Dead Wood and the Richness of Small Terrestrial Vertebrates in Southwestern Oregon[1]

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Abstract

In southwestern Oregon, 24 mature forest stands were used to test the hypothesis that species richness of small terrestrial vertebrates is positively correlated with dead wood volume, and to compare dead wood loads between capture and non-capture sites for species encountered. Dead wood was separated into two components: coarse woody debris (CWD)—defined as down wood of any length ≥ 10 cm in diameter—and snags, defined as standing dead wood ≥ 0.5 m in height and ≥ 25 cm in diameter. The volume of CWD in stands ranged from 50 to 860 m^3/ha and snag volumes ranged from 10 to 240 m^3/ha. Small terrestrial vertebrates numbered between 8 and 20 species per stand based on a pitfall sampling effort of approximately 3,600 trap nights per stand over 2 years. Regression analysis revealed that the species richness of all terrestrial vertebrates taken as a single group increased with increasing volumes of CWD. Viewed as separate taxonomic groups, species richness of small mammals, insectivores, and amphibians all correlated positively with CWD volume; rodent richness showed no significant relationship with CWD. None of the vertebrate groups disclosed significant correlations between species richness and snag volume. Although some individual species at the stand scale did not appear to associate with dead wood, the study results do not preclude the importance of dead wood as a microhabitat feature. The results of this study predict that if all stands are managed to Federal CWD targets in southwestern Oregon, the full component of small terrestrial vertebrates typical of Pacific Northwest forests will not be realized.

Introduction

Many species of wildlife use dead wood as breeding habitat, for cover, or as a source of prey (Bartels and others 1985). In the Pacific Northwest, regulations exist for the management of dead wood on forestlands for the purpose of accommodating wildlife (Oregon Department of Forestry 1991, USDA and USDI 1994). Despite specific number, dimensions, and decay class requirements, dead wood targets frequently vary little for vastly different forest community types partly because of limited available data on natural dead wood conditions and threshold levels of snags and down wood needed to maintain species diversity.

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effective than pitfall traps (Maguire, pers. observ.). Captured animals were transported to the laboratory and identified.

Voucher specimens from this study are housed in museums at Harvard in Cambridge, Massachusetts; Shippensburg University in Pennsylvania; Texas A & M in College Station; and the University of Alaska in Fairbanks. Museum staff verified species.

Table 1—*Pre-harvest characteristics of the 24 DEMO stands in the Umpqua National Forest in southwestern Oregon.*

Block/stand no.	Stand age (yr)	Elevation (m)	BA[1] (m^2/ha)	Mean DBH[2](cm)	Snags (m^3/ha)	CWD[3] (m^3/ha)
Watson Falls						
1	110	1,312	46.90	61	120.9	188.7
2	110	946	42.99	51	83.1	67.4
3	110	1,159	42.99	51	25.0	190.9
4	130	1,312	58.62	61	109.4	185.8
5	130	946	42.99	51	41.5	142.6
6	130	946	58.62	51	48.2	96.6
Little River						
1	400-520	1,281	128.74	122	193.2	547.9
2	250-300	1,373	91.95	91	175.3	205.4
3	300	1,281	103.45	97	70.9	219.0
4	200-250	1,312	80.46	114	240.1	183.2
5	300	1,251	103.45	97	100.0	261.7
6	225-325	1,312	74.71	86	25.7	94.1
Layng Creek[4]						
1	80	763	35.86	46	34.1	425.8
2	60	671	27.82	41	100.4	383.9
3	80	763	35.86	46	38.3	565.2
4	60	671	30.34	43	54.0	862.1
5	65	488	27.82	41	11.0	262.6
6	80	671	28.05	48	38.6	374.5
Dog Prairie						
1	165	1,647	68.97	61	78.7	58.4
2	165	1,647	68.97	61	54.8	91.1
3	165	1,525	68.97	61	125.5	180.0
4	165	1,647	68.97	61	57.1	62.4
5	165	1,647	68.97	61	28.4	50.5
6	165	1,525	68.97	61	142.5	232.9

[1] BA = basal area
[2] DBH = diameter at breast height
[3] CWD = coarse woody debris
[4] All six stands are second growth.

