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Terrestrial Arthropod Reviews 4 (2011) 203–220

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Habitats and seasonality of riparian-associated millipedes in southwest Washington, USA

Alex D. Foster* and Shannon M. Claeson

USDA Forest Service, PNW Research Station, 3625 93rd Avenue SW,
Olympia, Washington 98512, USA
*Corresponding author; e-mail: alexfoster@fs.fed.us
Received: 12 May 2011; accepted: 9 June 2011

Summary
Millipedes are a diverse and ancient group of poorly known terrestrial organisms. While recent advances in their taxonomy and distribution have occurred in some areas of the world, our knowledge about the distribution and ecology of many taxa in the Pacific Northwest is limited. We review the ecology of taxa we observed and present results from a field study relating millipede abundance and community composition to environmental conditions of geology, vegetation, and climate. Millipedes of southwest Washington State were surveyed in the spring and fall of 2005 and 2006 along twelve headwater streams in forested landscapes. Overall, we observed 10 families of millipedes, with confirmed identification of 15 species. Millipede community composition differed strongly between seasons and across sites. For each season, we report family-specific multiple regressions relating millipede abundance/presence to environmental conditions. Given the ecological importance of millipedes as detritivores, more information on taxonomy and environmental relationships is needed. This research provides insight into the patterns and distribution of riparian-associated millipedes in the Pacific Northwest.

Keywords
Diplopoda; ecology; Pacific Northwest; riparian; biodiversity; detritivore

Introduction

Millipedes, as detritivores, feed on decaying plant material and, as they are adapted for burrowing in the substrate, contribute to soil nutrient and mineral cycling. Millipedes increase forest floor organic decomposition rates by shredding leaf litter, making it more available to bacteria and fungi (Anderson, 1988; Wolters, 2000). By converting leaf litter to frass, millipedes enhance the release of nitrogen and carbon which accelerates bacterial activity and bio-assimilation (Carcamo et al., 2000).

Knowledge uncertainty regarding millipedes falls into three categories: 1) taxonomic, 2) distributional, and 3) ecological (Molina and Marcot, 2007). Millipedes are

DOI 10.1163/187498311X591102

a relatively uninvestigated group of organisms that play an important role in forest biodiversity. The millipede class Diplopoda is large and diverse, with more than 12,000 nominal species, but an estimated diversity of approximately 80,000 species worldwide based on known degrees of endemism (Sierwald and Bond, 2007). In North America, there are approximately 914 described species in 52 families (Hoffman, 1999); however we still lack basic knowledge concerning the taxonomy, distribution, and ecology of many species within this large group of organisms (Shelley, 2003; Sierwald and Bond, 2007). In a comprehensive review of soil fauna in terrestrial ecosystems worldwide, the highest millipede biomass reported in temperate coniferous forests occurred in the Pacific Northwest (Petersen and Luxton, 1982).

Most ecological studies of millipedes have a narrow geographic focus and tend to concentrate on few taxa. However, recent studies have addressed environmental factors affecting millipede abundance and diversity across biomes at sizeable spatial scales (Wytwer et al., 2009), and addressing large-scale ecosystem processes such as climate change (David, 2009). In the Pacific Northwest, interest in millipedes has increased with several recent discoveries of new taxa that includes two new families to the region, Microlympiidae (Shear and Leonard, 2003) and Anthroleucosomatoidae (Shear and Leonard, 2004), plus new additions to the Caseyidae, Tingupidae and Nearctodesmidae families (Shear and Leonard 2007; Shear and Shelley, 2007; Shelley and Shear, 2006). Millipede taxonomy in the Pacific Northwest includes at least 210 known species organized in 29 families and 10 orders (Parsons et al., 1991; Hoffman, 1999). Although there have been some recent developments with regard to taxonomy and distribution, practically nothing is known about the ecological aspects of millipedes found in this region.

The intent of this study is to better understand the distribution and ecology of millipedes in southwest Washington State. Based on millipede abundances observed along headwater streams in managed forests during the spring and fall of 2005 and 2006, we examine the relationships between millipede families, community composition, and environmental variables to describe millipede diversity, distribution patterns, and seasonal occurrence. Our objectives are to determine (1) if family-level millipede abundance and richness can be related to common environmental measures of riparian habitats; and (2) if millipede community composition varies across sites and environmental gradients. This exploratory analysis highlights possible relationships between millipede families and environmental factors. Although the sample size is relatively small, each stream was studied in depth, and since there is little information regarding the ecology of terrestrial millipedes, the results presented here offer a significant contribution to the current knowledge of a poorly known group of arthropods.

Methods

Study area

We investigated millipede communities in the riparian zones along headwater streams in three geographically separate sites (Tags, Split, and Ells) in southwest Washington

(Figure 1). These lands are managed by the Washington Department of Natural Resources (WADNR) for commercial forestry. The three sites were chosen as part of a larger project to assess the effects of experimental riparian buffer strips on a variety of biological and physical factors along headwater streams (USDA Forest Service, unpublished data). Timber harvest occurred in early 2004, one year prior to the data reported here. Our objectives were to examine millipede diversity and their seasonal and distribution patterns along environmental gradients; however, we also examined study design factors (e.g., buffer type) and their influence on millipede demographics.

