	100	17279	17.9
Pleiades I mat 2	middle	64.0	420	110	36285	50.8
Pleiades I mat 3	lower	42.5	222	86	14995	12.3
Prometheus mat 1	upper	72.0	370	210	61025	46.3
Prometheus mat 2	middle	61.0	430	90	30395	44.8
Prometheus mat 3	lower	52.0	530	190	79090	44.5
Atlas mat 1	upper	72.0	820	700	450819	58.5
Atlas mat 2a [†]	middle	70.7	180	120	16965	41.4
Atlas mat 2b [†]	middle	69.2	300	120	28274	36.4
Atlas mat 3	lower	27.9	380	100	29845	41.1

[†]Humus mat comprising two sections separated by a short distance (< 1m).

Table 1, continued.

Humus mat	<i>P. scouleri</i> fronds	Max. frond length	Max. pennae	Estimated <i>P. scouleri</i> biomass (g) [‡]	Estimated dead organic matter (g) [‡]
Bell mat 1	315	42	8	4013 ± 63	4402 ± 146
Bell mat 2	414	50	10	7721 ± 362	6147 ± 174
Bell mat 3	0	—	—	—	6956 ± 492
Ballantine mat 1	85	66	14	2672 ± 243	2712 ± 183
Ballantine mat 2a	136	60	14	3111 ± 210	2838 ± 147
Ballantine mat 2b	163	65	12	8362 ± 932	2803 ± 126
Ballantine mat 3	169	71	15	2909 ± 119	3391 ± 160
Pleiades I mat 1	232	62	14	3218 ± 59	4817 ± 183
Pleiades I mat 2	229	64	16	5899 ± 442	7014 ± 549
Pleiades I mat 3	150	81	21	2011 ± 37	4077 ± 269
Prometheus mat 1	65	61	16	4038 ± 482	8075 ± 1195
Prometheus mat 2	55	63	15	3824 ± 470	4497 ± 544
Prometheus mat 3	10	59	14	3390 ± 493	9417 ± 1647
Atlas mat 1	2280	86	19	25172 ± 854	74782 ± 8474
Atlas mat 2a	240	55	16	5225 ± 322	4970 ± 191
Atlas mat 2b	250	80	18	4904 ± 257	6442 ± 369
Atlas mat 3	215	90	19	4973 ± 333	6306 ± 419

[‡]Estimates of *P. scouleri* biomass and dead organic matter mass are reported ± 1.0 standard error.

frond encountered on Pleiades I mat 3 (lower mat at 42.5 m) had 21 pairs of penna; this represented the highest frond order yet encountered in our observations of redwood epiphytes (S. Sillett, *pers. comm.*). Estimated *P. scouleri* biomass ranged from 2011 ± 37 g to $25,172 \pm 854$ g. Huckleberry bushes also occurred on several of our study mats.

Our study mats in Atlas were among the humus mats included in a separate data-logger and telemetric study of humus mat microclimate variation conducted by Stephen Sillett and Anthony Ambrose. Data regarding temperature, moisture, and light variation within and adjacent to those mats were recorded during the arthropod sampling interval. Those data are still being processed by Sillett's group, but will be referenced in our manuscripts (as will the Save-the-Redwoods League support for that research).

Field work occupied the majority of time spent on this project during the duration of Save-the-Redwoods League support. Specimen sorting and identification was begun in the HSU entomology laboratory, however, and the results of preliminary data analyses were available. We sorted thirty of the humus core samples, thirty of the arboreal litter bag samples, sixty of the pitfall trap samples, and twenty of the forest floor litter bag samples. Taxonomic determinations are presently coarse, typically to order or sub-order, but nonetheless 309,851 animals have been categorized.

Collembola and Acari accounted for the vast majority of this abundance, representing 224,937 and 78,259 specimens respectively (Table 2). This was not surprising since springtails and mites are usually the dominant arthropod detritivores in forest soils. The overwhelming dominance of Collembola was unexpected, however, since the oribatid component of the acarine fauna usually dominates forest soil fungivore/microbivore assemblages.

