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Terrestrial and Aquatic Macroinvertebrate Assemblages as a Function of Wetland Type across a Mountain Landscape

Jeffrey G. Holmquist*‡
Jennifer R. Jones†
Jutta Schmidt-Gengenbach*
Lyra F. Pierotti* and
Jason P. Love*

*White Mountain Research Station, University of California San Diego, 3000 E. Line Street, Bishop, California 93514, U.S.A.
†Department of Forest, Rangeland, and Watershed Stewardship, Colorado State University, Ft. Collins, Colorado 80523, U.S.A.
‡Corresponding author: jholmquist@ucsd.edu

Abstract

Fens and wet meadows are important mountain wetland types, but influences on assemblage structure of associated invertebrates are poorly understood compared with other aspects of the ecology of these habitats. We sought to determine the relative contributions of terrestrial and aquatic invertebrates to diversity and abundance in these wetlands, the extent to which terrestrial and aquatic invertebrate assemblages differ with wetland type, and to what degree the aquatic assemblages vary as a function of slow sheet flow. We compared assemblages in fens and wet meadows, with and without flow, at 80 backcountry sites dispersed across the 6200 km^2 landscape of Yosemite, Sequoia, and Kings Canyon National Parks in the Sierra Nevada mountains of California, U.S.A., using standard aquatic and terrestrial sweep netting. Cicadellid leafhoppers, aphids, and thomisid crab spiders were the most abundant terrestrial taxa. Cicadellids, Lepidoptera, anthomyiid, muscid, chloropid, and ephydrid flies, and thomisids were more abundant in fens than in wet meadows. Only mirid leaf bugs were significantly more abundant in wet meadows than fens. Sphaeriid clams and chironomid midges dominated aquatic assemblages both with and without flow. Chloroperlid stoneflies, mites, clams, and flatworms were all more abundant in flow, and Hemiptera and mosquitos were significantly more abundant in quiescent water. Mosquitos were more abundant in wet meadows, but there were few other population differences as a function of wetland type. Terrestrial diversity was 1.1 to 2.0 times that of aquatic diversity, depending on metric and habitat. Fens had greater terrestrial abundance, richness, evenness, and diversity than wet meadows; there were fewer differences as a function of wetland type for aquatic fauna. Presence or absence of slow sheet flow had more effect on these aquatic assemblages than did wetland type. Cluster analyses, ordination, and multi-response permutation procedures were generally consistent with the univariate results. Vegetation-based wetland classifications should be extrapolated to faunal assemblages with caution, particularly for aquatic invertebrates.

Introduction

Fens and wet meadows are high diversity wetland habitats that are common in the mountain environment (Klikoff, 1965; Benedict and Major, 1982; Benedict, 1983; Bedford and Godwin, 2003). Fen peatlands are perennially saturated with water, whereas wet meadows are saturated with water during only part of the year and have mineral soils (Williams, 2006; Mitsch and Gosselink, 2007). The hydrology, soil characteristics, and flora of these habitats are well understood and are used in wetland classification schemes (Mitsch and Gosselink, 2007), but the distribution and abundance of invertebrate assemblages of mountain wetlands have received comparatively little attention (Wissinger et al., 1999). Further, although wetlands are often described as an aquatic-terrestrial ecotone (Batzer and Wissinger, 1996), aquatic and terrestrial fauna are rarely investigated simultaneously in these mountain wetlands.

Work to date in high elevation and/or high latitude environments suggests the importance of invertebrates in these wetlands. Finnamore (1994) for instance found that arthropods represented 77% of terrestrial taxa in an Alberta fen and related habitats, versus 16% and 6% for plant and vertebrate taxa, respectively (see also Keiper et al., 2002; Spitzer and Danks, 2006; Savage et al., 2011).

Simonson et al. (2001) found montane wet meadows to have disproportionately high butterfly diversity, despite accounting for a small proportion of the landscape. Studies in both North America and Europe have shown that invertebrate densities in these habitats can drive avian wetland use, size and spacing of territories, and breeding success (Orians, 1966; Rolando et al., 2007). Most work on aquatic invertebrates in peatlands has centered on permanent pond habitats versus shallower, ephemeral habitats with dense emergent vegetation (Batzer and Wissinger, 1996). Ephemeral mountain waters can have lower richness and abundance than permanent water bodies (Duffy, 1999; Wissinger et al., 1999; Euliss et al., 2004), and trophic complexity generally increases with increasing habitat permanence (Batzer and Wissinger, 1996; Duffy, 1999; Schneider, 1999). Temporary wetland pools nonetheless can support high abundances of chironomids, caddisflies, and dytiscid beetles, and chironomid species richness can be high in these habitats (Wiggins et al., 1980; Batzer and Wissinger, 1996; Wissinger et al., 1999). Detrital decomposition during waterless phases may make this food resource more available to fauna with resulting high insect productivity in ephemeral waters (Wiggins et al., 1980; Batzer and Wissinger, 1996). Insects are sensitive to subtle flow differences (Schowalter, 2006), and even low (<1 cm sec^{-1}) sheet flows

(Heinselman, 1970; Kadlec, 1990) in ephemerally inundated fens and wet meadows may be important in determining population densities of some taxa.

We examined three questions in the Sierra Nevada mountains of California, U.S.A.: (1) What are the estimated relative contributions of terrestrial (epigeal) and aquatic invertebrates to diversity and abundance in these wetlands, as information on relative diversity of habitats is critical to management decisions (Tierney et al., 2009; Hobbs et al., 2010; Thompson et al., 2011)? (2) Do aquatic and terrestrial invertebrate assemblages differ as a function of wetland type (fen versus wet meadow)? (3) To what extent do aquatic assemblages differ as a function of presence or absence of slow sheet flow across these wetlands? This initial study of Sierra Nevada wetland assemblages had a unique combination of elements: (1) a large, almost pristine, and remote study landscape of 6200 km^2 (Yosemite, Sequoia, and Kings Canyon National Parks); (2) extensive sampling (80 backcountry sites) at elevations as high as 3700 m; (3) simultaneous examination of aquatic and terrestrial assemblages; (4) analysis of all arthropod taxa rather than a subset of targeted groups; and (5) a focus on vernal waters versus permanent ponds or marshes.

Methods

We contrasted assemblage structure of the aquatic benthos using a 2 × 2 design (Wetland: Fen, Wet meadow; Flow: Absent, Present). Epigeal terrestrial invertebrates were compared as a function of wetland type (1 × 2). We did not sample infauna or soil fauna. We contrasted terrestrial and aquatic assemblages using a 2 × 2 design (Habitat: Aquatic, Terrestrial; Wetland: Fen, Wet meadow) for area-independent metrics (e.g., expected number of species), because samples were necessarily collected with different sampling techniques: standard sweep (cone) netting for terrestrial fauna and standard sweep (D-frame) netting for aquatic fauna. Area-dependent metrics (e.g., species richness) were not compared across habitats. The study was one component of a wetland "vital signs" program coordinated by the National Park Service (NPS; Davis, 2005; Fancy et al., 2009; Tierney et al., 2009). The goal was to address the questions outlined above at a large number of sites, each visited once, distributed across the sizeable landscape of three national parks, over a comparatively short period of time (two growing seasons).

STUDY AREA AND SITES

Sierra Nevada fens and wet meadows are relatively distinct environments and together comprise the majority of Sierra wetland habitat. Fen peatlands occur in basins, on slopes, and/or in association with distinct springs. Common plant taxa include Northwest Territory sedge (Carex utriculata L. Bailey), Rocky Mountain sedge (Carex scopulorum Holm), bog blueberry (Vaccinium uliginosum (A. Gray) Hultén), shooting star (Dodecatheon spp.), spikerush (Eleocharis spp.), and western cowbane (Oxypolis occidentalis J. Coulter & Rose). Wet meadows are often found in stream valleys and have fine textured soils with comparatively high organic content but little peat. Representative vegetation includes a reedgrass (Calamagrostis muiriana B.L. Wilson and S. Gray, formerly included in C. breweri Thurber), panicled bulrush (Scirpus microcarpus J. & C. Presl), arrowleaf ragwort (Senecio triangularis Hook), corn lily (Veratrum californicum Durand), and tinker's penny (Hypericum anagalloides Cham. & Schldl.) (see also Jones, 2011).