The Tags site is located in the Black Hills of Thurston County (46.99°N, 123.10°W, NAD 1983), approximately 15 km west of the city of Olympia, Washington. The other two sites, Split (46.58°N, 123.69°W) and Ells (46.64°N, 123.71°W) are located in the Willapa Hills of Pacific County about 17 km from the Pacific coastline. All sites share a maritime climate where the average annual precipitation is 125 cm, reaching its peak in November and low in August. The sites consisted of spatially close groupings of 3, 4, or 5 streams. Each stream within a site had one of four buffer configurations: fixed-width (40 m wide, continuous), patch (variable width, non-continuous), no-buffer, or control (no harvest).

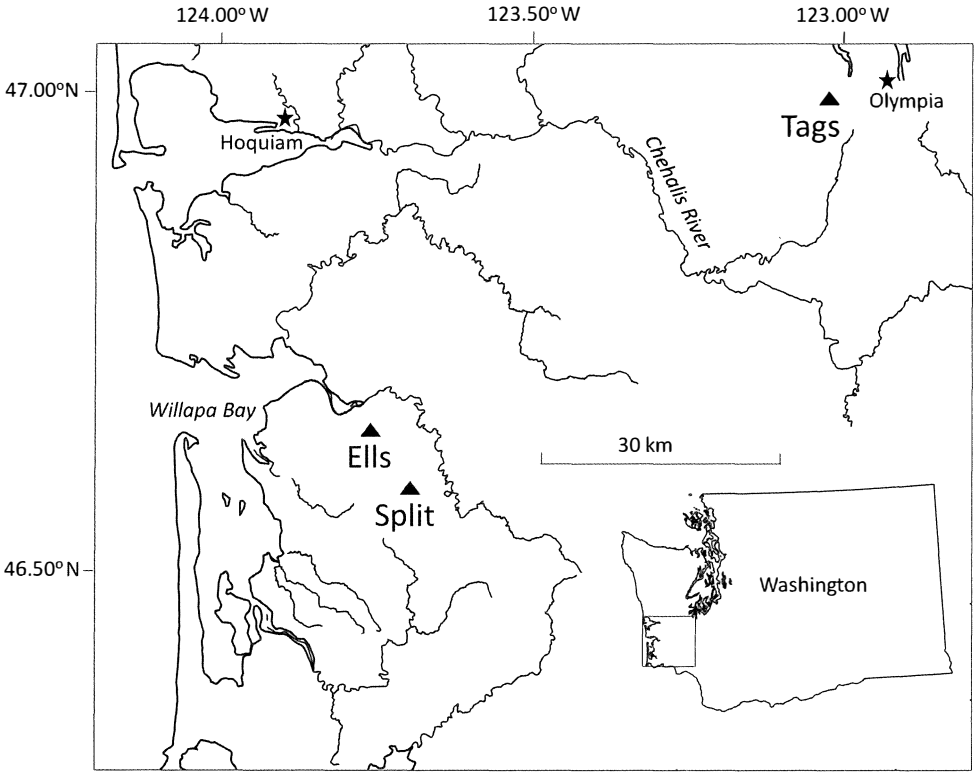

Figure 1. Study sites (triangles) Ells, Split, and Tags in southwest Washington State, USA.

Riparian forests at the Tags site consist of multi-story, mixed conifer and broadleaf tree species, including Douglas-fir *Pseudotsuga menziesii* (Mirb.) Franco (Pinaceae), western redcedar *Thuja plicata* (Donn) (Cupressaceae), red alder *Alnus rubra* (Bong) (Betulaceae), and black cottonwood *Populus trichocarpa* (Tor. & A.Gray) (Salicaceae). The dominant tree age class is approximately 50 years (Figure 2a). The well-established understory consists of red alder, western redcedar, devil's club *Oplopanax horridus* (Miq.) (Araliaceae), vine maple *Acer circinatum* (Pursh) (Aceraceae), and western sword fern *Polystichum munitum*(Kaulf.) (Dryopteridaceae). At the Ells site, the forest is primarily 60-year-old Douglas-fir trees intermixed with some western hemlock and Sitka spruce *Picea sitchensis* (Bong) (Pinaceae). Western hemlock and patches of sword fern comprise the understory at Ells, with some deciduous tree species present (Figure 2b). At the Split site (Figure 2c), forests are 45-year-old western hemlock *Tsuga heterophylla* (Sarg.) (Pinaceae) and there is little understory cover, deciduous or herbaceous.