Dead Wood Sampling

Dead wood was sampled on an average of 42 (range: 32 to 64) grid points per stand during snow-free months in 1994 through 1996. Selection of points was based on planned harvest treatments (Halpern and others 1999). Snags were counted on a

volumes are associated with both the youngest and the oldest stands *(fig. 1).* High numbers and volumes of down wood occur early in stand development after a catastrophic disturbance and in old-growth forests as dead wood accumulates (Spies and others 1988). Human disturbance in these forests did not significantly alter this pattern.

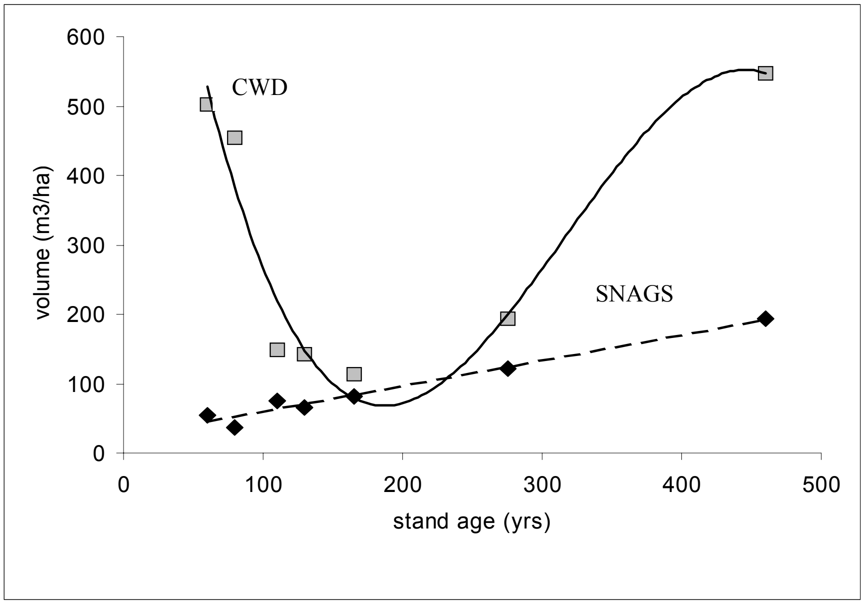

Figure 1—Mean stand volumes of coarse woody debris (CWD) and snags across stand ages for the 24 stands presented in *table 1.* Age groupings are 60/65, 80, 110, 130, 165, 275 (200-325), and 460 (400-520) years.

Snag volumes ranged from 10 to 240 m^3/ha across stands. Spies and Franklin (1988) also predicted a "U"-shaped developmental trajectory for snags in addition to CWD, but this pattern was not observed in these stands *(fig. 1),* possibly due to significant sacrifice or salvage of snags during past harvesting or the lack of snags during stand establishment. Nonetheless, similar non-"U" trends for snag volume have been found in other forest types (Sturtevant and others 1997, Tyrrell and Crow 1994). Snags and CWD volumes were poorly correlated (r^2 = 0.001, p = 0.87).

Species Richness

Regression analysis revealed that the species richness of all terrestrial vertebrates taken as a single group increased with increasing volumes of CWD and all dead wood (snags and CWD), but had no significant relationship with snag volume *(table 2).* Small mammals taken as a group, insectivores, and amphibians all reflected the same trends. The significance and linear relationship between richness and total dead wood volume was impacted by the substantial CWD component of total dead wood. Rodent richness was not correlated with any measure of dead wood volume.

Table 2—*Best fit regression models for the relationship between a variety of dead wood volumes and species richness of small terrestrial vertebrates estimated from the rarefaction technique (Krebs 1989). Species richness was estimated for the sample sizes in parentheses; sample sizes represent the mid-value of captures across 24 stands in the Umpqua National Forest, Oregon.*

Coarse woody debris volume (m^3/ha)			
Species group	**Model form**[1]	r^2	p
All vertebrates (n = 326)	log (SR) = 0.785 + 0.160 log (CWD)	0.42	0.0007
All mammals (n = 301)	log (SR) = 0.797 + 0.101 log (CWD)	0.32	0.004
Rodents (n = 117)	log (SR) = 0.451 + 0.105 log (CWD)	0.14	0.07
Insectivores (n = 212)	log (SR) = 0.507 + 0.109 log (CWD)	0.28	0.009
Amphibians (n = 20)	log (SR) = -0.152 + 0.289 log (CWD)	0.33	0.003