Mean arthropod abundance varied considerably from tree to tree, but the between-tree differences were not statistically significant (Figure 1a). Mean arthropod abundance in humus mats from Prometheus and Atlas was significantly lower than arthropod abundance in forest floor litter bags, however. This was largely because Prometheus and Atlas yielded lower numbers of Collembola than the other trees. However, neither the mean abundance of Collembola nor that of Acari differed significantly between trees

Table 2. Abundance of invertebrate taxa collected in arboreal pit fall traps ($n = 60$), humus cores ($n = 30$), and litter bags ($n = 30$), and in ground litter bags ($n = 20$) at PCRSP based upon sorting progress to date.

Taxon	Abundance
Acari	78,259
Annelida	200
Aphidae	2
Araneae	552
Chilapoda	128
Coleoptera	601
Collembola	224,937
Copepoda	163
Diplopoda	637
Diptera	2,998
Gastropoda	85
Heteroptera	23
Hymenoptera	10
Isopoda	3
Lepidoptera	3
Nematoda (macroscopic)	43
Paupropoda	356
Turbellaria	5
Pseudoscorpiones	494
Psocoptera	250
Sympyla	1
Thysanoptera	10
Unidentified arthropod larvae	91

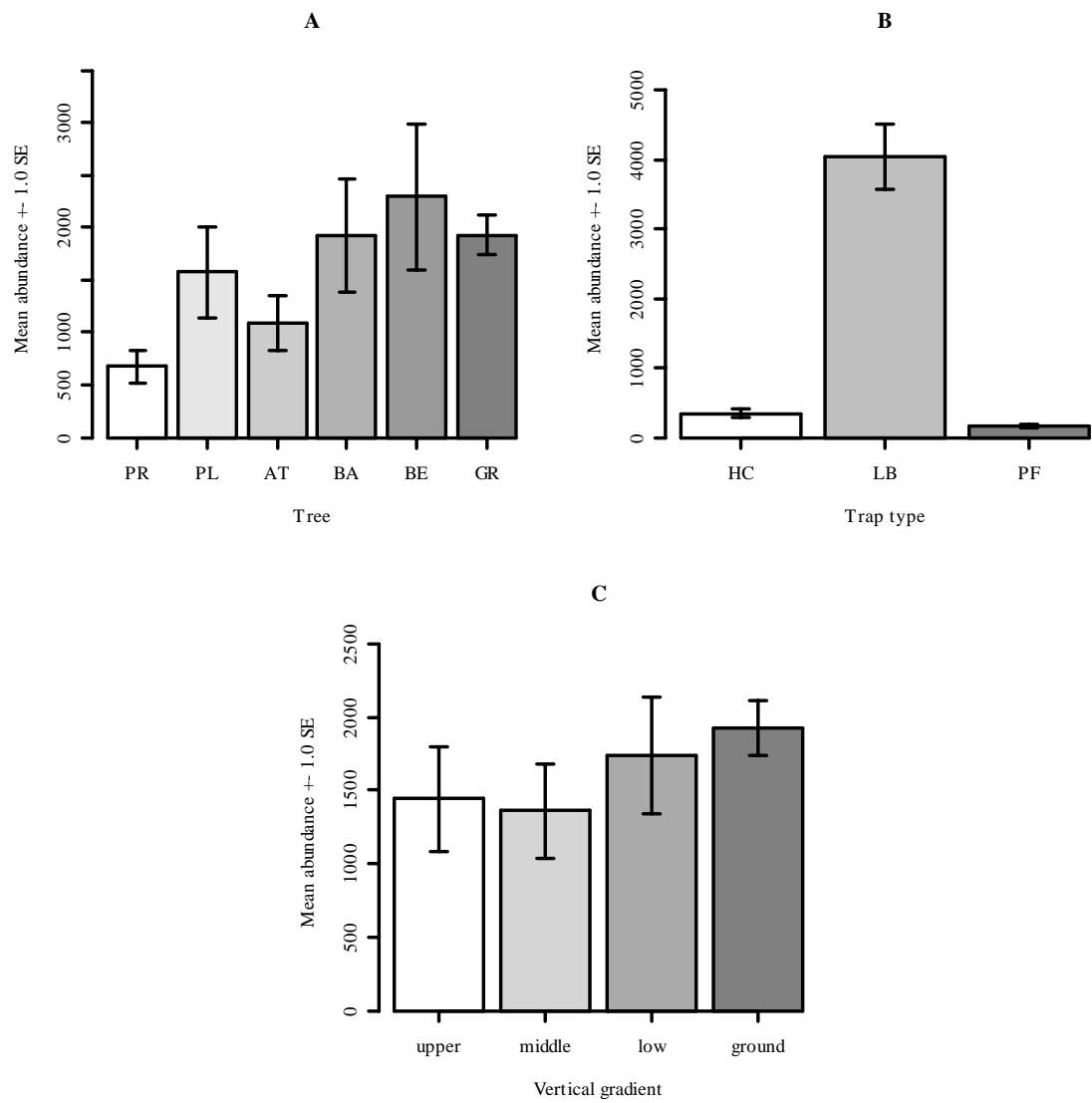


Figure 1. Mean abundance of arthropods \pm 1.0 standard error according to: (A) study tree (or the forest floor) in which samples were obtained; (B) the sampling method; (C) relative position along the forest vertical gradient from the ground to the upper canopy. Key to abbreviations: Prometheus (PR), Pleiades (PL), Atlas (AT), Ballantine (BA), Bell (BE), ground samples (GR), humus core samples (HC), litter bag samples (LB), and pit fall trap samples (PF).

($p > 0.05$). Nonetheless, all the study trees yielded significantly fewer mites than the ground samples and a greater mean abundance of springtails ($p < 0.001$).