Millipede sampling

Sampling for millipedes occurred at all sites in the spring (April-May) and fall (November-December) of 2005 and 2006. Two sub-season surveys were conducted within each season, one month apart, with the observations added together for an abundance count per season. At each site, two transects were established parallel to the headwater streams, one on each side. Each transect comprised five permanent sampling stations (Boag, 1982) alternately placed at 2 m and 5 m perpendicular to the stream channel and spaced 25 m apart, for a total of ten stations per stream (Figure 3). Each station consisted of four coverboards placed around a center point, 1 m apart. We made coverboards from two pieces of 30 x 30 cm cardboard stapled together along one edge (book-style), such that the total cardboard surface area was 0.36 m^2 and covered 0.09 m^2 of ground. Cardboard coverboards are a common method of surveying for terrestrial mollusks (Boag, 1990; Hawkins et al., 1998) that we also found to be a good method for live-trapping millipedes. Voucher specimens were collected early in the study, with taxonomic confirmation done by Dr. William A. Shear (Hampden-Sydney College, VA) and William P. Leonard (Olympia, WA). We used family as our lowest reliable taxonomic level for analysis because current descriptions of genera and species are experiencing taxonomic reevaluations and many unknown taxa are being described (W.A. Shear, pers. comm.)

Environmental variables

We measured various environmental site characteristics as potential explanatory variables for millipede abundance and community composition (Table 1). Stream basin size was derived from digital elevation data refined with low-altitude aerial photos. Slope (%) along the stream channel was measured with a clinometer. Air and soil temperatures (°C) were measured for each stream at 1 m above ground and 15 cm below ground, respectively, at the start and end of each day's survey. We acquired precipitation data from the National Climate Data Center weather stations closest to each sample site ('Hoquiam' ~40 km for the Split and Ells sites, 'Olympia' ~16 km for Tags)

Figure 2. Study sites showing vegetation structure. Tags site in figure A, Ells site in figure B, and Split site in figure C. All are mid-seral forest stands (overstory tree age ~50+ years). Courtesy of Jeffrey Ricklefs.

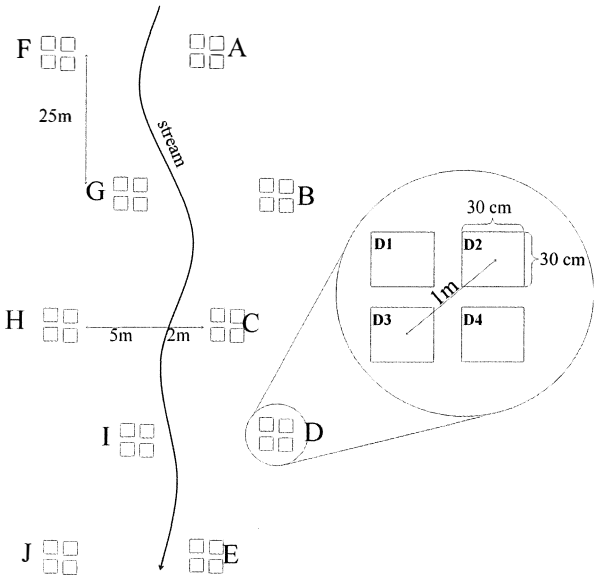

Figure 3. Sampling design consisting of four cardboard cover objects (each 900cm^2) grouped in five stations along each side of a headwater stream.

to calculate the precipitation totals for the 7 days prior to each survey day. The data are thus specific to sample times and sites, but not to individual streams. Once per stream, we measured the percent area occupied by small wetland features (% wetland) within a 10-m band on each side of the stream channel by surveying hydrophytic and wetland-obligate plant species along with soils and hydrologic expression, using a locally adapted method for small, forested wetland delineation (Janisch et al., 2011).

For each stream, once per year during the summer, we measured understory vegetation cover, overstory canopy cover, and coarse woody debris (CWD) volume within 12 m on each side of the channel (WADNR, unpublished data). We estimated understory vegetation cover (%) from 24 plots (3 x 3 m each) per stream with species grouped into five categories: 1) herbs, 2) ferns, 3) woody shrubs, 4) small hardwoods <10 cm diameter, and 5) small conifers <10 cm diameter. Overstory canopy cover (%) was estimated from hemispherical photographs taken at half of the vegetation plots. The photographs had a 20% filter around the periphery of the aperture to block out topographical variation. Coarse woody debris volume (m^3/ha) was estimated using three L-shaped transects, with each leg of the L being 10 m long. Wood pieces measured had a diameter ≥10 cm and a length ≥0.3 m and wood volume was calculated using the Van Wagner (1968) method.

Statistical analyses

We used multiple regressions to highlight relationships between millipede family abundance, or presence/absence, and the environmental variables measured from the 12 headwater stream riparian areas over the course of two years. Spring and fall

observations were analyzed separately because some families showed strong seasonal dominance, and vegetation characteristics varied between spring and fall. Life history accounts indicate that few millipede species live longer than one year (David, 1992; Baumeister, 2002; Youngsteadt, 2009), so data for each year could be treated as independent samples. Some explanatory environmental variables were correlated with each other (Pearson's product correlation coefficient > |0.6|), therefore we selected one representative variable having the highest correlation with our response variables to use in the regression models. No interactions between the explanatory variables were tested. The distribution of the data within each family or grouping (e.g., total abundance, taxa richness) and model residuals determined which General Linear Model (GLM) error structure was appropriate to use for the family-per-season dataset (Crawley, 2007). Data for total millipede abundance, taxa richness, and the fall abundance (count) data for the family Hirudosomatidae had sufficient sample sizes to be modeled using a normal distribution. The remainder of the count data by family did not, and was modeled using a Poisson distribution. For the few families observed in fewer than 50% of the samples per season, a logistic (binomial) GLM model was used for simple presence/absence determinations. Families observed in ≤ 25% of the samples in a given season were considered too rare for regression analysis, and were dropped. We began with a full model and used step-down model simplification to eliminate insignificant variables (Crawley, 2007). Once the significant environmental variables were selected, we

Table 1. Environmental variables describing site characteristics. The ranges of values, minimum-maximum, are from the streams within each site. For variables that change over time [temperatures, precipitation, vegetation and coarse woody debris (CWD)], individual stream values were averaged over the study period. Vegetation % cover may sum to >100% due to layering. See methods for specific information about each environmental variable.