Eighty wetland sampling sites were selected in the parks using a modified two-stage, spatially balanced, probability-based survey design at the watershed and site level (Stevens and Olsen, 2004). The goal of this design was to disperse sampling sites randomly while maintaining efficiency of backcountry travel and retaining the ability to make inference to the target population of fens and wet meadows at the desired spatial extent. The first stage of the design was a stratified random selection of watersheds. Watershed strata were based on physical drivers of wetland formation and type including precipitation, elevation, slope, and geology (Bedford and Godwin, 2003; James, 2003; Wohl et al., 2007). Extent of Pleistocene glaciers was used during exploratory analyses, but was removed due to correlation with elevation. Watersheds only partially contained within park boundaries were aggregated with adjacent watersheds and trimmed to the boundary so that areas outside of the parks were excluded from the study extent. The second stage involved a site-level selection from a sample frame of a target population (e.g., Thompson et al., 2011) of wet meadows and fens within stage one selected watersheds. At the site level, an unequal probability selection was used based on travel time (see also Thompson et al., 2011) and wetland type. Identification and delineation of wetlands into target types was based on landscape context, color signature, and vegetation map distinction. As many wilderness meadows in the parks are open to grazing by pack animals (Holmquist et al., 2010), potential sites with more than 0.5 annual pack stock grazing nights/0.4 ha over the past 18 years were excluded from consideration. A specified, site-level response design directed sampling at second stage selected wetland complexes. Each selection from the watershed to the plot level was made using the spsurvey package and the Generalized Random-Tesselation Stratified (GRTS) function in R (Stevens and Olsen, 2003, 2004; Tierney et al., 2009; Thompson et al., 2011). Final selections included 33 fens and 47 wet meadows; 38 sites were in Yosemite National Park, and 42 were in Sequoia and Kings Canyon National Parks. Mean elevation for fens and wet meadows was almost identical (fen $\overline{x}$ = 2680 m, SE = 42; wet meadow $\overline{x}$ = 2670 m, SE = 55); polygon areas from the second stage sample frame were also similar across wetland types (fen $\overline{x}$ = 2.97 ha, SE = 0.444; wet meadow $\overline{x}$ = 2.43 ha, SE = 0.454). The 300 km of the southern and central Sierra study range is crossed by only one road; one day of backpacking was necessary to reach most sites, and two days were necessary for one-way access to many others. Each site was sampled once. We thus sampled a large number of wetlands across a broad landscape with good replicate dispersion (Hurlbert, 1984). Gage et al. (2009) provided further details on site selection.

We sampled sites during July and August of 2007 and 2008. Upon arrival at each predetermined site, we verified wetland type via vegetation assemblage, hydrology, and soil characteristics (an unbroken peat layer from the soil surface to a depth of 30 cm was required for classification as a fen; assessed with an auger). All sites were sampled for epigeal terrestrial fauna. Mean canopy height was ~30 cm (fen $\overline{x}$ = 28 cm, SE = 2.1; wet meadow $\overline{x}$ = 33 cm, SE = 4.0). Vernal snowmelt ponds persist from one week to two months after snowmelt in these wetlands. If there was no ephemeral water at a predetermined site location, we sampled aquatic fauna in the nearest ephemeral water within the selected wetland. Most wetlands had aquatic habitat, and the aquatic habitat was usually of the same wetland type as the pre-selected site. Occasionally the aquatic sample was from a different wetland type than the predetermined wetland type that was sampled for terrestrial invertebrates, and in these instances the aquatic sample was categorized as being from the observed rather than the predetermined wetland type. We sampled 52 aquatic sites during the study: 25 fens and 27 wet meadows. Although snowmelt ponds did not persist all season, mean sampling dates were tightly clustered around ordinal day 205 (24 July) for all habitat types (terrestrial fen $\overline{x}$ = 204, SE = 3.0; terrestrial wet meadow $\overline{x}$ = 207, SE = 2.7; aquatic fen $\overline{x}$ = 205, SE = 3.6); aquatic

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wet meadow $\bar{x}$ = 204, SE = 3.4). Sheet flow, where present, was typically <0.5 cm sec^{-1}, and ambiguities were resolved by placing neutrally buoyant particles into the water column for observation. We did not sample the small streams that were sometimes present in the wetlands. Twenty-two aquatic sites had no flow, and 30 had flow; there was again little difference in sampling date across categories. Wetland area was also similar across flow types (no flow $\bar{x}$ = 2.64 ha, SE = 0.53; sheet flow $\bar{x}$ = 2.88 ha, SE= 0.51). Conductivity and total dissolved solids were generally low (30–80 μS cm^{-1} and 10–40 ppm, respectively), and pH ranged from 6.6 to 7.1 (Hanna model HI98129 combination meter). These values are similar to those recorded from analogous habitats (e.g., Wissinger et al., 1999). Canopy heights of the sampled aquatic habitat were, as in terrestrial habitat, ~30 cm (fen $\bar{x}$ = 29 cm, SE = 3.8; wet meadow $\bar{x}$ = 28 cm, SE = 6.9). Water depth was ~10 cm (fen $\bar{x}$ = 11 cm, SE = 2.9; wet meadow $\bar{x}$ = 9.0 cm, SE = 1.9).

FIELD AND LAB METHODOLOGY

Terrestrial Fauna

We used a cone net, a typical terrestrial sweep net with a handle (New, 1998; Southwood and Henderson, 2000), to sample epigeal terrestrial fauna. Sweep nets integrate terrestrial collections over a wide area and have a number of advantages for sampling remote wetlands (Holmquist et al., 2010). Sweep netting is the most common method used for sampling epigeal arthropods (Southwood and Henderson, 2000; Samways et al., 2010) and has been used in other investigations of arthropods in mountain vegetation (e.g., Wettstein and Schmid, 1999; Mysterud et al., 2005; Holmquist et al., 2010).

Each sample was the result of 50 sweeps, across 40 m of habitat, using a collapsible sweep net with a 30.5 cm aperture and mesh size of 0.5 × 0.75 mm (BioQuip #7112CP). Each terrestrial sweep sample was transferred to a self-sealing bag, killed with 99% ethyl acetate (Samways et al., 2010), and kept as cool as possible until the trailhead was reached and the samples could be transferred to a freezer. We sorted terrestrial sweep samples in the lab.

Aquatic Fauna

We used a D-frame sweep net (BioQuip #7512D; Merritt et al., 2008) to sample aquatic invertebrates. These nets produce samples with high abundance, richness, evenness, and precision, integrate a relatively large area, usually capture a high proportion of the taxa that are present, and are cost-effective (Kaminski and Murkin, 1981; Cheal et al., 1993; Turner and Trexler, 1997; New, 1998). This technique is recommended as a method of choice for sampling wetland invertebrates (Cheal et al., 1993; Turner and Trexler, 1997), is the most common method used in sampling shallow, vegetated freshwater wetlands (U.S. EPA, 2002), and has been used in other studies of mountain wetland invertebrates (e.g., Wissinger et al., 1999, 2003).

We briskly pushed the 30.5-cm-diameter D-frame net through 5 linear meters of vegetated aquatic habitat at each site, bouncing the net off of the substrate at intervals so as to disturb fauna living near the substrate and force animals into the water column where capture could occur (Usinger, 1956; Cheal et al., 1993; Turner and Trexler, 1997). Samples were sorted live in the field in a plastic tray and transferred to vials of 70% ethanol. Field sorting greatly reduced the volume and weight of material that had to be transported by backpack. Aquatic and terrestrial samples were sorted completely, rather than by subsampling, because complete sorting reduces the variance of metrics, improves proportion metrics, and increases taxon richness (Courtemanch, 1996; Doberstein et al., 2000).

We identified taxa to the family and morphospecies level. Higher taxonomic resolution was not possible due to the large collections, an abundance of immature specimens and undescribed species, and because a number of groups await revision. In cases in which taxonomic ambiguity (*sensu* Cuffney et al., 2007) was a factor, we used the ''distribute parents among children'' approach on a per sample basis, except where specific knowledge allowed more targeted allocation of ambiguous taxa.

