Legacy Trees Maintain Soil and Litter Microarthropod Abundance and Assemblage Organization in Managed Secondary Redwood Forests: A Report to Save-the-Redwoods League

Michael A. Camann, Karen L. Lamoncha, and Laura E. Hagenhauer

Recommended Citation:
Camann, Michael A., Lamoncha, Karen L., and Laura E. Hagenhauer. 2004. Legacy trees maintain soil and litter microarthropod abundance and assemblage organization in managed secondary redwood forests: A report to Save-the-Redwoods League. Humboldt State University. Arcata, CA.

Legacy trees maintain soil and litter microarthropod abundance and assemblage organization in managed secondary redwood forests. A project final report for the Save-the-Redwoods League.

Michael A. Camann[1], Karen L. Lamoncha, and Laura E. Hagenhauer, Humboldt State University.

30 March 2004

Summary

Remnant old growth "legacy trees" in commercially managed secondary redwood forests provide habitat for moderately to highly vagile wildlife species that depend upon late-seral tree characteristics, such as large size, complex crown structure, and stem cavities. Such trees also serve as habitat islands for ecologically important, relatively non-vagile soil and litter microarthropods that maintain crucial components of late-seral biodiversity and ecosystem processing within the matrix of managed second growth forest.

Redwood forest soil and litter microarthropods play critical ecosystem roles within the detritivorous decomposer community. They fragment organic litter and regulate the activities of fungal and microbial decomposers. Soil and litter microarthropod assemblages are sensitive to forest disturbance and responsive to seral development and forest structural alteration, making them ideal candidates for proximate bioindicators of forest ecosystem condition. Maintenance of late-seral soil and litter microarthropod assemblages associated with legacy trees might enhance sustainability of old growth ecosystem functions in managed second growth redwood forests and accelerate return to late-seral conditions in forests undergoing restoration.

Unfortunately, despite their recognized importance in forest ecosystem functioning, soil and litter microarthropod assemblages are poorly known in redwood forests. The role of legacy trees in maintaining late-seral microarthropod diversity in managed second growth redwood forests, as well as their ecosystem process attributes, has been hypothesized but never investigated. Furthermore, there are no specific requirements for the retention of old growth legacy trees, nor are there regulatory protections for such remnant trees that have escaped harvest on commercially managed timberlands. Harvest rotations on managed timberlands are unlikely to permit the reestablishment of late seral ecosystem processes independently. The need to understand the utility of legacy trees in maintaining forest diversity and processes characteristic of

---

[1] Corresponding author. Address correspondence to Michael A. Camann, Department of Biological Sciences, Humboldt State University, Arcata, CA 95521. E-mail: mac24@humboldt.edu

1

steady-state late-seral conditions is pressing, since approximately 95 percent of the remaining redwood forest is intensively managed for timber production, and much of it is in an early seral state.

This is a multi-year study that is approximately midway to completion. Nonetheless, our results to date strongly support our hypothesis that remnant old growth redwood trees provide habitat refugia for terrestrial arthropod communities that are much more characteristic of late seral forest development than of early seral forest replacement. We found significantly greater numerical abundance and species diversity of oribatid mites and Collembola, the most functionally important components of the soil and litter microarthropod detritivore assemblage, in association with legacy old growth trees. We also found early indications of significant habitat differences, e.g. deeper duff accumulations and microclimate moderation under old growth remnants. These suggest that legacy trees not only provide physical refugia for decomposers, but also functional refugia that retain aspects of late seral ecosystem characteristics. At the very least, retention of old growth trees assists in maintaining the biodiversity associated with soil and litter habitats in late seral redwood forests, and perhaps has the capacity to enhance metapopulation patch dynamics for detritivorous microarthropods during subsequent seral development.

Introduction

Previous coast redwood (*Sequoia sempervirens*) forest conservation efforts have focused upon preservation of the remaining intact old-growth forest, There has been great urgency for transferring as much of the roughly four or five percent of remaining primeval forest as possible to protected ownership in the public trust (Fox 1996, Thornburgh et al. 2000). Recently however, attention has shifted toward forest regeneration and seral development in the much larger proportion of coast redwood forest that has undergone stand replacing timber harvest or other disturbance. There is particular interest in accelerating the acquisition of late-seral characteristics in regenerating redwood forests by astute silviculture and forest management, especially when such forests are placed into public ownership following previous management for timber production.

There is growing concern that although we can articulate desirable outcomes of late-seral redwood forest restoration, there is as yet little consensus regarding the underlying ecosystem mechanisms that establish and maintain those characteristics under conditions of natural regeneration. Such desirable features as complex habitat structure, including snags, large trees with cavities, arboreal humus accumulations and other refugia, vegetation structure profiles similar to extant old growth forests (with equivalent physiographic characteristics), and habitat occupancy by old growth forest indicator taxa are the result of layered, interactive ecosystem processes. These include the influences of changing species composition and canopy structure during seral development as well as primary production, nutrient budgets, and energy fluxes.