Environmental variable	Ells	Split	Tags
Number of streams	3	4	5
Aspect	SW	NE	NE
Stream length (m)	100 – 250	250 – 400	200
Basin area (ha)	3.1 – 6.9	3.6 – 7.6	2.9 – 5.6
Elevation (m)	45 – 76	222 – 342	239 – 279
Slope (%)	14 – 18	21 – 27	38 – 46
Air temperature (°C)	9.4 – 10.8	3.9 – 11.4	7.6 – 11.0
Soil temperature (°C)	8.5 – 10.9	7.4 – 10.9	7.1 – 10.1
Precipitation (cm, 7-days)	1.7 – 2.3	1.5 – 1.9	1.9 – 3.0
Wetland (% area)	0 – 2	0 – 10	13 – 30
Canopy (% cover)	0.2 – 76.2	7.7 – 76.2	4.6 – 76.8
Conifer (% cover)	1.3 – 11.5	0.4 – 3.3	0.8 – 4.6
Hardwood (% cover)	0.1 – 2.4	0 – 1.4	12.6 – 31.6
Shrub (% cover)	3.3 – 22.5	2.8 – 6.2	5.3 – 24.2
Fern (% cover)	22.5 – 33.3	6.0 – 16.9	22.8 – 79.7
Herb (% cover)	3.1 – 28.3	12.6 – 33.0	5.5 – 31.0
CWD (m^3/ha)	125 – 776	246 – 390	207 – 313
Lithology	sandstone	sandstone	basalt
Soil type	silt loam	silt loam	gravelly silt loam

added categorical covariates of year, region, site, and buffer type into the model one at a time to test study design factors that may have influenced the results. A significant categorical variable in the regression indicates unaccountable variation not attributable to the environmental variables. Multiple regressions and correlation measures were conducted using the statistical package R (version 2.11.0).

To evaluate millipede community composition across seasons, sites, and environmental gradients we used nonmetric multideminsional scaling (NMS) with a Sorenson distance measure (McCune and Grace, 2002; PC-ORD® v.5.21). Family mean abundances were log(x+1) transformed to form a matrix of 10 millipede families and 24 sample points (12 stream riparian areas, 2 years). In one ordination, spring and fall seasons were analyzed together to look for community differences between seasons. Forty runs were performed for each ordination, and the run with the lowest stress (14.6) and a stability criterion of 0.00001 was selected. A 3-dimensional solution was recommended, representing 85% of the total variance. We then overlaid the environmental variables to display the strongest correlations (Pearson's *r*) between the variables and ordination axes.

Results

Over the entire study period, we counted 2092 millipedes distributed among 10 families, with 59% of the millipedes observed in the fall and 41% in the spring (Table 2). Daytime air and soil temperatures were warmer in the spring (air 11.5°C, soil 10.5°C) than fall (air 8.5°C, soil 7.5°C), whereas recent precipitation (previous 7 day total) was higher in the fall (3.3 cm) than spring (0.8 cm). Six of the millipede families were observed primarily in the fall, while four families were more common in the spring. Taxa richness at the family level was similar between seasons, although with different combinations of families (10 in spring, 9 in fall), years (10/year), and sites (10/site).

Table 2. Millipede abundance (number of individuals observed from all streams) and the proportion of total abundance (Total %) for each family over the entire study period, followed by the proportion of each family observed in spring versus fall (Spring %, Fall %).

Millipede Order	Millipede Family	Abundance (no. individuals)	Total (%)	Spring (%)	Fall (%)
Chordeumatida	Caseyidae	399	19	34	66
Chordeumatida	Conotylidae	206	10	9	91
Chordeumatida	Striariidae	26	1	42	58
Chordeumatida	Tingupidae	156	7	72	28
Julida	Parajulidae	243	11	37	63
Polydesmida	Nearctodesmidae	62	2	94	6
Polydesmida	Polydesmidae	86	4	35	65
Polydesmida	Xystodesmidae	27	1	70	30
Polyxenida	Polyxenidae	296	14	100	0
Polyxenida	Hirudisomatidae	591	28	13	87
All millipedes		2092	100	41	59

We did not detect any relationship between the riparian buffers and millipede abundances (i.e., the buffers were not a significant covariate in the NMS ordination or in the regression models). Any change in millipede abundance due to timber harvest was either incorporated into the environmental variables (e.g., canopy cover) or was not directly observable in our data.