ANALYSIS

We compared the influence of wetland type and flow on invertebrate assemblages with both uni- and multivariate approaches. Univariate analyses included 2 × 2 ANOVAs, *t*-tests, and tests for trends across suites of metrics using SYSTAT 12. We analyzed a variety of faunal metrics, including order and family population abundances and family and morphospecies richness. Reported abundances and richnesses were based on catch-per-unit-effort sampling: 50 cone net sweeps for terrestrial samples and five linear meters of D-frame sampling for aquatic samples. Frequencies represent the proportion of samples that included a given taxon. Large collections have more taxa than small collections, so we also assessed richness with expected number of morphospecies and families after scaling to the number of individuals in the sample with the fewest individuals (two; $E(S_2)$ and $E(F_2)$; Hurlbert, 1971; Simberloff, 1972; Magurran, 2004). Compensation for differing abundance also allowed comparison across sampling methods. We analyzed family and morphospecies dominance and used probability of interspecific encounter as a measure of evenness at both the morphospecies and family level (PIE; Hurlbert, 1971). We calculated E(S), E(F), and PIE using the application Diversity. We used GPower (Mayr et al., 2007) to estimate power using our sampling design and sample size with the standard *a priori* estimate for effect size of 0.5 (Cohen, 1988; Bausell and Li, 2002). Planned *t*-tests contrasting terrestrial assemblages as a function of wetland type had an *a priori* power of 0.70, and the suite of 2 × 2 ANOVAs had power of 0.94 or better. Metrics that demonstrated departures from normality via Lilliefors tests (Lilliefors, 1967) and/or showed heteroscedasticity (F$_{max}$ and Cochran's tests; Kirk, 1995) were corrected, by square-root transformations $((y)^{0.5} + (y + 1)^{0.5})$ of proportional data and log transformations (log $(y + 1)$) of other data, such that parametric assumptions were met. We examined meadow size (see also Savage et al., 2011), elevation, canopy height, water depth, and ordinal day as potential covariates in our analyses. Only variables that differ as a function of the design factor(s) should be considered for further analysis as covariates (Underwood, 1997), and these variables did not qualify. One-tailed sign tests were used to investigate trends across suites of metrics (two-tailed tests for aquatic populations). The sequential Bonferroni adjustment (Holm, 1979; Rice, 1989; Shaffer, 1995; Jaccard and Guilamo-Ramos, 2002) was used to calculate alternative, conservative probability values for families of contrasts such that the collective error rate was 0.05. Corrections were made with the application MacBonferroni. We used the Sørensen quantitative index (Magurran, 2004) to compare similarities among assemblage pairings. This index uses abundance data, rather than simple taxon presence-absence, and is equal to $2jN/(N_a + N_b)$, where N_a and N_b are the total number of individuals in each of the assemblages and jN is the sum of the lower of the two habitat abundances for each of the taxa collected in the study. The metric makes maximum use of quantitative data and is viewed as a superior index when sufficient data are available (Faith et al., 1987; Magurran, 2004). We supplemented metrics and contrasts with rank abundance plots to provide an additional perspective on diversity,
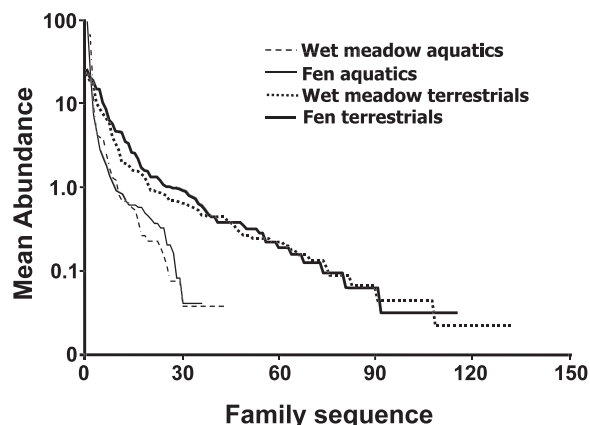
FIGURE 1. Rank abundance plot for families comparing terrestrial and aquatic faunas as a function of wetland type, based on mean abundances for study.

We assessed dimensionality of both terrestrial and aquatic data for NMS via stress tests and construction of scree plots. Multiple levels of dimensionality were evaluated, and the best balance of stress level and dimensionality was achieved at three dimensions for both data sets. We then used three dimensions as a starting configuration for 250 runs with real data. Final stress was 22.3 and 19.5 for terrestrial and aquatic data, respectively, and was less than expected by chance ($p = 0.0040$ and 0.0080; Monte Carlo test, 249 runs). There were 89 and 76 runs for the final terrestrial and aquatic solutions. We assessed stability with stress versus iteration plots; stress fell steeply and smoothly, stabilizing at 44 and 47 iterations for terrestrial and aquatic data, respectively. Nine complete additional NMS analyses confirmed consistency of results.

Results

We identified 14,805 wetland invertebrates from terrestrial and aquatic habitat. Terrestrial samples included 147 families, and aquatic samples yielded 48 families (Appendix 1). Sixty-seven percent of terrestrial families occurred in three or more samples, versus 60% for aquatic families. Rank abundance plots for terrestrial and aquatic faunas approximated a log normal distribution and log series, respectively; high dominance is apparent in the latter (Fig. 1). Although curves were almost congruent for each assemblage across wetland types within a given assemblage, there was slightly more abundance at mid-range family ranks for fen fauna in both terrestrial and aquatic assemblages, and there were more total families in wet meadow than in fen habitat for both terrestrial (134 versus 117) and aquatic (44 versus 37) fauna (Fig. 1, Appendix 1). Sampling terrestrial and aquatic habitat required different methodologies, but assemblage level comparisons across faunas were possible for metrics that were proportion based or had compensation for differing sample sizes (Table 1). Terrestrial fauna clearly contributed the majority of the total arthropod diversity present in these fens and wet meadows, as all assemblage contrasts were highly significant. Rarefied terrestrial family and morphospecies richnesses were 10–20% higher than those of the aquatic habitats, and associated variance was low (Table 1). Terrestrial evenness was up to twice that of the aquatics as indicated by Hurlbert's PIE, and terrestrial faunas had about half the dominance of the aquatics as assessed at both the family and morphospecies levels. Predators made up a higher proportion of the terrestrial assemblage, but there was a significant interaction term (Table 1). When terrestrial and aquatic assemblages were examined in combination, there were significant differences as a function of wetland type only for the two PIE metrics, but there was a significant trend of greater

richness, and evenness; these plots retain more information than individual assemblage metrics used in isolation (Magurran, 2004; Underwood and Fisher, 2006; Savage et al., 2011).

Multivariate analyses included hierarchical, polythetic, agglomerative cluster analyses; multi-response permutation procedures (MRPP); and nonmetric multidimensional scaling (NMS) using the approaches of McCune and Grace (2002) and Peck (2010) in PC-ORD 6. Response and explanatory matrices contained all sites. Terrestrial and aquatic taxa were analyzed separately. The response matrices of families included only taxa that were collected in at least three sites and were relativized by maximum abundance for each family. The final terrestrial response matrix contained 99 families, with a coefficient of variation (CV) of 56%, and 78% of the cells contained zeros. The aquatic response matrix contained 29 families, with a CV of 50% and 80% zeros. Explanatory matrices included habitat and flow coding, as well as ordinal day, elevation, meadow area, canopy height, and water depth as continuous variables. We used the Sørensen distance measure for all analyses. The cluster analyses used group average linkage. Habitat coding variables from the explanatory matrices were used in conjunction with the cluster analyses, and an additional group membership variable based on the four highest level groups from the resulting dendrograms, versus initially coded habitat types, was written to the explanatory matrices. We tested for differences among groups with MRPP, using both the pre-defined habitat types and the additional group membership variable. The distance matrices were rank-transformed prior to calculation.

TABLE 1

Means, standard errors, and results of 2 × 2 ANOVAs ($n = 133$; $df = 1,1,1,130$) comparing terrestrial versus aquatic faunas (Assemblage) and as a function of wetland type (Habitat). * and ** flag p-values less than 0.05 before and after, respectively, sequential Bonferroni correction across all assemblage metrics. See Methods for further metric description.