Moreover, there is little consensus regarding the choice of appropriate proximate indicators of ecosystem trajectories in managed redwood forests. Restoration of desirable late-seral characteristics provides the ultimate indicators of management success, but

unfortunately many of the desired changes occur on time scales that are not compatible with the need for near-term decision support. Managers need a suite of sensitive indicators that accurately reflect change in forest ecosystem processes in a timely manner. Our work in other systems suggests that ideal proximate indicators are often short-lived participants in the ecological mechanisms whose trajectories they reflect.

Nutrient cycling through the decomposer assemblage, in particular forest soil and litter microarthropods, is one such mechanism contributing to the maintenance of healthy late-seral redwood forests. Microarthropods, especially the Oribatei (Arachnida: Acari) and Collembola (Insecta), dominate redwood forest floor and arboreal fauna (Camann *et al., unpublished data*). Their assemblages are far more abundant and diverse than any corresponding vertebrate communities (Anderson 1977), with local assemblages commonly exceeding 100,000 individuals and dozens of species per m^2 (Behan-Pelletier and Bissett 1994, Hansen and Coleman 1998, Lamoncha and Crossley 1998). Soil microarthropods are crucial in forest ecosystem processes (Wallwork 1983, Kaneko et al. 1998). They regulate litter decomposition and nutrient mineralization rates in forest soils (Crossley 1977, Mitchell 1979, Swift et al. 1979, Seastedt 1984). Soil biota play pivotal nutrient dynamic roles in patchy habitats where nutrient levels fluctuate by enhancing mineralization of nutrients (Wagner et al. 1997). Detritivorous microarthropods dramatically shorten nutrient recycling intervals in forest soils. Litter decomposition and nutrient return slows when soil and litter microarthropods are excluded (Harding 1967, Santos and Whitford 1981). Disturbances that reduce microarthropod abundance or alter their assemblage organization affect litter decomposition and nutrient mobilization (Seastedt and Crossley 1980, Abbott and Crossley 1982). Soil and litter microarthropod community organization responds to forest seral condition (Camann *et al., unpublished data*).

Recent research in our laboratory (e.g. Rappaport *et al., in review*, Camann *et al.* 2001) suggests that microarthropods associated with detrital nutrient dynamics in western forests are especially sensitive proximate indicators of disturbance, i.e. of perturbation that disrupts steady-state conditions in late-seral forests, and of forest recovery following perturbation. This sensitivity of a whole functional trophic assemblage to disturbance of nutrient dynamics suggests in turn that detrital processing and forest nutrient budgets are crucial aspects of ecosystem health in steady-state, late-seral forests. Removal of forest canopies or alteration of stand structure affects forest floor microclimate and habitat suitability, i.e. by increasing insolation, reducing litter inputs and removing existing litter, compacting soil, and affecting moisture availability. For example, clear-cutting reduced litter microarthropod populations and biodiversity, and affected litter decomposition and soil nutrient dynamics at Coweeta Hydrologic Laboratory for nearly a decade (Abbott et al. 1980, Seastedt and Crossley 1981, Blair and Crossley 1988).

Approximately 95 percent of our remaining coast redwood forest is intensively managed for timber production (Fox 1996). Much of this forest is in an early seral condition, but there remain numerous instances of remnant old-growth "legacy" trees (Franklin 1990) and "legacy stands" interspersed among the matrix of second growth trees. Although relatively rare in commercial redwood forest management plans, and frequently in danger of subsequent harvest, legacy trees are especially valuable because they are often the only remaining repositories of old growth structure and late-seral

habitat in managed forests otherwise bereft of these characteristics. As such, they provide limited habitat refugia for taxa that depend upon old growth and opportunities for land managers wishing to maximize late-seral influence upon the surrounding matrix of regenerating forest.

Harvest rotations on most commercial timberlands do not allow regenerating forests to achieve late-seral ecosystem dynamics or to produce individual second-growth trees with mature ecosystem value. Retaining existing old-growth trees within the secondary-growth matrix offers an opportunity to realize at least some of the benefits of old-growth dependent soil processes at relatively low expense and effort. Unfortunately, our lack of concrete justification for the retention of these trees increases the uncertainty of their future. There is no specific requirement for their retention during timber harvest in redwood forests. Although the likely influence of legacy trees in regenerating forests is commonly acknowledged, little specific functional information is known (Hunter and Bond 2001), especially as regards such frequently overlooked but ecologically crucial fauna as soil and litter microarthropods. Most research to date has focused upon legacy tree habitat for vertebrates such as birds, bats, and small mammals who frequent structural refugia provided by tree cavities and extensive canopies (Mazurek and Zielinski 2002a). However, these vertebrate components of legacy tree fauna are moderately to highly vagile and while still dependent to some degree upon legacy tree habitat, they often utilize habitats in the surrounding second growth matrix as well. Their contribution to the maintenance of late-seral forest structure is poorly understood, but arguably minimal.

Soil and litter microarthropods, on the other hand, participate directly in crucial forest nutrient cycles and are far less vagile than vertebrates. Many are effectively sessile at stand and forest scales because their lifetime ranges encompass only a few cm^3, or at most a few m^2 of forest litter and organic humus. They are likely to exhibit strong legacy tree habitat dependencies and easily quantifiable population and community responses along habitat gradients extending from legacy trees into the surrounding matrix of regenerating forest. As such, they have enormous potential for proximate biomonitoring of ecological functional aspects of forest seral condition. We propose that as second growth forests reacquire late-seral characteristics, nutrient dynamic gradients extending from legacy trees might accelerate seral development, or at least support silvicultural efforts to achieve the same end.