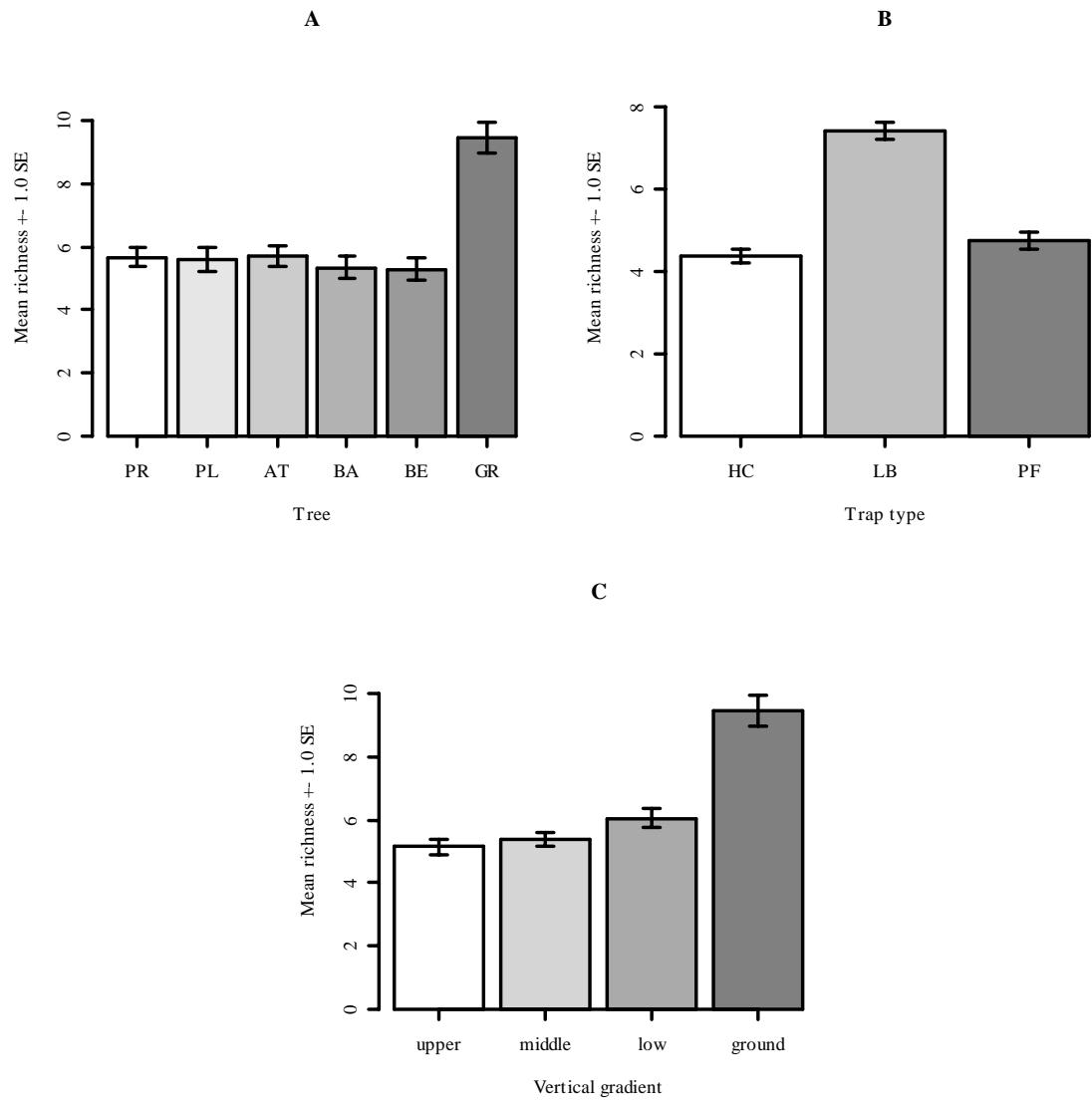


Figure 2. Variation in mean taxonomic richness ± 1.0 standard error according to: (A) study tree (or the forest floor) in which samples were obtained; (B) the sampling method; (C) relative position along the forest vertical gradient from the ground to the upper canopy. Richness estimates are based upon higher taxa, generally order or suborder. Key to abbreviations: Prometheus (PR), Pleiades (PL), Atlas (AT), Ballantine (BA), Bell (BE), ground samples (GR), humus core samples (HC), litter bag samples (LB), and pit fall trap samples (PF).

Taxonomic richness was significantly lower in the canopy than on the forest floor despite greater diversity of sampling effort in the canopy ($p < 0.001$, Figure 2a). We presume this to be the result of both dispersal limitations of soil/humus fauna, especially

the Acari, and habitat constraints imposed by canopy humus mats with limited area and volume for colonization, harsher microclimate, decreased habitat heterogeneity, and higher species turnover rates. These factors appear to act uniformly within the redwood canopy itself, at least at the higher taxon level, because we observed no significant differences in taxonomic richness between trees. This might change, of course, when we obtain greater taxonomic resolution.

Arthropod assemblage heterogeneity was greater for the forest floor samples than for the canopy samples (Brillouin index, Figure 3a), but unlike the taxonomic richness component, there was significant diversity variation between trees. Samples from the crowns of Prometheus and Atlas were somewhat more diverse than samples from the other three trees. However, it must be emphasized that our understanding of arthropod diversity in all of the samples remained preliminary since it was derived from higher taxa only.