	Terrestrial				Aquatic				ANOVA		
	Fen		Wet Meadow		Fen		Wet Meadow				
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Assemblage	Habitat	Assemblage × Habitat
Expected no. families E(F)	1.84	0.02	1.82	0.02	1.54	0.06	1.45	0.06	<0.001**	0.158	0.393
Expected no. morphospp. E(S)	1.88	0.01	1.85	0.02	1.64	0.06	1.60	0.05	<0.001**	0.415	0.968
PIE (family)	0.83	0.02	0.80	0.02	0.51	0.05	0.41	0.05	<0.001**	0.019*	0.112
PIE (morphospecies)	0.87	0.01	0.83	0.02	0.60	0.06	0.54	0.05	<0.001**	0.019*	0.204
% Family dominance	32.26	2.26	34.29	2.60	60.72	4.85	69.58	4.24	<0.001**	0.169	0.322
% Morphospecies dominance	26.57	2.00	30.78	2.34	52.10	5.42	58.46	4.30	<0.001**	0.119	0.706
% Predators	21.74	2.09	26.72	2.15	20.70	4.47	9.51	2.56	<0.001**	0.094	0.003**

TABLE 2

Mean relative abundance (number of individuals/50 sweeps), standard errors, frequency of occurrence across all samples, and results of one-tailed, independent t-tests (fen $n = 33$, wet meadow $n = 47$, $df = 78$) comparing terrestrial orders, plus Acari, and the 10 most abundant families as a function of wetland type. Psocoptera lacked sufficient abundance for testing. * and ** flag p-values less than 0.05 before and after, respectively, sequential Bonferroni correction for all taxa within a given order.

	Fen			Wet meadow			
	Mean	SE	Frequency	Mean	SE	Frequency	p
Odonata	0.18	0.13	0.09	0.13	0.07	0.09	0.414
Orthoptera	0.12	0.07	0.09	0.19	0.08	0.13	0.281
Plecoptera	0.03	0.03	0.03	0.02	0.02	0.02	0.404
Hemiptera	40.06	7.00	0.91	52.04	14.95	0.96	0.382
Miridae	2.49	0.82	0.42	8.32	3.42	0.43	0.050*
Cicadellidae	24.58	5.85	0.88	16.43	6.37	0.85	0.023*
Aphidae	4.30	1.14	0.64	21.83	10.86	0.66	0.116
Thysanoptera	0.88	0.61	0.21	0.43	0.14	0.26	0.439
Psocoptera	0.06	0.04	0.06	0.00	0.00	0.00	ID
Coleoptera	11.91	4.90	0.85	11.40	3.65	0.75	0.244
Mordellidae	8.27	4.94	0.49	5.70	3.21	0.34	0.172
Neuroptera	0.21	0.14	0.09	0.26	0.13	0.11	0.416
Hymenoptera	6.30	1.18	0.88	7.09	1.20	0.89	0.477
Trichoptera	0.36	0.36	0.03	0.23	0.20	0.04	0.497
Lepidoptera	2.33	0.53	0.64	1.64	0.44	0.38	0.050*
Diptera	95.76	12.85	1.00	51.55	14.35	1.00	<0.001**
Anthomyiidae	17.63	4.45	0.91	7.28	2.06	0.72	<0.001**
Muscidae	9.85	3.74	0.91	3.83	0.75	0.79	0.004**
Chloropidae	19.61	5.01	0.82	6.40	1.88	0.70	0.007**
Drosophilidae	3.36	1.36	0.42	17.81	12.40	0.40	0.357
Ephydridae	14.15	5.25	0.78	2.66	0.65	0.55	0.001**
Araneae	20.33	3.20	0.97	14.51	1.98	0.89	0.050*
Thomisidae	14.18	2.96	0.85	9.79	1.70	0.79	0.141
Acari	0.33	0.19	0.15	0.26	0.14	0.13	0.364

ID = insufficient data.

diversity in fens than wet meadows when all metrics were considered ($p < 0.0025$).

When terrestrial fauna were considered in isolation for all assemblage metrics, there were additional significant differences as a function of wetland type (one-tailed, independent t-tests; fen $n = 33$, wet meadow $n = 47$, $df = 78$). There was greater abundance in fens ($\bar{x} = 178$ individuals/50-sweep sample, SE = 20.4) than in wet meadows ($\bar{x} = 137$, SE = 25). Morphospecies richness per sample was also higher in fens ($\bar{x} = 38.1$, SE = 3.63) than in wet meadows ($\bar{x} = 29.0$, SE = 2.51), as was morphospecies PIE (Table 1). There was a higher proportion of predators in wet meadows (Table 1). Several other metrics were consistent with the trend of higher diversity in fens, and had low ($p < 0.15$), but not significant, p values (family richness, E(S), species dominance, and family PIE), and there was again a significant overall trend of higher diversity in fens ($p < 0.025$).

The terrestrial fauna was dominated by Diptera, in terms of family richness (43), abundance (mean = 70/50-sweep sample), and frequency of occurrence (1.0, Table 2, Appendix 1). Hymenoptera (28 families), Coleoptera (24), and Hemiptera (19) were also diverse. Cicadellid leafhoppers had the greatest morphospecies richness. Other abundant groups included Hemiptera and Araneae (Table 2, Appendix 1). Only Diptera were found in each sample, but Hemiptera, Araneae, and Hymenoptera all had frequencies of ~0.8. Cicadellids had the greatest overall family abundance (mean = 20/sample), followed by another hemipteran family (Aphidae, 15/sample), thomisid crab spiders, and chloropid, drosophilid, and anthomyiid flies (all ~12/sample, Table 2, Appendix 1). Cicadellids, thomisids, and muscid and anthomyiid flies had the highest frequencies of occurrence. Less

than 1% of the terrestrial fauna was composed of taxa with early aquatic life stages. The proportion of such taxa was positively and significantly related to meadow area, although the proportion of the variance explained was small (linear regression, $p = 0.016$, $R^2 = 0.064$, $df = 1{,}79$).

There were a number of terrestrial population differences as a function of wetland type (Table 2, Appendix 1). The two most abundant families in wet meadows, Aphidae and Drosophilidae, were not among the 10 most abundant families in fens, although the rest of the dominant families were broadly similar in rank between the two wetland types. Cicadellids, Lepidoptera, Diptera, anthomyiid, muscid, chloropid, and ephydrid flies, and thomisids were all significantly more abundant in fens than in wet meadows. Only mirid leaf bugs were significantly more abundant in wet meadows than fens, and there was an overall trend of higher population abundances in fens ($p < 0.05$). Frequencies of the most common fauna were similar across habitats. Fens and wet meadow had 105 families in common and 12 and 29 families unique to fens and wet meadows, respectively (Appendix 1). The Sørensen quantitative similarity index for these two assemblages was 0.63.

Cluster analysis of terrestrial sampling sites showed separation of some wet meadows from other locations (Appendix 2). A low MRPP p-value (0.0012, randomization test) suggests that fens and wet meadows were compositionally distinct, but the low within-group agreement value, or effect size (A = 0.030), indicates a substantial variation within each habitat type. A second MRPP using the new group membership variable generated from cluster analysis resulted in a lower p value (<0.0001) and higher A (=0.18), underscoring the potential importance of other factors in addition
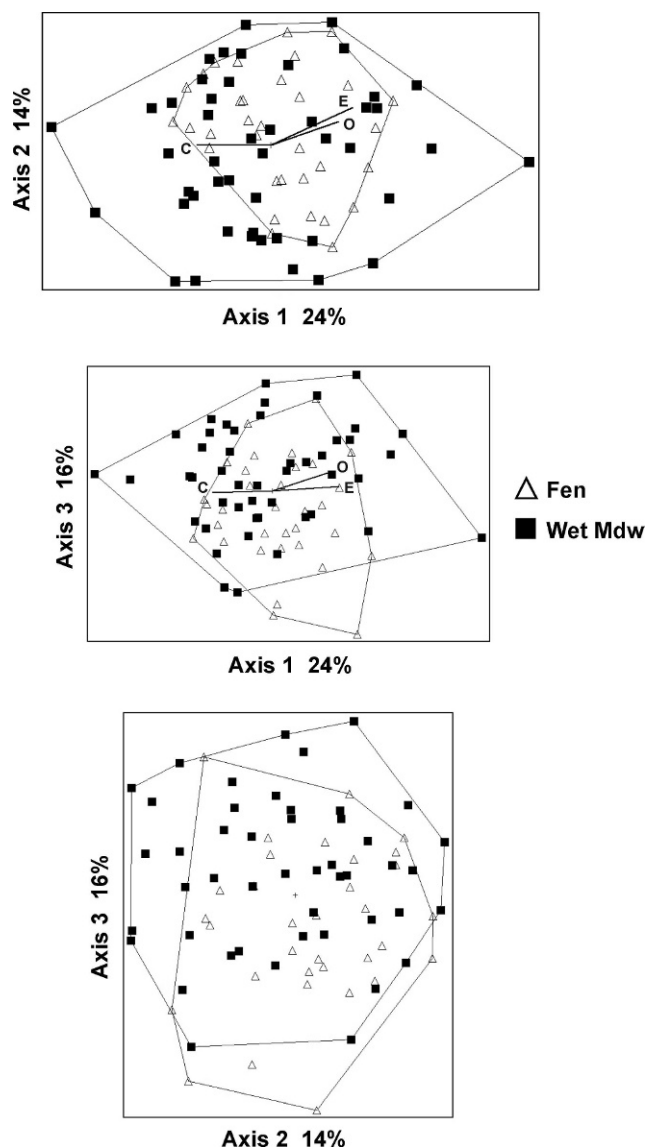
FIGURE 2. Ordination (joint) plots of terrestrial assemblage structure across sites in two-dimensional space using nonmetric multidimensional scaling. Distance between site icons approximates dissimilarity between sites; convex hulls surround sites of a given habitat type. Plots are scaled by proportion of maximum; orthogonality was 100% for each axis pairing. Axis labels include R^2 values estimating post-hoc percent of variation within the distance matrix that is explained by each axis. Cumulative R^2 was 0.54. Explanatory variables in joint plot: C = canopy height, E = elevation, O = ordinal day. Minimum explanatory variable-axis correlation for inclusion in the joint plot was $R^2 = 0.20$.