Millipede community composition

Millipede community compositions showed strong seasonal and site differences, along with relationships to some environmental variables. Season and climatic conditions were strongly correlated with axis 1 of the NMS ordination (Figure 4ab), with spring samples associated with greater air and soil temperatures (r = 0.49 and r = 0.59, respectively) and fall samples associated with greater precipitation (r = 0.66). Sites are arrayed in a gradient along axis 2 (Figure 4a). Greater overall millipede abundance (r = 0.58) and taxa richness (r = 0.48), greater percent cover of shrubs (r = 0.62), ferns (r = 0.68), understory hardwood trees (r = 0.60), wetlands (r = 0.45), and greater stream slope (r = 0.51) were positively associated with axis 2. Axis 3 was not associated with any measured variable (Figure 4b), indicating that 23% of the variation in the

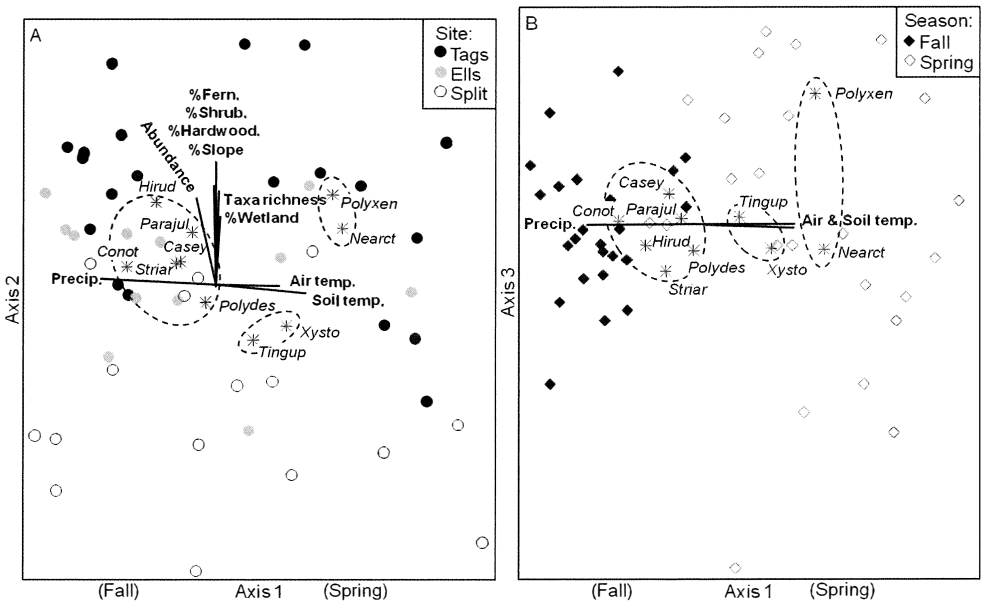

Figure 4. Nonmetric Multidimensional Scaling (NMS) was used to depict relationships between sample units (48 stream riparian areas) in terms of millipede community composition (10 families). The resulting 3D ordination explained 85% of the variance in the millipede communities. Samples are coded by site (circles) in figure A, and season (diamonds) in figure B. Millipede families are denoted by an * (abbreviated taxon names are italicized). Environmental variables correlated with the ordination are denoted by the line vectors (abbreviated variable names are in bold). Circles of dashed-lines group similar occurring millipede families.

ordination is due to factors not included in this study or that the factors measured were at too coarse of a resolution.

The percent cover of shrubs, ferns, small hardwood trees, wetlands, and stream slope (hereafter called the 'shrub group' of variables) were all positively correlated with each other ($r > |0.6|$). Riparian areas along the Tags streams had relatively high amounts of this 'shrub group', compared to the Ells or Split streams (Table 1). Thus millipedes that were observed in greater abundance at the Tags site tended to be associated with the 'shrub group' of environmental variables (Figure 4a). We also observed a consistent negative relationship between regression coefficients of the 'shrub group' versus herb percent cover (Table 3), probably because in landscapes with heavy shrub, fern, and small hardwood tree cover, the amount of space and/or light available to herbs would be limited.

Millipede families

Millipede families within the NMS ordination form three groups defined by their seasonality, abundance, relationship with the 'shrub group', or some combination of these variables. The groups are the (1) fall-dominant taxa of Caseyidae, Conotylidae, Hirudisomatidae, Parajulidae, Polydesmidae, and Striariidae; (2) spring-dominant taxa of Polyxenidae and Nearctodesmidae that were high in abundance and positively correlated with the 'shrub group' of variables; and (3) spring-dominant taxa of Tingupidae and Xystodesmidae that were low in abundance and negatively correlated with the 'shrub group'.