We have begun testing aspects of this hypothesis with help from the Save-the-Redwoods League. First, we are inventorying the primary soil and litter microarthropods, especially the Oribatei and Collembola, associated with remnant old-growth and young trees within commercially managed redwood forests in the central portion of the coast redwood range (Sawyer et al. 2000). There is presently no information regarding this abundant, diverse, and ecologically important fauna in regenerating redwood forests (we have preliminary data from several other projects underway in our laboratory, but only from the more mesic and decidedly late-seral forests at Prairie Creek Redwoods State Park and Redwoods National Park).

Second, we are assessing the abundance and species assemblage structure of forest soil and litter microarthropods along habitat gradients and disturbance continua emanating from paired old growth legacy trees and nearby second growth trees in

4

regenerating commercial stands. This will provide information regarding the extent of old growth habitat influence from legacy trees into the surrounding matrix of regenerating forest on a scale that is directly relevant to important ecosystem processes, e.g. detritivory and nutrient dynamics.

Third, we are assessing the degree to which legacy trees serve as "habitat islands" for soil and litter microarthropods within the surrounding matrix, conserving late-seral biodiversity for future metapopulation processes during seral development and buffering against biodiversity loss within this important faunal component of regenerating forests.

Fourth, we hope to determine whether legacy trees foster local metapopulation habitat quality for redwood forest soil and litter microarthropods, e.g. through nutrient interactions. If so, removal of legacy trees threatens ecologically important faunal assemblages that are less likely to occur elsewhere within regenerating redwood forests.

Finally, our work on remnant old-growth associated microarthropods compliments similar studies recently completed by colleagues investigating vertebrate habitat use and dependency upon old growth legacy redwood trees (Mazurek and Zielinski 2003). Soil and litter microarthropods occupy one end of an animal vagility continuum whose other endpoint is characterized by by wide-ranging taxa such as birds and bats. It is likely that animals in such widely differing dispersal classes will respond differently to habitat modification, and will have correspondingly different habitat dependencies upon legacy redwood trees.

Materials and Methods

Study area and tree selection. Field sampling was conducted in Mendocino County in cooperation with the USDA Forest Service Pacific Southwest Research Station, Redwood Sciences Laboratory, on land owned by the Mendocino Redwood Company, the Jackson State Demonstration Forest, and the Hawthorne Timber Company. We used 40 paired legacy and non-residual second growth control trees previously selected during companion studies supported by Save-the-Redwoods League (Mazurek and Zielinski, 2002a, 2002b, 2003). The legacy trees included trees with and without basal cavities. Control trees were randomly drawn from trees in the largest size class within the surrounding regenerating stands with environmental parameters similar to the legacy trees. Physical characteristics (e.g. diameter at breast height, tree height, and basal structure) and vertebrate wildlife visitation and habitat use data were previously obtained (Mazurek and Zielinski 2003).

Microarthropod sampling. We established equal length tree-centered transects on opposite sides of each legacy and control tree extending from the tree bole to the approximate tree-crown drip line of the tree with the largest diameter crown. Transect directions were randomly determined, but subject to the constraint that they minimize management related soil and litter disturbance whenever possible, e.g. avoiding slash piles and road cuts. Four soil and litter samples were taken at 2.0 m intervals along each transect using a cylindrical metal template 25.4 cm in diameter, i.e. at approximately 2.0 m and 4.0 m from the tree bole in each direction, but once again adjusted to avoid obviously disturbed locations. Litter, woody debris, and organic humus were collected

from within the template, either to mineral soil or to 25 cm if the organic layer exceeded that depth. We recorded the mean depth of humus removal and each sample's proximity to large woody debris on the ground. Two additional samples were taken from within cavities of trees with basal hollows, one from the approximate center of the cavity and one from the interior edge nearest the opening. Humus samples were returned to Humboldt State University within 48 hours for high-gradient photo-extraction of microarthropods for 72 hours. Following extraction, litter and humus samples were dried at 60 °C and weighed, and the proportional masses of coarse and fine components measured.

Habitat quality. We used litter depth as a correlate of microarthropod habitat quality in these preliminary analyses. This was appropriate for at least three reasons. First, soil and litter fauna live within decaying humus where they forage for detritus and microbial detritivores. All other habitat conditions being equal, greater volumes of decaying organic litter should yield greater microarthropod abundance and perhaps greater species diversity. Second, humus retains water and decreases temperature variation, moderating seasonal and diel microhabitat extremes. Finally, we reasoned that deep litter accumulations are themselves a likely legacy tree contribution to soil and litter microarthropod habitats in second growth forests where mechanized harvest operations and lower subsequent litter imput during stand regeneration might decrease fine organic detritus availability, especially after the first year or two following timber removal.