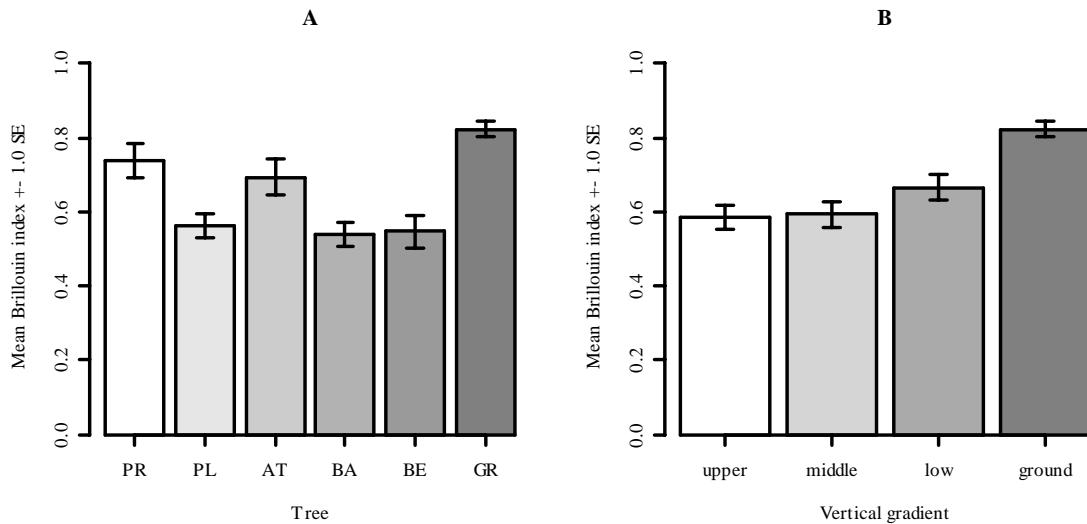


Figure 3. Mean invertebrate assemblage heterogeneity \pm 1.0 standard error. The index of heterogeneity used was the Brillouin diversity index. Key to abbreviations: Prometheus (PR), Pleiades (PL), Atlas (AT), Ballantine (BA), Bell (BE), and ground samples (GR).

Considering only the samples obtained in the forest canopy (since only litter bags were deployed on the forest floor), the mean number of arthropods collected from litter bags was significantly higher than from either humus cores or pitfall traps ($p < 0.001$, Figure 1b). This suggests that litter bags were the most effective way to sample humus

mat arthropods, at least in terms of numbers of specimens yielded per unit of sampling effort. This was especially true for the Collembola and Acari since litter bags are widely regarded as an efficient, non-destructive means for sampling these litter associated fauna. However, Collembola and Acari comprised greater than 95 percent of all samples, regardless of trapping method.