Of the fall-dominant group, Hirudisomatidae was the most numerous, making up 28% of total detections, most of which were in the fall (Table 2). This family was most abundant at the Tags streams, positively associated to the 'shrub group' and negatively associated with herb cover in both seasons (Table 3). Caseyidae was the second most abundant family (19% of total), was found at all sites, and was generally more abundant in the fall. In both seasons, Caseyidae abundance was associated with streams at lower elevation, less understory conifer cover, the 'shrub group', and more CWD, plus other environmental variables specific to each season. Parajulidae represented 11% of total detections, was somewhat more common in the fall than spring, and was found at all sites. There were twice as many individuals observed in the fall of 2006 as in the fall of 2005, producing a significant year effect on Parajulidae abundance. Regression models indicated that a number of environmental variables were significantly associated with Parajulidae abundance in the spring, but few in the fall, possibly because of the high variability between years. Conotylidae, with 10% total detections, was observed primarily in the fall and at the Ells streams. Conotylidae was positively associated with stream basin size in both seasons, and with other environmental variables specific to each season. The families Polydesmidae and Striariidae made up 4% and 1% of the total detections, respectively. They were both observed slightly more frequently in the fall and were found in similar abundances at all sites. Polydesmidae spring abundance in 2005 was more than twice that in 2006; year was a significant covariate with no other explanatory variables. Polydesmidae fall abundance was associated with cooler

Table 3. Multiple regression correlation coefficients for significant environmental variables related to millipede family abundance (Normal and Poisson models) or presence/absence (Binomial models). Binomial model coefficients are back-transformed (e^B) and italicized. Spring and fall abundances are analyzed separately. Max sample size (n) is 24 per group. Millipede families per season with a sample size ≤ 6 are considered too rare for regression analysis (Model = "none").

Millipede	Season	n	Model	Basin (ha)	Elev. (m)	Air[1] (°C)	Precip.[2] (cm)	Canopy (%)	Conifer (%)	Shrub[3] (%)	Herb (%)	CWD[4] (m^3/ha)	Year
Caseyidae	Spring	21	Poisson	−0.605	−0.010		1.049		−0.317	−0.041	0.081	0.004	
	Fall	23	Poisson		−0.005	−0.098			−0.102	0.018		0.001	
Conotylidae	Spring	10	Binomial	2.670		1.765				1.183			
	Fall	23	Poisson	0.317			0.137	−0.010	0.106				
Hirudisomatidae	Spring	12	Poisson	0.647	−0.011	0.284			−0.466	0.181	−0.087		
	Fall	20	Normal							0.116	−0.051		
Nearctodesmidae	Spring	14	Poisson		0.035				0.484	0.062	−0.096	−0.015	
	Fall	3	None										
Parajulidae	Spring	23	Poisson	−0.715	−0.013		−0.985	0.018	−0.292	−0.048	0.115	0.003	
	Fall	20	Poisson				0.197			0.060	−0.030		0.868
Polydesmidae	Spring	14	Poisson										−0.847
	Fall	16	Poisson			−0.310	0.516		0.128				
Polyxenidae	Spring	10	Binomial										33.016
	Fall	0	None										
Striariidae	Spring	6	None										
	Fall	9	Binomial					1.039					
Tingupidae	Spring	21	Poisson			0.177				−0.081	0.019	0.002	
	Fall	18	Poisson	0.308				−0.020		−0.042			
Xystodesmidae	Spring	9	Poisson		0.017							0.005	
	Fall	5	None										
All millipedes	Spring	24	Normal			0.131	0.593		−0.095			0.002	0.864
	Fall	24	Normal			−0.108				0.059	−0.026		
Taxa richness	Spring	24	Normal										
	Fall	24	Normal										

[1] Air temperature is correlated with soil temperature.
[2] Precipitation is the sum of the previous 7 days rainfall from time of data collection.
[3] Shrub % cover is correlated with fern, hardwood, and wetland % covers, and basin slope.
[4] Coarse woody debris (CWD).

air/soil temperatures, recent precipitation, and more understory conifer cover. Striariidae detections in the spring were too rare to analyze with multiple regression; however fall presence/absence was modeled using logistic multiple regression, resulting in understory conifer cover as the only significant explanatory factor of Striariidae presence.

Among the spring-dominant groups, Polyxenidae was the third most abundant family (14% of total, Table 2), was found at all sites, but was found primarily in the spring of 2006. None of the environmental variables significantly explained Polyxenidae presence besides year as a covariate (Table 3). Nearctodesmidae made up 3% of the total detections and was found almost exclusively in the spring and at the Tags site (only 1 individual was found at Ells). Nearctodesmidae was positively associated with the 'shrub group', understory conifer cover, and elevation, but negatively associated with herb cover and CWD. Tingupidae, with 7% of total detections, was most abundant along the Split streams. Tingupidae was negatively associated with the 'shrub group' in both seasons, and with other environmental variables specific to each season. Xystodesmidae made up only 1% of the total detections and was found most often in the spring and predominantly at the Split site. Xystodesmidae spring abundance was positively associated with elevation and CWD.

Discussion

The ten millipede families detected at the sites belonged to five orders: Chordeumatida, Polyzoniida, Julida, Polydesmida, and Polyxenida.

Chordeumatida millipedes tend to be most abundant in the temperate and moist Atlantic forests of Europe where stable and predictable climatic conditions permit numerous, early-maturing millipede species to exist (Kime and Golovatch, 2000). Climatic conditions in these forests are very similar to the stable conditions found in the forests of western Washington where local weather is dominated by onshore marine flow. We observed four families of the order Chordeumatida, including the fall-dominant families Caseyidae, Conotylidae and Striariidae and the spring-dominant family Tingupidae.