to wetland type; some of the new groupings had a latitudinal component. Ordination via NMS showed some separation of sites by habitat type, particularly along Axis 1 (Fig. 2). The ordination suggests that the two habitat types were not strongly compositionally distinct, but there was less within-group variation in ordinal space for fens than wet meadows. The explanatory variables canopy height ($R^2 = 0.31$), elevation ($R^2 = 0.34$), and ordinal day ($R^2 = 0.28$) were most strongly associated with Axis 1 (Fig. 2).

Aquatic fauna examined in isolation for all assemblage metrics showed notably few significant differences as a function of either wetland type or flow (Table 3). There was a higher proportion of predators in fens, and there was a higher proportion of Ephemeroptera, Plecoptera, and Trichoptera (%EPT) in sites with sheet flow. There were significant trends across all metrics for overall higher

diversity in flow and in fens ($p < 0.001$ and $p < 0.025$, respectively), despite greater absolute family richness in wet meadows.

The aquatic fauna, like the terrestrials, was dominated by Diptera in terms of family richness (12) and frequency of occurrence (0.94), but Diptera were second to clams (Veneroida) in terms of abundance (50 versus 78/sample; Table 4, Appendix 1). Family richnesses of other groups were well below Diptera: Acari (6), Ephemeroptera (6), Trichoptera (5), and Odonata (5), and abundances of these groups were far below those of Diptera and Veneroida (Table 4). Chironomids had the highest morphospecies richness. Beetles, clams, and mites followed Diptera in frequency and were the only taxa with frequencies above 0.5. Sphaeriid clams and chironomids were by far the most abundant families (Table 4, Appendix 1).

There were comparatively few differences for aquatic assemblage metrics as a function of habitat and flow, but a number of population differences were apparent (Table 4, Appendix 1). Although clams and chironomids were the most abundant families in both wetland types, mosquitos, flatworms, and ephemerellid mayflies were abundant in wet meadows but not fens (ephemerellids were absent), and coenagrionid damselflies were abundant in fens but were almost absent in wet meadows. Variance among samples was high, and there were significant differences as a function of wetland type for Diptera and Culicidae only (more abundant in wet meadows). Clams and chironomids were the two most abundant taxa both with or without flow. Mosquitos and damselflies were abundant in no-flow habitats, but almost absent if even very slow sheet flow was present. Flatworms and ephemerellids were common with flow, but absent from still water. There were more significant population differences as a function of flow than for wetland type: Plecoptera, chloroperlid stoneflies, mites, clams, and flatworms were all significantly more abundant in flow, and Hemiptera, Diptera, and mosquitos were significantly more abundant in quiescent water. There were significant interaction terms for mosquitos and dysticid predaceous diving beetles. Although individual taxa had different abundances as a function of wetland type or water flow, there was not an overall directional trend for either factor across all taxa ($p > 0.25$ for both factors). Frequencies of the most common fauna were relatively similar across habitats, but mites occurred about 50% more frequently in fens than wet meadows. Fens and wet meadow had 33 families in common and only 4 and 11 families unique to fens and wet meadows, respectively (Appendix 1). The Sørensen quantitative similarity index for aquatic assemblages was 0.66. In contrast, there were only 22 families common to aquatic habitats across flow regimes but 9 families found only where flow was absent and 17 found only where flow was present (Appendix 1). In turn, the similarity index for no-flow and flow assemblages was 0.34—about half that of either the terrestrial or aquatic wetland assemblage similarities.

There was some clustering of aquatic sites as a function of flow regime; in particular, a number of wet meadow sites with flow showed higher level separation from other sites (Appendix 3). As with terrestrial assemblages, MRPP suggested some relative similarity within habitat groups ($p = 0.031$) but also high within-group variation (A = 0.048). The MRPP based on the group membership variable from the cluster analysis again had a lower p value (<0.0001) and higher A (0.25). Some of the new cluster groupings suggested latitudinal differences. Ordination (NMS) plots showed more similarities than differences across habitat types, but some dissimilarity was observed for wet meadows with flow (Fig. 3). Aquatic explanatory variables were more weakly correlated with axes than in the terrestrial NMS. The strongest

TABLE 3

Means, standard errors, and results of 2×2 ANOVAs ($n = 52$; $df = 1,1,1,48$) comparing aquatic fauna as a function of wetland type and water flow. Metrics are based on 5 m sweep samples. * and ** flag p-values less than 0.05 before and after, respectively, sequential Bonferroni correction across all assemblage metrics. See Methods for further metric description.

| | Fen | | | | Wet Meadow | | | | ANOVA | | |
| | No Flow | | Flow | | No Flow | | Flow | | | | |
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Habitat	Flow	Habitat × Flow
Total individuals	83.18	32.74	193.21	68.99	188.55	90.24	145.06	49.60	0.439	0.628	0.273
Family richness	4.70	1.04	7.14	0.90	6.00	0.62	7.00	1.28	0.549	0.374	0.240
Morphospecies richness	8.70	1.68	10.79	1.38	9.73	0.79	10.80	1.85	0.603	0.785	0.449
Expected no. families E(F)	1.49	0.08	1.57	0.08	1.43	0.08	1.47	0.09	0.355	0.529	0.791
Expected no. morphospp. E(S)	1.63	0.08	1.64	0.09	1.54	0.07	1.64	0.08	0.662	0.573	0.571
% Family dominance	65.99	6.19	56.26	7.25	68.15	6.47	70.56	5.77	0.192	0.477	0.311
% Morphospecies dominance	55.40	6.39	49.29	8.59	60.34	6.51	57.17	5.85	0.296	0.371	0.696
PIE (family)	0.47	0.08	0.54	0.08	0.42	0.07	0.40	0.07	0.280	0.854	0.480
PIE (morphospecies)	0.60	0.08	0.60	0.09	0.53	0.07	0.55	0.07	0.649	0.921	0.942
%EPT	7.23	4.91	8.75	3.42	5.28	4.40	11.35	3.22	0.750	0.018*	0.345
% Predators	18.60	7.13	22.48	5.86	8.90	3.79	9.95	3.53	0.019*	0.600	0.602

explanatory variable correlations were water depth with Axis 1 ($R^2 = 0.19$) and elevation with Axis 3 ($R^2 = 0.16$; Fig. 3).

Discussion

The terrestrial assemblage accounted for most of the diversity in these wetlands and had more evenness and morphospecies richness as well as three times the family richness and half the dominance of the aquatic assemblage. The log normal distribution approximated by the terrestrial fauna in both fens and wet meadows also indicated high evenness (see also Savage et al., 2011) and typifies a large, mature, and varied assemblage, whereas the log series approximated by the aquatic fauna in both wetland types indicates a smaller number of abundant taxa (clams and midges in this study) and the dominance of one or a few factors in controlling an assemblage's ecology (Magurran, 2004). Hydroperiod is one such major determinant of aquatic diversity in mountain ponds (Duffy, 1999; Schneider, 1999; Wissinger et al., 1999; but see Batzer et al., 2004; Hanson et al., 2009), and the ephemeral waters that we investigated harbored a simpler assemblage than is found in more persistent waters and one that was lacking in vertebrates such as amphibians (Wissinger et al., 1999) and fishes (Zedler, 2003). Top predators were instead insects, such as diving beetles, damselflies, stoneflies, mites, and flatworms, as has been observed in other vernal and autumnal ponds (Wiggins et al., 1980; Batzer and Wissinger, 1996; Wissinger et al., 1999). Many of these predators were absent in our most ephemeral habitats, which were often dominated by chironomids and sphaeriid clams, and were only relatively diverse and abundant in the vernal ponds that persisted until mid-summer (see also Neldner and Pennak, 1955; Wiggins et al., 1980; Batzer and Wissinger, 1996).