Data analyses. Microarthropods are presently being determined to the lowest practical taxon, generally species or morphospecies for the Oribatei and Collembola, in the Humboldt State University Entomology Laboratory. Ecological correlations between microarthropod species assemblage gradients in legacy and control transect samples, and habitat and microarthropod community structure will be identified with indirect ordination (e.g. non-metric multidimensional scaling) after omitting taxa that did not occur in at least 10 percent of the samples. Microarthropod assemblage similarities will be quantified with multi-response permutation procedure (MRPP) analysis and dendrograms of assemblage similarities constructed using pairwise Morisita similarity coefficients. Relevant indices of species assemblage organization (identified with indirect ordination) will be compared using non-parametric rank-sum tests, e.g. Kruskal-Wallis and pairwise Wilcoxon rank sum comparisons of mean values of corresponding community structure indices, e.g. the Brillouin coefficient (heterogeneity), Camargo index (evenness), and the dominance-rank coefficient (dominance). Species richness will be compared by interpolation with rarefaction and by extrapolation of total species richness using jack-knife estimates. Individual microarthropod species characterizing legacy tree and control tree microarthropod assemblages will be identified using indicator species analysis.

Table 1. Legacy tree project milestones and current status as of mid-March 2004.

Project Milestone	Current Status	Anticipated Completion
Field sampling	Completed	
Microarthropod recovery	Completed	
Sample sorting	70 % completed	June 2004
Oribatid mite separation	60 % completed	June 2004
Collembola identifications	Not started	Oct. 2004
Oribatid mite identifications	5 % completed	Oct 2004
Data analyses	10 % completed	Nov. 2004

6

Results and Discussion

Progress to date. This is a multi-year project partly funded by the Save-the-Redwoods League (SRL). Although the SRL supported portion is completed, the project will culminate with publication of Ms. Laura Hagenhauer's Master's Degree thesis in the Department of Biological Sciences at Humboldt State University (HSU). We anticipate completion during late 2004 or early 2005.

We are pleased to report substantial progress with the aid of SRL (Table 1). Field work was completed, as was microarthropod recovery from soil samples collected in the field. Due to the high abundance of microarthropods collected (Table 2), we reduced the number of sample units for subsequent analyses from 20 pairs (40 trees) to 10 pairs (20 trees), yielding a total of 80 soil and litter samples (although microarthropods were recovered from all of the field samples and the unprocessed samples are archived at HSU). We have completed sorting microarthropods from 56 of those samples. Despite our early reporting, preliminary analyses have proved quite informative.

Litter thickness. The mean depth of organic litter sampled was greater beneath the legacy trees than beneath second growth trees in the surrounding matrix (9.6 cm ± 0.6 cm and 5.4 ± 0.4 cm respectively, $p < 0.001$). Undoubtedly this affected microarthropod abundance and diversity to some extent because the organic litter layer is habitat for detritivores. However, the differences in microarthropod abundance and community organization exceed the differences in litter availability, suggesting that habitat quality has been affected as well as simple habitat quantity. Moreover, a thicker duff layer beneath legacy old growth trees, with larger, more complex crowns, is itself likely a legacy characteristic. Given the limited vagility of detritivorous microarthropods, remnant old growth redwoods appear to provide valuable habitat reserves for maintaining detritivore community complexity.
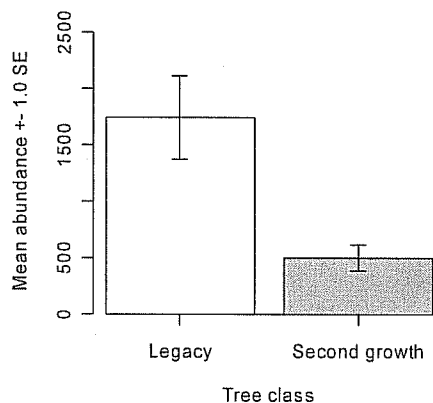

Figure 1. Mean abundance of soil and litter microarthropods collected under legacy old growth and second growth redwoods (± 1.0 SE).

Microarthropod community organization. We have recovered, sorted, and coarsely determined 48,660 microarthropods (generally to taxonomic order or sub-order), a mean abundance of 1,747 ± 374 specimens in the legacy tree soil samples and 508 ± 118 in the second growth controls ($p < 0.001$, Figure 1).

Nonmetric multidimensional scaling (NMS) of the samples yielded a solidly supported two dimensional solution (stress = 1.79, Figure 2). The first axis reflected organization along a gradient significantly correlated with microarthropod community abundance ($r = 0.85$), coarse taxonomic richness, ($r = 0.80$), and evenness of taxonomic abundance distributions ($r = -$
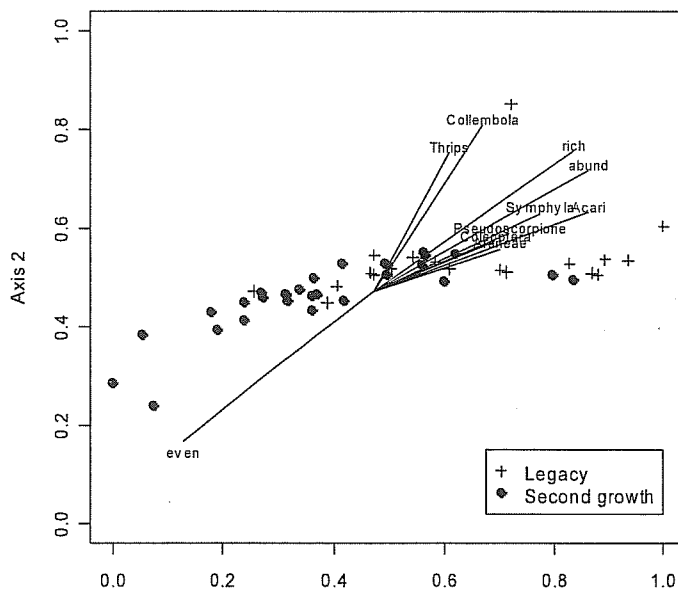
Figure 2. NMS ordination of the microarthropod abundance data and community structure parameters.