Snag volume (m^3/ha)			
Species group	**Model form**	r^2	p
All vertebrates (n = 326)	SR = 14.890 - 0.007 SNAG	0.02	0.48
All mammals (n = 301)	SR = 11.203 - 0.006 SNAG	0.05	0.30
Rodents (n = 117)	SR = 5.559 - 0.007 SNAG	0.12	0.09
Insectivores (n = 212)	SR = 5.905 - 0.002 SNAG	0.01	0.59
Amphibians (n = 20)	log (SR) = 0.311 + 0.103 log (SNAG)	0.04	0.33

Total dead wood volume (m^3/ha)			
Species group	**Model form**	r^2	p
All vertebrates (n = 326)	log (SR) = 0.744 + 0.166 log (DW)	0.30	0.005
All mammals (n = 301)	log (SR) = 0.786 + 0.099 log (DW)	0.20	0.03
Rodents (n = 117)	log (SR) = 0.481 + 0.086 log (DW)	0.06	0.24
Insectivores (n = 212)	log (SR) = 0.480 + 0.113 log (DW)	0.20	0.03
Amphibians (n = 20)	log (SR) = -0.296 + 0.329 log (DW)	0.29	0.007

[1]SR = species richness = number of species estimated for a sample of n individuals; CWD = coarse woody debris volume; SNAG = snag volume; DW = total dead wood volume = CWD + SNAG volumes.

The results indicate that CWD volume is a better predictor of species richness at the stand level for small terrestrial vertebrates than either snag or total dead wood volumes in southwestern Oregon, even though snags provide a future source of down wood (Spies and others 1988). Many amphibians and mammals exploit snag cavities, flaking bark on snags, or insect and fungal food resources inhabiting snags (Dupuis and others 1995); but for many small terrestrial vertebrates, the absence of snags does not appear to be a limiting factor (Bunnell and others 1997).

Mammals represent the largest number of terrestrial vertebrate species associated with down wood (Brown 1985). Although species abundance may increase as dead wood abundance increases, many mammalian species that use down wood are not believed to require it (Bunnell and others 1997). The exception may be the insectivores. Down wood and insect levels often are tightly linked (e.g., Torgersen and Bull 1995), and insect outbreaks frequently are associated with unnaturally high levels of dead wood resulting from active fire suppression (Campbell and Liegel 1996). Because of the insect/dead wood linkage, animals that primarily consume insects, such as the insectivores, often have close ties to CWD, as is evident in this study. Conversely, insects represent only a portion of most rodent diets, and rodent richness was not strongly tied to down wood.

Amphibians also feed on insects, and they too had richness levels significantly correlated with CWD volume. In addition, amphibians, particularly salamanders, require moist habitat conditions, and the stable, moist micro-environment provided by the space beneath logs or the decomposing interior of logs is well suited to their life requisites (Bury and Corn 1988, Corn and Bury 1991a, DeMaynedier and Hunter 1995).

Individual Species

The number and type of animal species encountered varied widely across the 24 stands *(table 3).* Twenty-nine species were captured, including 7 salamanders, 2 frogs, 6 insectivores, 13 rodents, and 1 carnivore. The number of species in any stand ranged from 8 to 20, a richness range consistent with other studies (Bury and Corn 1988, Gomez and Anthony 1998).

With the exception of the rough-skinned newt *(Taricha granulosa)* and the spotted frog *(Rana pretiosa)*—species that both spend a major portion of their lives in or near water—previous studies suggest that the remaining seven species of amphibians associate with down wood when on land (Brown 1985, Bury and Corn 1988, Bury and others 1991, Corn and Bury 1991a, Stelmock and Harestad 1979). To evaluate the consistency of these relationships, CWD volumes between capture and non-capture stands for each species were tested for differences. Results did not always reflect the trends noted above. Dunn's salamander *(Plethodon dunni)* and western red-backed salamander *(P. vehiculum)* were captured on stands with greater volumes of CWD than non-capture stands. This positive association with down wood also extended to the rough-skinned newt. Conversely, Pacific treefrog *(Pseudacris regilla)* was located on stands with less CWD. Species that did not express significant relationships with down wood include clouded salamander *(Aneides ferreus),* northwestern salamander *(Ambystoma gracile),* and Pacific giant salamander *(Dicamptodon tenebrosus).* The spotted frog and ensatina *(Ensatina eschscholtzii)* were not analyzed because spotted frog was captured on only one stand while ensatina was captured on all stands but one *(table 3).*