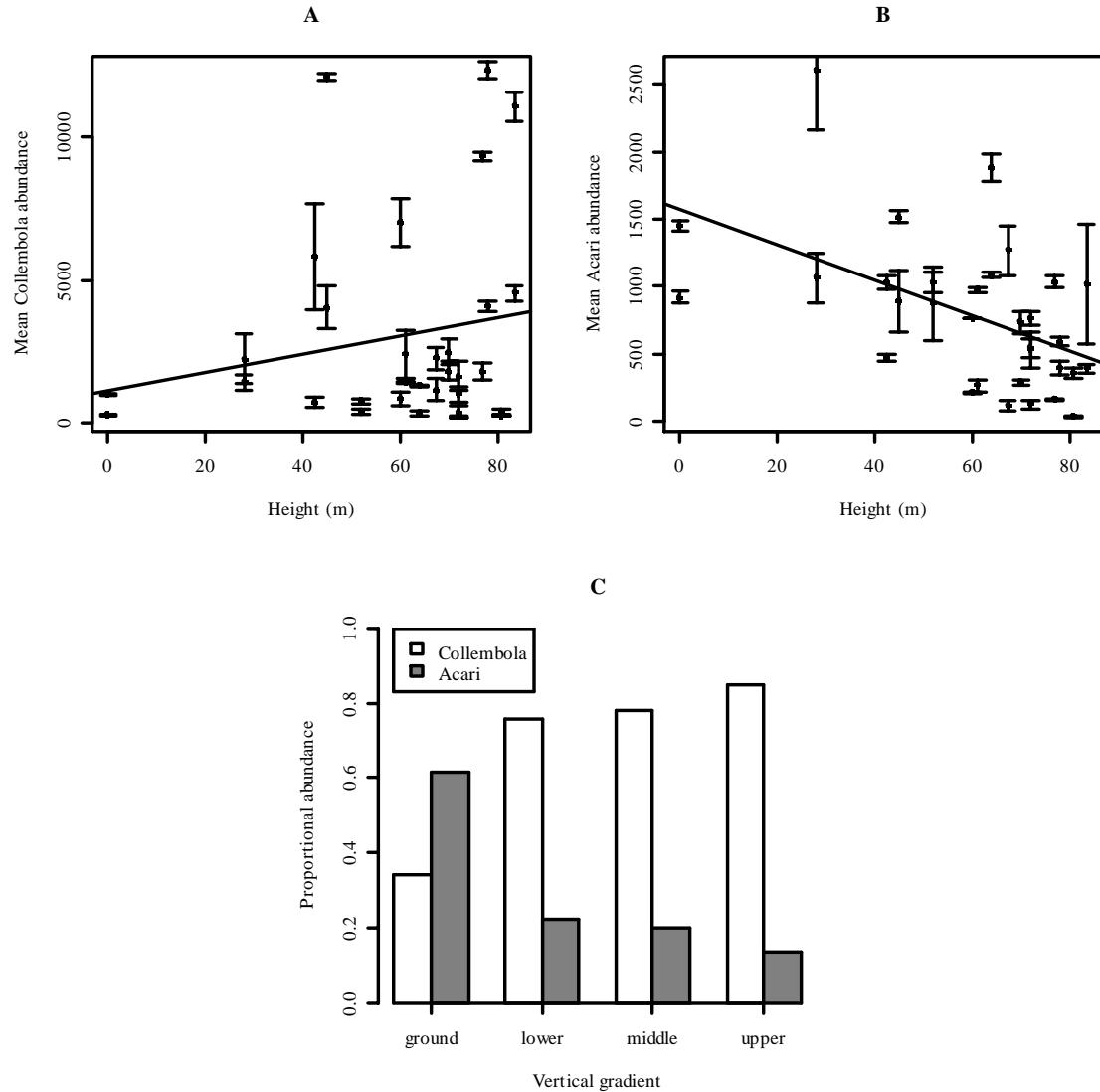


Figure 4. Mean abundance of the two most dominant taxa ± 1.0 standard error for (A) Collembola and (B) Acari. In both (A) and (B) the diagonal line represents the least-squares regression relationship between mean taxon abundance and height in meters. Regression lines are given to illustrate the direction of the general trend only; in neither instance does the simple linear relationship adequately describe variation in mean abundance. In (C), the relative proportional abundance of the two most dominant taxa are illustrated in response to relative position along the forest vertical gradient.

Litter bags also yielded significantly greater taxonomic richness than either pitfall traps or humus cores ($p < 0.001$, Figure 2b). We anticipate even greater differences as taxonomic resolution increases.

The mean number of arthropods in the canopy samples, regardless of within-crown position, was significantly lower than the mean number obtained from the forest floor litter bags ($p < 0.001$, Figure 1c). There are several possible explanations for this, but we presently favor an island-biogeographic rationale, since faunal assemblages in canopy humus are likely to be comprised primarily of emigrants from the forest floor community, but limited by both emigration difficulty and habitat constraints imposed by individual humus mats. Arboreal humus mats serve as "habitat islands" for forest soil fauna much as oceanic archipelagos serve as colonization sinks for emigrating mainland populations.