0.75). Even at coarse taxonomic resolution, microarthropod communities associated with legacy old growth trees differed markedly from those beneath second growth trees (MRPP, $p < 0.001$).

Microarthropod taxa that were positively correlated with the first NMS axis included Acari ($r = 0.85$), Collembola ($r = 0.44$), Coleoptera ($r = 0.48$), Pseudoscorpiones ($r = 0.54$), Aranae ($r = 0.51$), Symphyla, ($r = 0.66$), and Thysanoptera ($r = 0.30$). Although we have not yet included habitat quality data in these analyses, a casual examination of the data strongly suggests that litter depth was also positively correlated with the first NMS axis.

None of the data included in the NMS analysis thus far has assisted us in interpreting the second NMS axis except descriptively in terms of Collembola and thrips contributions to community organization ($r = 0.74$ and $r = 0.61$, respectively) and decreasing evenness of microarthropod species abundance distribution ($r = -0.66$). This was not especially problematical, however, because the greatest proportion of sample variation was clearly captured by the first NMS axis. Furthermore, it should be noted that these analyses will be improved by the greater taxonomic resolution obtained when the dominant oribatid mites and collembolans have been determined to species and morphospecies in all of the samples.

These results provide further evidence that legacy old growth redwoods retain elements of remnant detritivore communities within the matrix

Table 2. Higher taxa collected from soil samples beneath legacy and second growth redwood trees. The p values are for significant abundance differences between legacy old growth and second growth tree samples. Empty rows had $p \geq 0.05$.

| Taxon	Abundance	Percent	p
Acari	39,514	81	< 0.001
Collembola	7,738	16	< 0.001
Pauropoda	274	0.6	0.03
Coleoptera	184	0.4	
Pseudoscopriones	180	0.4	
other Aranae	178	0.4	0.002
Diplopoda	147	0.3	0.049
Protura	92	0.2	
Symphyla	81	0.2	< 0.001
Thysanoptera	78	0.2	
Diptera	57	0.1	
Hymenoptera	44	0.1	
Diplura	33	0.1	
Chilopoda	30	0.1	0.045
Gastropoda	10	< 0.1	
Undetermined	9	< 0.1	
Isopoda	9	< 0.1	
Homoptera	2	< 0.1	
Annelida	1	< 0.1	

8
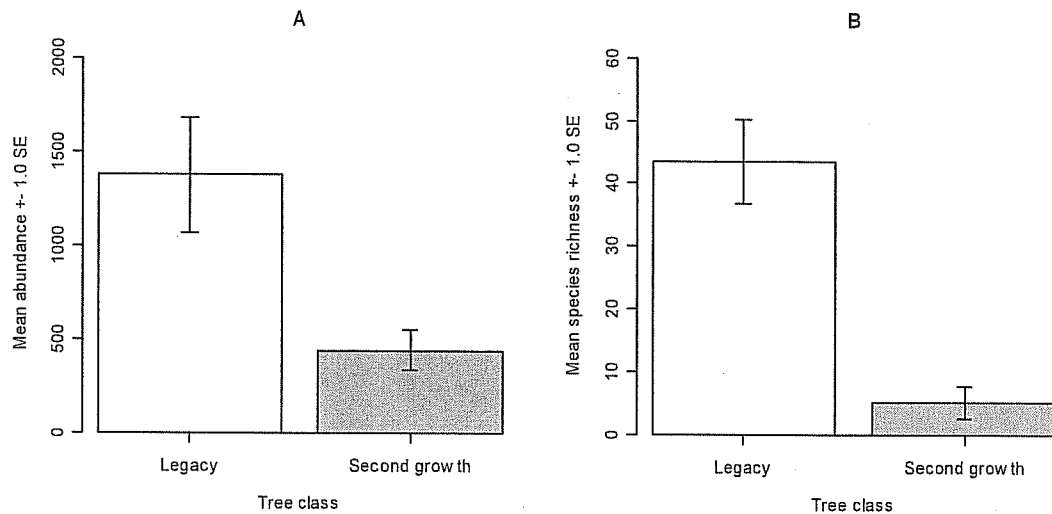
Figure 3. Mean oribatid mite abundance (A) and species richness (B) in soil samples beneath legacy old growth and second growth redwood trees (± 1.0 SE).

of second growth, regenerating forest. Such occupied habitat patches might serve as metapopulation source patches during the reestablishment of late-seral nutrient dynamics. We might also expect the differences in microarthopod assemblage organization to decline as late-seral processes are restored in the regenerating forest matrix. This might be a valuable indicator of ecosystem convergence.