Fens and wet meadows are ecotones that contain terrestrial and aquatic habitats that interdigitate in space and time as ephemeral ponds cyclically flood and dry (see also Haslett, 1997, 2001; Wettstein and Schmid, 1999). The aquatic fauna of ephemeral ponds often have relatively low diversity (Wissinger et al., 1999; Williams, 2006), but when aquatic diversity is combined with that of the terrestrial assemblage of these wetlands, this ecotonal environment has rather high overall diversity. Inclusion of terrestrial soil fauna and aquatic infauna would increase diversity still further.

It was striking that adult forms of taxa with the most abundant aquatic nymphs or larvae were almost absent from our terrestrial samples. Adult caddisflies, odonates, stoneflies, mos-

quitos, and chironomids accounted collectively for only 0.32% of total terrestrial individuals despite representing 38% of the aquatic assemblage. Adults of these taxa were similarly uncommon (2.7%) in the terrestrial assemblage examined by another study of Sierra wet meadows (Holmquist et al., 2010). Such taxa are frequently observed in upland habitats, so export from wetlands is at least a partial explanation for the discrepancy. The vernal ponds have less spatial extent than the rest of these wetlands, so these populations would necessarily be less dense upon emergence and dispersion in the terrestrial environment. The positive relationship between wetland area and presence of adult forms of aquatic taxa offers additional support to the possible influence of meso-scale landscape structure on boundary dynamics and ultimate retention of such fauna. More emigration would be expected from smaller patches (i.e., wetlands in the current study) with a larger perimeter:area ratio (Wiens et al., 1985; Ims, 1995) potentially resulting in lower proportions of adults of aquatic taxa. The wetland-upland interface should be a low contrast boundary with high permeability (Wiens et al., 1985; Stamps et al., 1987; Holmquist, 1998) for many terrestrial fauna, ultimately allowing high connectivity between wetlands and uplands. Indeed, Haslett (1997) and Wettstein and Schmid (1999) found significant numbers of upland fauna in subalpine wetland samples in the Austrian and Swiss Alps. In contrast to our current study, adult phases of aquatic insects can comprise 31% of terrestrial arthropod assemblages in desert wetlands (Holmquist et al., 2011) isolated in a xeric matrix (Tiner, 2003). This higher relative abundance of terrestrial adult phases of aquatic taxa at desert springs suggests fidelity of aquatic taxa that may be driven by the higher contrast boundaries encountered at the spring margins. We may also have missed some short adult phases in our fen and wet meadow sampling, and predation may account for some of the disparity as well. Interestingly, two less common dipterans, ceratopogonid biting midges and tipulid crane flies, were proportionally more abundant in our terrestrial mountain wetland samples than in the aquatic samples. It is possible that these midges have more fidelity to the wetland environment throughout their life cycles than do some of the more abundant groups.

Wetland type had an influence on invertebrates, particularly terrestrial fauna. The higher diversity and abundance of terrestrial fauna that we observed in fens may have been due to greater soil moisture and plant biomass relative to wet meadows; NMS ordination suggests that variation in canopy height may be an

TABLE 4

Mean relative abundance (number of individuals/5 m sweep), standard errors, frequency of occurrence across all samples, and results of 2 × 2 ANOVAs ($n = 52$; $df = 1,1,1,48$) comparing aquatic orders, plus Acari, and the 10 most abundant families as a function of wetland type and water flow. WM = wet meadow; * and ** flag p-values less than 0.05 before and after, respectively, sequential Bonferroni correction for all taxa within a given order.

| | Fen | | | | | Wet Meadow | | | | | | ANOVA | | |
| | No Flow | | Flow | | Fen | No Flow | | Flow | | WM | | | | |
	Mean	SE	Mean	SE	Freq.	Mean	SE	Mean	SE	Freq.	Habitat	Flow	Habitat × Flow
Collembola	0.00	0.00	0.08	0.08	0.04	0.55	0.55	0.00	0.00	0.04	0.430	0.430	0.163
Ephemeroptera	1.58	1.20	4.15	4.07	0.16	3.36	3.07	9.81	6.23	0.37	0.223	0.440	0.321
Ephemerellidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.44	6.24	0.11	0.280	0.280	0.280
Leptophlebiidae	0.42	0.42	3.77	3.77	0.08	0.00	0.00	0.00	0.00	0.00	0.194	0.730	0.730
Odonata	9.17	8.63	0.77	0.50	0.28	0.27	0.19	0.13	0.09	0.15	0.098	0.388	0.610
Coenagrionidae	8.42	8.42	0.54	0.46	0.12	0.09	0.09	0.00	0.00	0.04	0.172	0.458	0.670
Plecoptera	0.08	0.08	1.39	0.78	0.28	0.00	0.00	4.25	2.00	0.30	0.412	0.003**	0.267
Chloroperlidae	0.08	0.08	1.08	0.76	0.24	0.00	0.00	2.75	1.82	0.22	0.658	0.019*	0.437
Hemiptera	1.08	0.91	1.23	1.15	0.20	0.91	0.55	0.06	0.06	0.15	0.303	0.050*	0.262
Coleoptera	5.50	2.77	2.54	0.75	0.68	5.27	2.04	2.06	0.73	0.67	0.512	0.144	0.292
Dytiscidae	2.83	2.12	2.54	0.75	0.60	3.82	1.93	1.44	0.60	0.52	0.734	0.384	0.043*
Neuroptera	0.67	0.43	0.23	0.23	0.16	0.45	0.25	0.75	0.52	0.19	0.795	0.422	0.504
Trichoptera	13.67	13.58	3.23	1.24	0.44	0.73	0.56	5.81	4.25	0.37	0.610	0.123	0.781
Limnephilidae	13.00	12.91	1.54	0.53	0.40	0.73	0.56	5.69	4.19	0.33	0.573	0.421	0.732
Diptera	30.36	14.16	20.00	6.97	0.88	143.27	93.43	26.56	8.35	1.00	0.035*	0.063	0.156
Culicidae	1.82	1.82	0.00	0.00	0.04	21.45	16.99	0.06	0.06	0.30	<0.001**	0.001**	0.001**
Chironomidae	28.21	15.20	16.08	5.55	0.84	121.00	94.40	25.19	8.22	0.96	0.140	0.161	0.517
Acari	1.33	0.92	5.85	2.66	0.60	0.82	0.38	2.44	1.06	0.41	0.255	0.012*	0.116
Veneroida	15.25	4.91	163.46	71.48	0.72	32.09	17.67	85.75	42.48	0.63	0.588	0.041*	0.357
Sphaeriidae	15.25	4.91	163.46	71.48	0.72	32.09	17.67	85.75	42.48	0.63	0.588	0.041*	0.357
Tricladida	0.00	0.00	2.08	1.39	0.12	0.00	0.00	6.94	4.43	0.11	0.725	0.046*	0.725
Planariidae	0.00	0.00	2.08	1.39	0.12	0.00	0.00	6.94	4.43	0.11	0.725	0.046*	0.725