Insectivores as a group were encountered more frequently than amphibians *(table 3).* Both the Trowbridge's and Pacific shrews *(Sorex trowbridgii* and *S. pacificus*, respectively) were present in all stands, and the vagrant shrew *(S. vagrans)* was located in all but one stand. Trowbridge's shrew is the most common shrew in Pacific Northwest forests west of the Cascade crest (Carey and Johnson 1995, Gomez and Anthony 1998); however, Dalquest (1941) stated that it is rarely found when the vagrant shrew is present. The results of the current study document the consistent overlap of Trowbridge's and vagrant shrews. Some research suggests that the vagrant shrew prefers moist open areas (Gomez and Anthony 1998, Hawes 1977) and is uncommon or absent in Douglas-fir forests (Terry 1981). These findings are inconsistent with the results of this study as all 23 sites where the vagrant shrew was found were upland Douglas-fir stands *(table 1).* Although some past research indicates that the vagrant shrew does indeed inhabit forested areas (e.g., Corn and Bury 1991b, Hooven and Black 1976), this earlier work has been met with skepticism because of the lack of voucher specimens (Verts and Carraway 1998) and earlier confusion concerning the taxonomic status of the species (Carraway 1990).

Table 3—*Species of terrestrial vertebrates captured in pitfall traps in 24 stands located in 4 blocks across the Umpqua National Forest in southwestern Oregon. Number 1 indicates that the species was captured; 0 represents no capture.*

	Research blocks Stand No.			
	Watson Falls 1 2 3 4 5 6	**Little River** 1 2 3 4 5 6	**Layng Creek** 1 2 3 4 5 6	**Dog Prairie** 1 2 3 4 5 6
Amphibians				
Salamanders				
Ambystoma gracile	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 0 1 1	1 1 1 0 0 1
Aneides ferreus	0 0 0 0 0 0	1 0 0 1 1 1	1 1 0 0 1 1	0 0 0 0 0 1
Dicamptodon tenebrosus	0 0 0 0 0 0	1 0 1 0 1 1	1 1 0 1 0 0	0 0 0 0 0 0
Ensatina eschscholtzii	1 1 1 1 1 1	1 1 1 1 1 0	1 1 1 1 1 1	1 1 1 1 1 1
Plethodon dunni	0 0 0 0 0 0	0 0 0 0 0 0	0 1 1 0 0 1	0 0 0 0 0 0
Plethodon vehiculum	0 0 0 0 0 0	0 0 0 0 0 0	1 1 1 1 1 1	1 0 0 0 0 0
Taricha granulosa	0 1 1 1 1 1	1 0 1 1 1 1	1 1 1 1 1 1	0 0 0 0 0 0
Frogs				
Pseudacris regilla	0 1 0 0 1 0	0 0 0 0 0 0	0 0 0 0 0 0	0 1 0 0 0 0
Rana pretiosa	0 0 0 0 0 0	0 1 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 0
Mammals				
Insectivores				
Neurotrichus gibbsii	1 1 1 1 1 1	1 1 1 0 1 1	1 1 1 1 1 1	0 1 1 0 1 1
Scapanus orarius	1 0 1 0 0 0	0 0 1 1 0 0	1 1 1 1 1 1	0 1 0 1 0 1
Sorex bendirii	0 0 0 0 0 0	0 1 0 1 1 0	1 1 1 1 1 1	0 1 0 0 0 0
Sorex pacificus	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1
Sorex trowbridgii	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1
Sorex vagrans	1 1 1 1 1 1	1 1 0 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1
Rodents				
Arborimus albipes	0 0 0 0 0 0	0 0 0 0 0 0	0 0 0 1 1 1	0 0 0 0 0 0
Arborimus longicaudus	0 0 0 0 0 0	1 0 1 0 1 1	1 1 1 0 0 0	0 1 0 0 0 0
Clethrionomys californicus	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1
Glaucomys sabrinus	0 0 0 0 0 0	1 0 1 1 0 0	0 0 1 0 1 1	0 0 1 0 0 0
Microtus oregoni	1 1 1 1 1 1	1 1 0 1 1 1	1 1 0 1 1 1	1 1 1 1 1 1
Microtus richardsoni	0 0 0 0 0 0	1 0 0 0 0 0	0 0 1 0 1 1	1 0 0 0 0 0
Microtus townsendii	0 0 0 0 0 0	0 1 0 1 1 1	0 0 0 0 1 1	0 0 0 1 0 0

(*table 3* continued)