The greatest proportion of the total microarthropod abundance was accounted for by the acarine mites and the hexapod Collembola (Table 2), both of which were more numerous in association with legacy trees. This was consistent with our expectations based upon previous work in old growth redwood forests and bolsters our confidence that these two taxa are the most numerically dominant members of the detritivorous microarthropod community. There is ample evidence that they are the most speciose as well. This increases their sensitivity as proximate indicators of ecosystem change within forest soils.

Other higher taxa with significantly greater abundances beneath legacy trees included Coleoptera (beetles), Diplopoda (millipedes), Pauropoda, Chilopoda (centipedes), Aranae (spiders), and Symphyla. The insect order Thysanoptera (thrips) was more frequently encountered in the second growth matrix (17 samples) than beneath legacy old-growth trees (9 samples), as were Hymenoptera (primarily ants, 11 and 7 samples, respectively) and Diplopoda (18 and 9 samples). This was despite the higher mean abundance of thrips and centipedes in the legacy tree samples, suggesting differences in the spatial distribution of those taxa beneath legacy trees and the surrounding second growth matrix.

These changes suggest that retention of old growth trees within the regenerating redwood forest matrix affects other terrestrial arthropod trophic levels as well as detritivores. As a group, beetles exhibit broad, complex trophic relationships, although ground and litter associated species are often either predaceous or fungivorous. Centipedes and spiders are predators. Many ant species are opportunistic and establish

9

colonies in disturbed areas. Moreover, ants generally prefer warmer, dryer habitats, and are often sparsely distributed in old growth redwood forests.

There was significantly greater taxonomic richness at the higher taxon level beneath the old-growth legacy trees, although rarefaction of the more numerous legacy tree specimens suggested that at the present taxonomic resolution this was likely attributable to differences in abundance. However, the abundance difference was unambiguous, so we are confident that improved taxonomic resolution will demonstrate that remnant old-growth trees supported greater soil and litter microarthropod species richness than second growth trees within the surrounding matrix. At coarse taxonomic resolution we are still making comparisons near the base of the rarefaction curves where between-group differences are least apparent.

Table 3. A list of 64 oribatid mite species and morphospecies identified to date. All of these species were obtained from samples taken beneath legacy old growth redwood trees. Species indicated with an asterisk were also obtained beneath trees in the second growth matrix.

Morphospecies	Morphospecies	Morphospecies	Morphospecies
Allosuctobelba sp.	*Epidamaeus* sp. a	*Joshuella* sp. *	*Oribatritia* sp. b
Ametroproctus sp. *	*Epidamaeus* sp. b	*Lasiobelba* sp.	*Parhypochthonius* sp.
Autogneta sp.	*Epidamaeus* sp. c	*Lepidozetes* sp. *	*Peltenuiala* sp.
Belba sp.	*Epidamaeus* sp. f	*Liacarus* sp. a	*Platynothrus* sp.
Belba sp. b	*Eueremaeus* sp. a *	*Liacarus* sp. b	*Pthiracarus* sp. a
Benibates sp. *	*Eueremaeus* sp. b *	*Liacarus* sp. c	*Pthiracarus* sp. b
Brachychthonius sp.	*Eupelops* sp. *	*Licnodamaeus* sp.	*Quadroppia* sp.
Carabodes sp. a	*Eupthiracarus* sp. a	*Liochthonius* sp.	*Ramusella* sp. *
Carabodes sp. b	*Eupthiracarus* sp. b	*Liochthonius* sp. b	*Scheloribates* sp. *
Ceratoppia sp. a *	*Galumna* sp. *	*Liochthonius* sp. c	*Sphodrocepheus* sp.
Ceratoppia sp. b	*Gustavia* sp.	*Microppia* sp.	*Spinozetes* sp.
Ceratozetes sp.	*Hermaniella* sp. a	*Oppia* sp.	*Suctobelbella* spp.
Cosmochthonius sp.	*Hermaniella* sp. b	*Oppiella* sp.	*Synchthonius* sp.
Cultoribula sp.	*Hermannia* sp.	*Oppiellla* nova	*Tenuiala* sp.
Dentachipteria sp. *	*Hermannis* sp. b	*Oribatella* sp. *	*Trichoribates* sp. *
Dyobelba sp.	*Hypochthonius* sp.	*Oribatiritia* sp.	*Zachvatkinibates* sp.

Oribatei. The oribatid mites accounted for the greatest proportion of Acari recovered from soil samples under both legacy trees and second growth trees ($p < 0.001$ for both), and indeed the greatest total proportion of microarthropods recovered. We have so far recovered 24,812 oribatid mites. Mean oribatid mite abundance was significantly greater beneath legacy trees ($p < 0.001$, Figure 3a).