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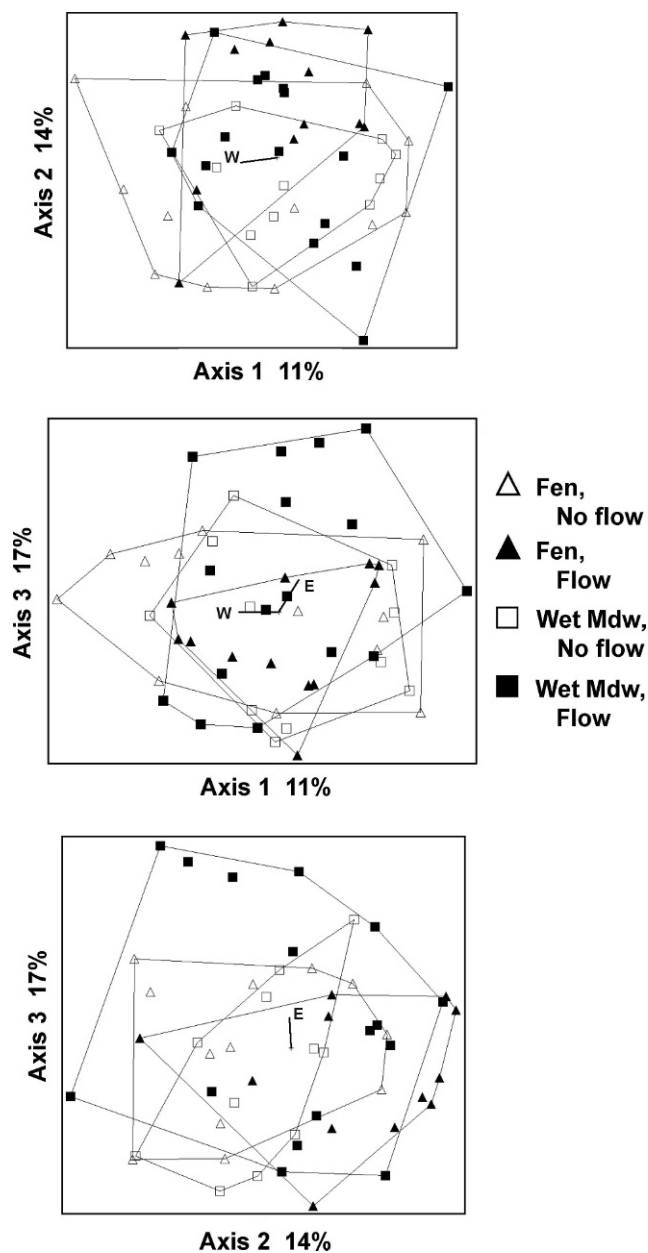
FIGURE 3. Ordination (joint) plots of aquatic assemblage structure across sites in two-dimensional space using nonmetric multidimensional scaling. Cumulative R^2 was 0.42. Explanatory variables in joint plot: E = elevation, W = water depth. Minimum explanatory variable-axis correlation for inclusion in the joint plot was $R^2 = 0.15$. See Figure 2 caption for additional information.

influence on wet meadow fauna in particular. In contrast, aquatic taxa of peatlands and other wetlands are often dominated by generalists that are widely distributed across wetland types (Danks and Rosenberg, 1987; Euliss et al., 1999).

The presence or absence of slow flow had more effect on aquatic assemblages than did wetland type. Although this general relationship was anticipated, the strength of this trend was greater than expected. There were more significant population differences as a function of sheet flow (9) than wetland type (2), and there was a trend across assemblage metrics of higher diversity in flow. The strongest evidence for the importance of flow, relative to wetland type, in structuring assemblages was the low similarity (0.34) between assemblages with and without slow sheet flow, in contrast to the much higher terrestrial and aquatic assemblage similarities as

a function of wetland type (0.63 and 0.66, respectively). Insects are sensitive to flow in part because flow lowers water temperature and increases oxygen availability (Erman, 1973; Schowalter, 2006). The high variance and relative lack of trend as a function of wetland type may also be due to the likely multiplicity of faunal sources. For instance, ephemeral waters primarily support lentic and lotic taxa that can tolerate the fluctuating water levels, but also some animals that are specialized for these habitats, and even some upland and semi-terrestrial taxa (Wiggins et al., 1980; Zedler, 2003). Similarly, upland specialists can be found in terrestrial wetland vegetation (Haslett, 1997; Wettstein and Schmid, 1999). Peatland specific flies make up only about 20% of certain Canadian bog and fen faunas (Marshall, 1994), yet this low percentage is viewed as representing comparatively high peatland specificity, as such percentages are typically lower still (Keiper et al., 2002; Savage et al., 2011). Although classification of wetlands into various types (overview in Mitsch and Gosselink, 2007) has been an important component in both the understanding of larger scale vegetation patterns and in developing wetland conservation measures, these classifications should be extended to faunal assemblages with caution, particularly for aquatic fauna (see also Euliss et al., 2004).

The importance of invertebrates in ecosystem function is widely acknowledged, but invertebrates are often "consigned to the 'too hard' basket" (Andersen and Majer, 2004) during design of monitoring programs (see also Agosti et al., 2000; Samways et al., 2010). The inclusion of invertebrates in the NPS Sierra Nevada Inventory and Monitoring Network's Vital Signs is commendable, and our work and that of others (Oliver and Beattie, 1993, 1996; Andersen and Majer, 2004; Underwood and Fisher, 2006) indicate that invertebrates can be sampled and processed efficiently and on a large scale. Our rapid assessment approaches were combined with vegetation and hydrological monitoring, resulting in further efficiencies; multiple sites, all distant from trailheads, were sampled daily throughout each of our field seasons. Invertebrates make up a large portion of the overall abundance, diversity, and food web structure of ecosystems, and simple protocols can capture much of this complexity quickly and easily. We urge other land managers to strongly consider increased emphasis on invertebrates, including terrestrial fauna, in monitoring and research programs. As noted above, however, invertebrate assemblage structure may or may not align with that of vegetation; differing response to some predictors should be anticipated, and is indeed one reason to include invertebrates in ecosystem assessment.

Acknowledgments

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APPENDIX 1.

Mean relative abundance and standard errors for all terrestrial and aquatic family abundances as a function of wetland type and flow. Zeros are omitted for clarity. Abundances are only comparable among terrestrial (number of individuals/50 sweeps) or aquatic (number of individuals/5 m sweep) taxa due to necessarily different sampling methodology.

	Fen						Wet Meadow					
	Terrestrial		Aquatic				Terrestrial		Aquatic			
			No flow		Flow				No flow		Flow	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Collembola					0.08	0.08			0.55	0.55		
Hypogastruridae									0.55	0.55		
Sminthuridae					0.08	0.08						
Ephemeroptera			1.58	1.20	4.15	4.07			3.36	3.07	9.81	6.23
Ameletidae			1.17	1.17					0.09	0.09		
Baetidae					0.39	0.31			0.18	0.18	1.88	1.09
Ephemerellidae											6.44	6.24
Heptageniidae											1.50	1.31
Leptophlebiidae			0.42	0.42	3.77	3.77						
Siphlonuridae									3.09	3.09		
Odonata	0.18	0.13	9.17	8.63	0.77	0.50	0.13	0.07	0.27	0.19	0.13	0.09
Aeschnidae			0.17	0.17					0.09	0.09		
Cordulegastridae											0.06	0.06
Libellulidae			0.58	0.34	0.23	0.17			0.09	0.09	0.06	0.06
Coenagrionidae	0.03	0.03	8.42	8.42	0.54	0.46	0.09	0.05	0.09	0.09		
Lestidae	0.15	0.12					0.04	0.04				
Orthoptera	0.12	0.07					0.19	0.08				
Acrididae	0.09	0.07					0.19	0.08				
Tetrigidae	0.03	0.03										
Plecoptera	0.03	0.03	0.08	0.08	1.39	0.78	0.02	0.02			4.25	2.00
Chloroperlidae	0.03	0.03	0.08	0.08	1.08	0.76	0.02	0.02			2.75	1.82
Nemouridae					0.31	0.31					0.94	0.54
Perlodidae											0.56	0.56
Hemiptera	40.06	7.00	1.08	0.91	1.23	1.15	52.04	14.95	0.91	0.55	0.06	0.06
Aradidae							0.02	0.02				
Anthocoridae	0.06	0.04					0.19	0.08				
Berytidae	0.03	0.03					0.09	0.05				
Corixidae					0.69	0.61			0.55	0.39		
Geocoridae	0.06	0.06					0.13	0.06				
Gerridae			0.08	0.08	0.54	0.54					0.06	0.06
Lygaeidae	1.27	0.54					0.83	0.25				
Miridae	2.49	0.82					8.32	3.42				
Nabidae	0.30	0.12					0.62	0.43				
Notonectidae			1.00	0.91					0.36	0.28		
Pentatomidae							0.02	0.02				
Reduviidae							0.02	0.02				
Rhopalidae	0.03	0.03					0.21	0.13				
Saldidae	0.03	0.03										
Scutelleridae	0.18	0.08					0.79	0.43				
Thyreocoridae							0.02	0.02				
Aphididae	4.30	1.14					21.83	10.86				
Cercopidae	0.03	0.03					0.02	0.02				
Cicadellidae	24.58	5.85					16.43	6.37				
Delphacidae	5.52	1.55					0.87	0.43				
Psyllidae	0.85	0.39					1.06	0.45				
Thysanoptera	0.88	0.61					0.43	0.14				
Thripidae	0.88	0.61					0.43	0.14				
Psocoptera	0.06	0.04										
Coleoptera	11.91	4.90	5.50	2.77	2.54	0.75	11.42	3.65	5.27	2.04	2.06	0.73
Anobiidae							0.04	0.03				
Anthicidae	0.06	0.04					0.02	0.02				
Bostrichidae	0.06	0.04					0.09	0.04				
Brentidae	0.03	0.03					0.06	0.06				
Buprestidae							0.04	0.03				
Cantharidae	0.36	0.12					0.11	0.05				