	Research blocks Stand No.			
	Watson Falls	**Little River**	**Layng Creek**	**Dog Prairie**
	1 2 3 4 5 6	1 2 3 4 5 6	1 2 3 4 5 6	1 2 3 4 5 6
Peromyscus maniculatus	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1
Phenacomys intermedius	0 0 0 1 0 0	0 0 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 0
Tamias siskiyou	1 1 1 1 0 0	0 0 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 0
Tamias townsendii	0 0 0 0 0 0	0 1 1 1 1 1	0 0 1 1 0 0	0 0 0 0 0 0
Thomomys mazama	1 1 1 1 0 1	0 0 1 0 0 1	0 0 0 0 0 0	0 1 1 1 0 0
Zapus trinotatus	0 1 0 0 1 0	1 0 0 0 1 0	1 1 1 1 1 1	1 0 0 0 0 0
Carnivores				
Mustela erminea	0 0 1 0 1 1	1 0 0 0 0 0	0 0 1 0 1 0	0 0 0 0 0 1

All six of the insectivorous species observed in this study are believed to derive habitat benefits from down wood (Brown 1985, Carey and Johnson 1995, Gilbert and Allwine 1991). The almost uniform presence of Pacific, Trowbridge's, and vagrant shrews across the 24 stands would imply that these shrews are not limited by CWD. However, studies at the micro-habitat scale suggest otherwise (reviewed in Verts and Carraway 1998). Of the three insectivorous species for which t-tests could be performed *(table 4),* coast mole *(Scapanus orarius)* did not demonstrate differences in CWD volume between capture and non-capture stands, but both the shrew-mole *(Neurotrichus gibbsii)* and the Pacific water shrew *(Sorex bendirii)* were captured on stands where CWD volumes were more than twice that found on non-capture stands. Interestingly, although the shrew-mole and the Pacific water shrew are both thought to favor moist habitats (Gomez and Anthony 1998), they only overlapped on 9 stands while one or the other species was present on 22 of the 24 study stands. These results suggest that for at least some species, down wood likely works in conjunction with other habitat features to influence stand suitability.

Rodents had a wide range in site occurrence, but only two species showed significant differences in CWD volumes between capture and non-capture stands *(table 4)*. Western pocket gopher *(Thomomys mazama)* was observed on stands with less down wood, and Pacific jumping mouse *(Zapus trinotatus)* was observed on stands with greater down wood compared with non-capture sites. Neither species is believed to have strong dead wood habitat relationships (Brown 1985, Gilbert and Allwine 1991, Gomez and Anthony 1998); however, little is known of the habitat requirements of the jumping mouse (Verts and Carraway 1998) despite its apparent preference for riparian areas (Gomez and Anthony 1998). In addition, Verts and Carraway (1998) contend that the western pocket gopher does not occupy dense forest areas, but results from this study and others, and confirmed voucher specimens conflict with this claim.

Table 4—*Results of Welch's approximate t-tests for comparing differences in mean coarse woody debris (CWD) volumes (m^3/ha) in stands in the Umpqua National Forest, Oregon, where small terrestrial vertebrate species were and were not located.*

	Located		Not located				
	Stands (n)	CWD	Stands (n)	CWD	t	df	p
Amphibians							
Salamanders							
Ambystoma gracile	21	236	3	325	0.33	2	0.77
Aneides ferreus	9	307	15	211	1.32	21	0.2
Dicamptodon tenebrosus	7	399	17	185	2.14	7	0.07
Ensatina eschscholtzii	23	254	1	94	--	--	--
Plethodon dunni	3	441	21	219	2.97	4	0.04
Plethodon vehiculum	7	419	17	176	2.46	7	0.04
Taricha granulosa	16	304	8	133	2.85	20	0.01
Frogs							
Pseudacris regilla	3	100	21	268	3.42	19	0.003
Rana pretiosa	1	205	23	249	--	--	--
Mammals							
Insectivores							
Neurotrichus gibbsii	21	268	3	101	2.79	8	0.02
Scapanus orarius	13	311	11	172	1.88	20	0.07
Sorex bendirii	10	362	14	166	2.51	13	0.03
Sorex pacificus	24	247	0	--	--	--	--
Sorex trowbridgii	24	247	0	--	--	--	--
Sorex vagrans	23	248	1	219	--	--	--
Rodents							
Arborimus albipes	3	500	21	211	1.54	2	0.26
Arborimus longicaudus	8	324	16	209	1.40	14	0.18
Clethrionomys californicus	24	247	0	--	--	--	--
Microtus oregoni	22	234	2	392	0.89	1	0.54
Microtus richardsoni	5	362	19	217	1.40	5	0.22
Microtus townsendii	7	206	17	264	0.86	21	0.4
Peromyscus maniculatus	24	247	0	--	--	--	--
Phenacomys intermedius	1	186	23	250	--	--	--
Thomomys mazama	10	138	14	326	3.01	15	0.009
Zapus trinotatus	11	359	13	152	2.78	11	0.02