We have identified 64 species of oribatid mites in the soil samples processed so far. Most are currently determined to genus and morphospecies (Table 3). This is undoubtedly an underestimate of the actual species richness because oribatids from only a relative few samples have been identified. All 64 oribatid species were retrieved from the legacy tree soil samples, while only 14 species were obtained in the second growth matrix. Mean oribatid species richness was 44 ± 6.8 species beneath the legacy trees and 5 ± 2.6 species under second growth redwoods (Figure 3b).
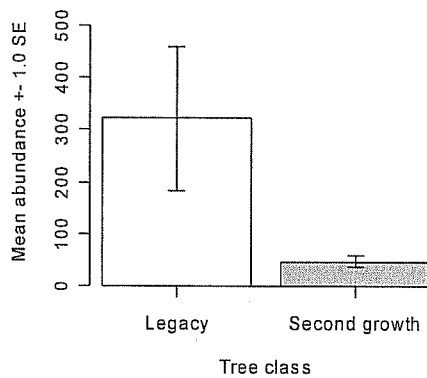
Figure 4. Mean abundance of Collembola collected beneath legacy old growth redwood trees and second growth threes (± 1.0 SE).

Although we are not entirely comfortable drawing conclusions from quantitative analyses of the oribatid species data at this early stage, we nonetheless note the striking contrast in oribatid species distribution in habitats provided by legacy trees and those afforded by second growth trees in the regenerating forest matrix. This is entirely consistent with our hypotheses that remnant old growth trees provide habitat refugia for these ecologically valuable detritivores.

Collembola. Collembolans accounted for the second greatest proportion of the microarthropod taxa recovered from our soil samples (7,738 specimens at present). Mean Collembola abundance was also greatest under legacy old growth trees ($p < 0.001$, Figure 4). As noted in Table 1, Collembola have not yet been identified beyond order.

We are especially interested in completing analyses of Collembola species diversity and assemblage structure for several reasons. First, Collembola are among the more vagile members of the detritivorous microarthropod community and thus are generally capable of colonizing disturbed and recovering habitat patches more quickly than are oribatid mites. This quality makes them *potentially* more dynamic proximate indicators of ecosystem change. Second, we believe that many Collembola species are somewhat more sensitive to harsh microclimate conditions, particularly hot and dry habitats. This is not to suggest that Collembola cannot colonize and persist under such conditions (our own data from other forest systems suggest otherwise). Rather, we expect to find either reduced Collembola species diversity away from the relatively moderate microhabitat conditions maintained beneath old growth redwood trees or a distinct change in Collembola species assemblages as desiccation tolerant species are favored.

Conclusions

Although our data analyses are preliminary, and data collection is still ongoing, the analyses to date unambiguously support our hypothesis that legacy old growth redwood trees serve as ecologically valuable habitat islands within a matrix of regenerating second growth, managed forest. The data strongly suggest that remnant old growth trees provide habitat refugia for a detritivore community that provides valuable ecosystem services.

The data also support our proposal that soil and litter microarthropods species assemblages constitute an important proximate bellwether of ecosystem change in regenerating redwood forests. This conclusion has both ecological and management implications. From an ecological perspective, it suggests that species assemblages which participate in ecological processes characterizing ecosystem conditions are themselves often the best proximate indicators of change in those systems. Nutrient cycling in forest

soils is certainly one such process with characteristic seral states. This is important from a management perspective because the ultimate objective of redwood forest restoration is reestablishment of ecological processes that maintain– and reflect– desirable seral conditions. Ultimate indicators of such processes are likely to develop at time scales too long to inform management efforts or to allow for adaptive management of redwood forest restoration.

This study did not address the functional attributes of detritivorous microarthropod community organization, however previous work has demonstrated the general importance of detrivorous microarthropods as facilitators of nutrient mineralization and reuse in forest ecosystems, and as regulators of the fungal and microbial decomposer communities. Nonetheless, the implications for future reseach needs are clear. We need to look critically at the specific functional relationships between soil microarthropod associations and seral development in redwood forests. This study, which characterizes the effect of seral disturbance on soil microarthropod communities, is a necessary first step in this process, but much remains to be done in the future. In particular, we would like to examine the dynamics of the entire organic nutrient cycle in old growth and regenerating redwood forests. We believe that there are likely seral stages in nutrient cycling that mirror seral development in forest structure and habitat quality, and that good proximate indicators of these changes will be useful tools for understanding ecosystem development and for managing redwood forest restoration for the future.

Acknowledgments

Literature cited

Abbott, D. T., and D. A. Crossley Jr. 1982. Woody litter decomposition following clear-cutting. Ecol. 63: 35-42.

Abbott, D. T., T. R. Seastedt, and D. A. Crossley Jr. 1980. Abundance, distribution, and effects of clear-cutting on Cryptostigmata in the southern Appalachians. Environ. Entomol. 9: 618-623.

Anderson, J. M. 1977. The Organization of Soil Animal Communities. *In* Soil Organisms as Components of Ecosystems, Ecol. Bull. (Stockholm) 25:15-23.

Behan-Pelletier, V. M. and B. Bissett. 1994. Oribatida of Canadian peatlands. Mem. Entomol. Soc. Can. 169: 73-88.