Consistent with this view, taxonomic richness and assemblage diversity also declined in the canopy ($p < 0.001$, Figure 2c and 3b). Within the canopy, mean taxon richness and arthropod diversity declined with increasing height, but not significantly so. Some taxa, such as isopods, pauropods, and symphylans occurred only in the ground samples, but some taxa were encountered only in the canopy, i.e. Psocoptera (bark-lice) and Thysanoptera (thrips). We expect stronger within-canopy richness gradients when we achieve better taxonomic resolution because the coarsely resolved data suggested that dispersal limitations were a fundamental constraint on the organization of canopy humus arthropod communities. We anticipate further dispersal variation within lower taxa, for example in the Acari which dominated forest floor assemblages but comprised a conspicuously declining proportion of the arthropod assemblage with increasing height.

As noted previously, the most numerically dominant arthropods were Collembola and Acari, both in the canopy humus and on the forest floor. The third most dominant taxon in the canopy was Araneae (spiders). On the forest floor the third dominant taxon was Paupropoda. However, the third dominant taxon accounted for less than one percent of the arthropod assemblage in both cases. Mites comprised 61.5 percent of the forest floor arthropods sampled (dominance index = 0.95) and Collembola were sub-dominant, accounting for 34.0 percent of the assemblage (dominance index = 0.55, Figure 4). In the canopy humus mats Collembola were increasingly dominant along the vertical gradient.

In the lower, middle, and upper canopy mats Collembola accounted for 74.2 percent, 76.1 percent, and 84.5 percent of the sampled arthropods, respectively, while Acari declined to 23.8 percent, 22.6 percent, and 13.4 percent of the assemblage.

The dominance of Collembola in redwood canopy humus mats was somewhat unexpected since the Acari are usually dominant in forest soils and decomposing litter. Indeed, the Acari are regarded as among the most functionally important detritivores regulating nutrient mineralization in forest soils. This is especially true of the acarine sub-order Oribatei which usually accounts for most of the diversity among soil microarthropods. Although we know of no data comparing the ecosystem roles of Collembola and oribatids, we suspect that the dominance of canopy Collembola influences the persistence of decomposing redwood litter in arboreal humus since Collembola are unlikely to fragment litter as effectively as oribatids. Indeed, decomposing litter in the humus mat litter bags lost less mass than litter bags on the forest floor. Canopy litter bags lost 19.3 ± 0.57 percent of their starting mass during 16 months of decomposition while forest floor litter bags lost 24.2 ± 8.03 percent. The difference was not statistically significant, however (Kruskal-Wallis rank sum test, $p = 0.66$).

The observed decline in acarine dominance along the canopy vertical gradient might result from dispersal and recruitment limitations of the Acari, especially the oribatids. Oribatid mites disperse slowly and they have relatively long life-cycles with low reproductive capacity. Collembola are quite mobile, on the other hand, have shorter generations, and can be very fecund when conditions are amenable. Habitat quality of redwood canopy humus mats is exceptionally good for both Collembola and the Oribatei, but we suspect that Collembola are more effective at overcoming dispersal barriers between mats and at exploiting resources rapidly within the mats themselves. This becomes progressively more important in the upper canopy where dispersal barriers are strongest.

Collembola dominance in the canopy might also influence resource quality for wandering salamanders. The close cogener *A. ferreus* occurs on the redwood forest floor and is known to consume both mites and springtails. Although little is known about the dietary preferences of either salamander species, we may surmise that Collembola are at least as beneficial a resource as mites and quite possibly more so. Most adult Collembola

are larger than most mites, for example. Furthermore, many mite species are highly sclerotized (especially the acarine-dominant oribatids), reducing the proportion of ingested mass that is accessible to digestion by salamanders. Collembola are relatively soft-bodied and were exceedingly abundant in the canopy humus mats. Availability of this rich resource might be one of the important advantages of arboreality for canopy-dwelling salamanders.