Of the remaining species, four are believed to require down wood in their habitat and four appear little impacted by it (Brown 1985). Three of the four species that use CWD were common across the study sites and their routine occurrence in Oregon forests is well documented (e.g., Carraway and Verts 1985, Doyle 1987, Gomez and Anthony 1998, Rosenberg and others 1994, and reviewed in Verts and Carraway 1998). These include western red-backed vole *(Clethrionomys californicus),* creeping vole *(Microtus oregoni),* and deer mouse *(Peromyscus maniculatus).* The fourth species, white-footed vole *(Arborimus albipes),* is one of the rarest microtines in North America (Voth and others 1983). Although it is captured infrequently in a variety of habitats (reviewed in Verts and Carraway 1998), it appears to closely associate with abundant deciduous vegetation (Gomez and Anthony 1998, McComb and others 1993, Voth and others 1983).

The four rodent species captured that do not appear to associate with dead wood at the stand level include red tree vole *(Arborimus longicaudus),* water vole *(Microtus richardsoni),* Townsend's vole *(M. townsendii)* and heather vole *(Phenacomys intermedius).* Red tree voles are primarily arboreal rodents, water voles inhabit streamsides, Townsend's voles occupy moist environments, and heather vole habitat remains under review (Verts and Carraway 1998). Only one heather vole was captured in this study.

There are a number of potential reasons for the inconsistency of some of the wildlife/CWD relationships observed in this study versus other published works: Type I or Type II errors may occur in the statistical analysis of species associations with down wood; the prospective rather than experimental nature of the study may have produced some false results; sampling method bias may have affected the number of species encountered; stand scale associations may not adequately reflect microhabitat associations; and sampling an incomplete range of all possible down wood conditions may have masked species sensitivities to low CWD levels.

The lack of representation of all possible dead wood conditions in any given study is probably the biggest disadvantage to using mean CWD values to evaluate species relationships with dead wood based on capture/non-capture data. In addition, capture and non-capture site comparisons unite stands with varying amounts of down wood based solely on the encounter of as few as a single individual with no consideration of population size. Because population abundance for dead wood associates likely correlates with amount of dead wood, regression analysis is more suited to express this relationship and also to identify volumes above which populations are no longer served by additional dead wood. The reliability of regression results, however, is significantly influenced by the reliability of the abundance estimate. Regardless, mean dead wood comparisons between capture and non-capture stands or stands of different age, structure, or management history is the most published statistic for animal/dead wood relationships, and it is frequently used to compare results among studies. Included in the scope of the current study, regression analysis was performed with animal abundance data to expand on the CWD mean comparisons, but regression results will be reported elsewhere.

Conclusions

Although some small terrestrial species at the stand scale do not appear to associate with dead wood, current results do not preclude the importance of dead wood as a micro-habitat feature. Amphibian and insectivore richness correlates highly with CWD volume and most likely is linked to the importance of dead wood as a habitat moderator for these species and as a source of insect food items. Because of the tie between small vertebrates and CWD coupled with the noted importance of down wood at the micro-habitat scale for many species, CWD manipulation at the stand scale should have a large impact on the richness of ground dwelling vertebrates.

The CWD volumes examined in the 24 stands of this study were greater than five times the current CWD Federal targets for southwestern Oregon. If the richness trends observed with down wood volume determined in this study extend to the lower Federal target levels of CWD, then terrestrial vertebrate richness is predicted to be lower than richness observed in this study on sites where minimum Federal CWD targets are implemented. To maintain the full component of small vertebrates typical of Pacific Northwest forests, a logical dead wood management strategy would be to provide for heterogeneity in down wood across the landscape representing the full range of natural levels. The challenge, however, will be to determine the natural range of CWD conditions and to provide an ecological rationale for the proportional allocations of different CWD volumes.

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