Caseyidae individuals have been found in a variety of deciduous and conifer litter along the Pacific coast (Gardner and Shelley, 1989). Similarly, we found the Caseyidae to be associated with the 'shrub group' and CWD. We had two confirmed Caseyidae taxa, *Caseya borealis* (Gardner and Shelley) and *Opiona spp*. (Chamberlin); both taxa were found at all sites. Ecology descriptions for Conotylidae are also rare in the literature, although Shear (1971) noted that conotylids were found in leaf litter and rotted wood in West Virginia and in sites supporting hemlock, spruce, and fir in the western U.S.A. Members of the genus *Bollmanella* (Chamberlin) were also found in the duff and litter of deciduous species (Shear, 1974). *Bollmanella complicata* (Shear) was our only confirmed species of Conotylidae and it was found at all sites. Unlike Caseyidae, we did not find Conotylidae to be associated with deciduous shrub or

tree cover, although there was a positive association with understory conifer coverage. Conotylids are active throughout the winter months and at exceedingly high elevations (Shear, 1971) and both Caseyidae and Conotylidae are found as far north as SE Alaska (Shelley et al., 2007, 2009a), thus at least some species within these families persist in cold environments. We observed both Caseyidae and Conotylidae individuals moving about underneath the cardboard cover objects under a blanket of snow during the months of November and December.

Overall, we had very few detections of the family Striariidae in riparian areas of southwest Washington State, with one individual confirmed in the genus *Striaria* (Bollman). However, subsequent taxonomic work creates some uncertainty of the genus type confirmed (Shear and Krejca, 2007). Regardless, Striariidae had a positive association to canopy cover and was a fall-dominant family, although a fair number of detections also occurred in the spring. We could find no other published accounts regarding the ecology of Striariidae.

The most recent taxonomic revision for North America (Shear, 1981) listed ten species of Tingupidae, of which six occur in the Pacific Northwest region, including *Tingupa benedictae* (Shear), our only confirmed species. Unfortunately, very little is known about the ecology of this family. We found Tingupidae primarily in the spring where it was associated with greater air/soil temperatures, herb cover, and CWD, and with lower amounts of the 'shrub group' in both spring and fall. Like Caseyidae and Conotylidae, recent discoveries of Tingupidae in remote areas of the Northwest such as southeast Alaska and as far west as Kodiak, Alaska, suggest its persistence in cold environments (Shear and Shelley, 2007; Shelley et al., 2009b).

Hirudisomatidae, order Polyzoniida, was the most abundant family we found and was observed more in the fall season and at the Tags streams. The predominant species occurring at all the sites was confirmed as *Octoglena anura* (Cook). *O. anura* occurs from the Pacific coast inland to the west slope of the Cascade Range from British Columbia south to Douglas County, Oregon (Shelley, 1995). This large area includes not only our study sites, but encompasses the central core of the Pacific Northwest region where weather is reasonably stable, temperatures are moderate, and precipitation is high. Habitat notations for the genus *Octoglena* along the Pacific coast include mixtures of deciduous and conifer litters, "under log", "under wet rotting branches," or "under rock on damp, muddy floor" (Shelley, 1995). The Tags site had the densest understory of the three sites, a NE aspect decreasing solar exposure, and several small, forested wetlands and seep features, all of which features helped to create humid riparian areas. Our results confirm that moist conditions with abundant deciduous cover are preferred habitats of this species.

Of the order Julida, our specimens were entirely from the family Parajulidae, with adult specimens showing the characteristic elongated, often hooked epiproct (Shelley, 2002). Parajulidae is the largest family of millipedes in North America, yet it is essentially unstudied, and some 200 undiscovered species are anticipated in this taxon alone (Shelley, 2010). Only one genus, *Bollmaniulus* (Chamberlin), was confirmed from this study. The genera *Litiulus*, *Saiulus* and *Uroblaniulus* may have also occurred at our

study sites (Hoffman, 1999). The relationship of parajulid abundance to environmental variables in this study is not clear because many environmental variables were significant for spring abundances, whereas fewer variables were significant, yet in the opposite direction, for fall abundances. Some of this variability may result from the apparent increase in abundance from 2005 to 2006, primarily in the fall. The nascent state of Parajulidae taxonomy very likely confounds their association with ecological traits. Given that there are many known and unknown species within this family, our attempt at establishing environmental relationships at the family level should be viewed cautiously.

We observed three families of the Polydesmida order; Polydesmidae, Nearctodesmidae, and Xystodesmidae. Polydesmidae was primarily found in the fall, whereas both Nearctodesmidae and Xystodesmidae were spring-dominant families. Within the Polydesmidae, we observed only the medium-sized, pinkish millipede *Scytonotus bergrothi* (Chamberlin), although *S. insulanus* (Attems) is also known to be found in the region (Shelley, 1993; Hoffman, 1999). Habitat descriptions for *Scytonotus* include a combination of deciduous (*Alnus* spp. and *Acer* spp.) and conifer litter, or under the bark of decaying logs or Douglas-fir trees, or on moss (Shelley, 1993). Other studies conducted in forests on the west slope of Oregon's Cascade Range showed that seasonal changes in litter-dwelling arthropods, including several taxa of millipedes were closely tied to seasonal litter moisture levels or microclimate (Rykken et al., 2007; Yi and Moldenke, 2008). We found fall abundance of *Scytonotus* to be associated with understory conifer cover, recent precipitation, and cooler temperatures, suggesting their preference for moist coniferous litter.