These results suggested that redwood canopy humus mats and their arthropod associates were an ideal model system for investigating the role of island-biogeographic processes such as dispersal limitation and the species-area relationship in regulating community structure. At the scale at which these meso- to microarthropods interact with their environment, canopy humus mats represent a far-flung archipelago of habitat islands within easy reach of ecologists. The discrete separation of humus mat islands in redwood crowns is especially useful; in some co-occurring tree species, such as Sitka spruce, most surfaces are covered with essentially continuous humus and epiphytic growth, while in redwoods there is clear separation between humus mats. Redwood canopy humus mat composition varies somewhat, but not a great deal, resulting in near homogeneity of resource quality for all mats. Microclimate variation can be either controlled or exploited by carefully selecting mats for study. Mats and inter-mat dispersal corridors are easily manipulated. Arthropod assemblages associated with canopy mats in redwood forest have sufficient diversity to yield useful data but are not so diverse as to be taxonomically overwhelming. Trophic organization within humus mat communities is as complex as in other systems but is also constrained somewhat by the common, and somewhat uniform, resource base shared by most redwood canopy mats.

Surprisingly, we found harpacticoid copepods in decomposing litter on the forest floor and in the redwood forest canopy up to 84 m (Figure 5). Harpacticoid copepods are semi-aquatic microcrustaceans that occur interstitially in benthic sediments and in groundwater. They were previously reported in wet leaf litter (although not in redwood forests), into which they presumably migrated from the groundwater. We obtained them from forest floor litter bags and from litter bags in the canopy at all three crown positions. This represented a first report of this organism in redwood forests and especially in the redwood forest canopy. The migratory scale of such colonization was impressive. These

copepods were approximately 200 μm long; their emigration to 84 m represents a vertical displacement of 420,000 times their body length. Some harpacticoids are known to encyst during dry periods and others presumably produce desiccation resistant eggs. Colonization of the upper canopy could therefore have occurred in stages, perhaps requiring many generations. Indeed, we think this most likely. Nonetheless, the occurrence of these tiny crustaceans in the redwood forest canopy was quite remarkable. We have found 163 specimens so far, so although somewhat infrequent, they are not rare in the redwood forest at PCRSP.



Figure 5. Photomicrograph of a harpacticoid copepod species collected from litter bags on the forest floor and on canopy humus mats up to 84 meters.

Although our taxonomic determinations and data analyses are not yet complete, we are certain that several important publications will result from this research as well as a number of additional directions for future study. First, there is much interest in the arthropod taxa that regulate litter decomposition and nutrient mobilization in forest soils, and even more so regarding similar assemblages in forest canopies, about which very little is known. Prior to this study, absolutely nothing was known about this assemblage

in redwood forest canopies. Once the species assemblage is known, we can begin to design studies to illuminate their functional ecosystem roles. We would also like to determine the relative contribution of arboreal humus to the nutrient budgets of old-growth redwood trees, and the functional role of canopy arthropods in processing those nutrients.

Second, there is considerable interest among ecologists regarding the extrinsic factors that organize species assemblages. Our data will provide insights into the roles that dispersal limitation, reproductive capacity, resource quality, and habitat area/volume play. We are very excited by the utility of the redwood canopy humus system for studying these processes further. Two of us (Camann and Lamoncha) are presently collaborating with another graduate student to study the roles of canopy microarthropods regulating decomposition and nutrient mobilization from epiphytic lichens in redwood crowns, and conversely, the influence of lichen secondary metabolites upon arthropod community structure and detritivory. We also hope to directly test some hypotheses regarding arthropod colonization and species persistence in redwood canopy humus mats.

Third, these data will yield information about the survival strategies of the wandering salamander, and perhaps help us to understand some of the advantages of arboreality for this and other such "terrestrial" vertebrates. We are discussing future collaboration with a mammalogist interested in exploring this issue further.

Finally, this study will greatly extend our understanding of the biodiversity and ecosystem resources that characterize old-growth redwood forests.