Blair, J. M., and D. A. Crossley, Jr. 1988. Litter decomposition, nitrogen dynamics, and litter microarthropods in a southern Appalachian hardwood forest 8 years following clearcutting. J. Appl. Ecol. 25: 683-698.

Camann, M. A., K. L. Lamoncha, and C. B. Jones. 2001. Old-growth redwood forest canopy arthropod prey base for arboreal wandering salamanders: a report prepared for the Save-the-Redwoods League.

Crossley, D. A. Jr. 1977. Oribatid mites and nutrient cycling. In Dindal (ed), *Biology of Oribatid Mites*. Syracuse State Univ., New York, pp. 71-85.

Fox, L. 1996. Current status and distribution of coast redwood. Pp. 18-19 *In* J. LeBlanc, editor. Coast Redwood Forest Ecology and Management, University of California, Berkeley.

Franklin, J. F. 1990. Biological legacies: A critical management concept from Mount St. Helens. Trans. North American Wildlands Natural Resource Conference 55: 216-219.

Hansen, R. A. and D. C. Coleman. 1998. Litter complexity and composition are determinants of the diversity and species composition of oribatid mites (Acari: Oribatida) in litterbags. Appl. Soil Ecol. 9: 17-23.

Harding, D. J. L. 1967. Faunal participation in the breakdown of cellophane inserts in the forest floor. *In* Graff and Satchell (eds), *Progress in soil biology*. North-Holland Publ. Co., Amsterdam. Pp. 162-170.

Hunter, J.E. and M.L. Bond. 2001. Residual trees: Wildlife associations and recommendations. Wildlife Society Bulletin 29:995-999.

Kaneko, N., M. A. McLean, and D. Parkinson. 1998. Do mites and Collembola affect pine litter fungal biomass and microbial respiration? Appl. Soil Ecol. 9: 209-213.

Lamoncha, K. L., and D. A. Crossley Jr. 1998. Oribatid mite diversity along an elevation gradient in a southeastern Appalachian forest. Pedobiologia 42: 43-55.

Mazurek, M.J. and W. J. Zielinski. 2002a. The Importance of Legacy Old-growth Trees in the Maintenance of Biodiversity in Commercial Redwood Forests - A report of progress: June 2001 – October 2001, Redwood Sciences Laboratory, Pacific Southwest Research Station, Arcata, CA.

Mazurek, M.J. and W. J. Zielinski. 2002b. The Importance of Legacy Old-growth Trees in the Maintenance of Biodiversity in Redwood Forests Managed for Multiple Uses. Redwood Sciences Laboratory, Pacific Southwest Research Station, Arcata, CA.

Mazurek, M.J. and W. J. Zielinski. 2003. The Importance of Legacy Old-growth Trees in the Maintenance of Biodiversity in Commercial Redwood Forests. Final Report. Redwood Sciences Laboratory, Pacific Southwest Research Station, Arcata, CA.

Mitchell, M. J. 1979. Energetics of oribatid mites(Acari: Cryptostigmata) in an aspen woodland soil. Pedobiologia 19: 89-98.

Rappaport, N., M. A. Camann, and K. L. Lamoncha. Response of forest soil Acari to prescribed fire following stand structure manipulation in the Southern Cascade Range. Pedobiologia. *In review*.

Santos, P. F., and W. G. Whitford. 1981. The effects of microarthropods on litter decomposition in a Chihuahuan desert ecosystem. Ecology 62(3):654-663.

Sawyer, J. O., S. C. Sillett, J. H. Popenoe, A. LaBanca, T. Sholars, D. L. Largent, F. Euphrat, R. F. Noss, and R. VanPelt. 2000. Characteristics of Redwood Forests. *In:* The Redwood Forest: History, Ecology, and Conservation of the Coast Redwoods. R.F. Noss (ed.) Island Press, Covelo. 339 pp.

Seastedt, T. R. 1984. The role of microarthropods in decomposition and mineralization processes. Ann. Rev. Entomol. 29: 25-46.

Seastedt, T. R., and D. A. Crossley Jr. 1980. Effects of microarthropods on the seasonal dynamics of nutrients in forest litter. Soil Biol. Biochem. 12: 337-342.

Seastedt, T. R., and D. A. Crossley Jr. 1981. Microarthropod response following cable logging and clear-cutting in the southern Appalachians. Ecol. 62: 126-135.

Swift, M. J., O. W. Heal, and J. M. Anderson. 1979. *Decomposition in Terrestrial Ecosystems*. Univ. California Press, Berkeley. 372 pp.

Thornburgh, D. A., R. F. Noss, D. P. Angelides, D. M. Olson, F. Euphrat, and J. J. Welsh. 2000. Managing Redwoods *In:* The Redwood Forest: History, Ecology, and Conservation of the Coast Redwoods. R.F. Noss (ed.) Island Press, Covelo. 339 pp.

Wagner, D., M. J. F. Brown, and D. M. Gordon. 1997. Harvester ants nests, soil biota, and soil chemistry. Oecologia 112:232-236.

Wallwork, J. A. 1983. Oribatids in forest ecosystems. Ann. Rev. Entomol. 28: 109-130.