Nearctodesmidae is an abundant and common family along the Pacific Northwest coast, ranging from San Francisco to the southern tip of SE Alaska and inland into western Montana (Shelley, 1994a). We confirmed the species *Kepolydesmus anderisus* (Chamberlin) and the closely related species, *Nearctodesmus insulanus* (Chamberlin) (Shelley, 1994a). Adult members of this family are usually maroon colored and large, second in body size only to those of the Xystodesmidae. However, despite their size, little is known about this family in the Pacific Northwest. Hoffman (1999) notes "The content and affinities of this taxon are far from being settled." We found them almost exclusively in the spring and at all sites; however the family was most abundant at the Tags site, with positive associations with understory conifer cover and the 'shrub group'. Since 94% of the individuals of Nearctodesmidae we encountered were found in the spring and most were fully formed or late instar adults, it is possible that spring is a time of migration and breeding.

Within the Xystodesmidae, we encountered the large and conspicuous *Harpaphe haydeniana* (Wood). We found no individuals from the related genera *Chonaphe* (Cook) or *Tubaphe* (Causey) whose distribution includes our study sites (Shelley, 1994b). Surprisingly, we had few detections of *H. haydeniana*; however their large body size makes for a greater contribution to biomass than numbers alone would indicate. Mature *Harpaphe* individuals weigh between 750-1000 mg, in contrast to other millipedes that weigh from 10-100 mg (N. Baumeister, pers. com.). In the spring, *H. haydeniana* adults are known to aggregate in large numbers at a specific location for

mating, and then disperse, thus adults may be present in a given location only briefly (Buckett and Gardiner, 1968; Baumeister, 2002). Individuals have been found in mixed coniferous forests, occasionally with a deciduous component that included red alder and bigleaf maple (Buckett and Gardiner, 1968; Baumeister, 2002). Our Tags and Ells sites generally have these attributes, but most of our detections of *H. haydeniana* came from the Split site where the overstory is western hemlock, which is reported to be their least- preferred food source and one that provided the slowest growth rate of *H. haydeniana* in laboratory experiments (Carcamo et al., 2000; Baumeister, 2002).

Very little information exists about the minute, hairy millipedes of the order Polyxenida in North America; taxonomic information is sparse and distributional and ecological information is rare. *Polyxenus pugetensis* (Kincaid), of the family Polyxenidae, was the most likely species we detected based on known range descriptions (Hoffman, 1999), however no specimens have yet been taxonomically confirmed. We observed individuals in fairly high abundance at select streams within each of the three sites, but only in the spring, and 99% of the observations occurred in 2006. Weather station temperature and precipitation records showed nothing unusual about the spring of 2006, although rainfall in January of 2006, four months prior to survey, was 161% of normal. Because the year to year difference in abundance was so large, the multivariate regression with environmental variables was not informative in terms of correlated habitat (i.e., the year effect likely masks any stream-scale environmental relationships). A related species, *Polyxenus lagurus* (Linnaeus), is found in mixed coniferous forests in Greece and has been positively correlated with air temperature and negatively correlated with rainfall (Karamouna, 1990). In Great Britain, *P. lagurus* was observed to be present on "solid surfaces open to more or less direct sunlight…" (Alexander, 2006). These accounts and our results suggest that Polyxenidae individuals prefer warm areas in the spring.

Conclusion

Relatively less motive organisms, such as terrestrial mollusks and millipedes, tend to develop unique habitat and environmental associations, especially on the peripheries of their ranges (Molina and Marcot, 2007), and many millipede species have likely developed specialized niches or life-history requirements that are yet to be discovered. However, the "appreciation of the ecological importance of a group of organisms is directly proportional to the understanding of its taxonomy, which has advanced to the level at which broadly based biological research is feasible in only a few millipede families" (Shelley, 2010). The ecological relationships of certain millipede families of the Pacific Northwest described in this review are an introductory step in acknowledging and understanding this poorly known group of animals. As millipede taxonomic and distributional knowledge improves, awareness and conservation will contribute to safeguarding this vital component of Pacific Northwest forest biodiversity.

Acknowledgements

This work was part of a larger collaborative effort with the Washington State Departments of Natural Resources and Ecology, and the University of Washington. Funding for this study was primarily through the US Forest Service PNW Research Station, with in-kind assistance from the other named collaborators. We gratefully acknowledge Joan Ziegltrum, Dr. William Shear, and Bill Leonard for their contributions to the study. Special thanks go to Wren Wolf, Kim Gridley, and several others for their help with millipede surveys. The comments provided by Bruce Marcot, Nancy Baumeister, and Brent Matsuda greatly improved the manuscript. Additional review was provided by Lara Boyd and Kathryn Ronnenberg. We thank E. Ashley Steel for her statistical assistance.

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