	Fen						Wet Meadow					
	Terrestrial		Aquatic				Terrestrial		Aquatic			
			No flow		Flow				No flow		Flow	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Cerambycidae	0.06	0.04					0.04	0.03				
Chrysomelidae	0.73	0.29					0.83	0.50			0.13	0.13
Cleridae							0.02	0.02				
Coccinellidae	0.42	0.16					0.51	0.18				
Curculionidae	0.18	0.11					0.15	0.07				
Dermestidae							0.13	0.13				
Dytiscidae			2.83	2.12	2.54	0.75			3.82	1.93	1.44	0.60
Elateridae	0.06	0.04					0.02	0.02				
Hydraenidae			0.08	0.08			0.02	0.02	0.18	0.18	0.31	0.18
Hydrophilidae			1.42	0.78					1.09	0.50	0.13	0.09
Latridiidae	0.97	0.47					0.15	0.06				
Melyridae	0.03	0.03										
Mordellidae	8.27	4.94					5.70	3.21				
Nitidulidae							0.06	0.04				
Phalacridae	0.06	0.04					0.09	0.04				
Scirtidae			1.17	1.17					0.18	0.18	0.06	0.06
Staphylinidae	0.61	0.34					3.19	1.55				
Tenebrionidae							0.02	0.02				
Neuroptera	0.21	0.14	0.67	0.43	0.23	0.23	0.26	0.13	0.45	0.25	0.75	0.52
Chrysopidae	0.21	0.14					0.26	0.13				
Sialidae			0.67	0.43	0.23	0.23			0.45	0.25	0.75	0.52
Hymenoptera	6.30	1.18					7.09	1.20				
Apidae	0.15	0.08					0.09	0.04				
Bethylidae	0.03	0.03										
Braconidae	1.27	0.27					1.55	0.55				
Ceraphronidae	0.06	0.04										
Chalcididae							0.02	0.02				
Chrysididae							0.04	0.03				
Colletidae							0.23	0.08				
Diapriidae	0.27	0.13					0.15	0.07				
Dryinidae	0.03	0.03										
Eucoilidae	0.09	0.05					0.13	0.05				
Eulophidae							0.02	0.02				
Eurytomidae	0.36	0.36					0.15	0.10				
Figitidae							0.02	0.02				
Formicidae	0.18	0.09					0.55	0.31				
Halictidae	0.09	0.07					0.21	0.07				
Ichneumonidae	0.94	0.19					1.49	0.35				
Megachilidae	0.03	0.03					0.09	0.04				
Megaspilidae	0.03	0.03										
Pemphredonidae	0.03	0.03					0.02	0.02				
Platygastridae	0.03	0.03					0.04	0.04				
Proctotrupidae	0.03	0.03					0.06	0.05				
Pteromalidae	2.09	0.75					1.83	0.46				
Scelionidae	0.03	0.03					0.02	0.02				
Sphecidae	0.09	0.07										
Tenthredinidae	0.30	0.13					0.30	0.10				
Vespidae	0.03	0.03					0.02	0.02				
Trichoptera	0.36	0.36	13.67	13.58	3.23	1.24	0.23	0.20	0.73	0.56	5.81	4.25
Brachycentridae					1.62	1.04					0.06	0.06
Lepidostomatidae					0.08	0.08					0.06	0.06
Limnephilidae	0.36	0.36	13.00	12.91	1.54	0.53	0.23	0.20	0.73	0.56	5.69	4.19
Polycentropodidae			0.67	0.67								
Lepidoptera	2.33	0.53					1.64	0.44				
Coleophoridae	0.12	0.07					0.04	0.03				
Elachistidae							0.04	0.04				
Gelechiidae	0.03	0.03					0.17	0.13				
Geometridae	0.27	0.15					0.28	0.15				

	Fen						Wet Meadow					
	Terrestrial		Aquatic				Terrestrial		Aquatic			
			No flow		Flow				No flow		Flow	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Heliodinidae							0.02	0.02				
Hesperiidae							0.09	0.07				
Incurvariidae							0.04	0.04				
Lycaenidae	0.30	0.13					0.23	0.12				
Noctuidae	1.27	0.38					0.43	0.21				
Pterophoridae							0.02	0.02				
Pyralidae	0.21	0.14					0.02	0.02				
Tortricidae	0.12	0.09					0.23	0.15				
Yponomeutidae							0.02	0.02				
Diptera	95.76	12.85	30.36	14.16	20.00	6.97	51.55	14.34	143.27	93.43	26.56	8.35
Agromyzidae	4.45	2.69					1.89	0.55				
Anthomyiidae	17.64	4.45					7.28	2.06				
Asilidae							0.06	0.04				
Bibionidae	0.03	0.03					0.04	0.03				
Bombyliidae	0.03	0.03					0.13	0.06				
Cecidomyidae							0.06	0.04				
Ceratopogonidae	3.18	1.06			0.08	0.08	0.66	0.27			0.06	0.06
Chaoboridae									0.18	0.12		
Chamaemyiidae	0.52	0.31					0.43	0.16				
Chironomidae	1.52	0.81	28.21	15.20	16.08	5.55	0.34	0.16	121.00	94.40	25.19	8.22
Chloropidae	19.61	5.01					6.40	1.88				
Culicidae	0.15	0.09	1.82	1.82			0.21	0.09	21.45	16.99	0.06	0.06
Dixidae			0.33	0.26	0.39	0.24			0.27	0.20	0.25	0.11
Dolichopodidae	6.03	2.02					0.77	0.22				
Drosophilidae	3.36	1.36					17.81	12.40				
Empididae	0.91	0.26					0.87	0.19				
Ephydridae	14.15	5.25					2.66	0.65	0.09	0.09		
Heleomyzidae	0.03	0.03					0.23	0.11				
Lauxaniidae							0.17	0.17				
Lonchopteridae	0.36	0.22					0.04	0.03				
Micropezidae	0.36	0.28					0.04	0.03				
Muscidae	9.85	3.74					3.83	0.75				
Mycetophilidae	0.30	0.13					0.43	0.27				
Opomyzidae	0.09	0.07					0.04	0.03				
Phoridae	0.45	0.18					0.66	0.22				
Pipunculidae	0.58	0.30					0.36	0.11				
Psilidae	0.03	0.03										
Psychodidae	0.21	0.18					0.02	0.02				
Rhagionidae	0.36	0.16					0.43	0.17				
Sarcophagidae	0.09	0.05					0.06	0.04				
Scathophagidae	0.97	0.54					0.53	0.22				
Scatopsidae	0.06	0.04										
Sciaridae	4.39	1.07					1.38	0.39				
Sciomyzidae	0.21	0.09					0.06	0.05				
Sepsidae	1.03	0.24					1.28	0.64				
Simuliidae	0.03	0.03			3.39	2.21	0.06	0.05			0.63	0.50
Sphaeroceridae	0.94	0.33					1.49	0.53				
Stratiomyidae											0.06	0.06
Syrphidae	1.15	0.45					0.13	0.05			0.06	0.06
Tabanidae	0.09	0.07					0.04	0.04	0.09	0.09		
Tachinidae	0.12	0.06					0.23	0.08				
Tephritidae	0.36	0.22					0.38	0.18				
Tethinidae							0.04	0.03				
Therevidae							0.02	0.02				
Tipulidae	1.64	0.62			0.08	0.08	0.23	0.12	0.09	0.09	0.31	0.31
Vermileonidae							0.02	0.02				
Araneae	20.33	3.20					14.51	1.98				
Araneidae	1.48	0.40					0.64	0.18				
Dictynidae	2.45	1.21					1.78	1.13				

	Fen						Wet Meadow					
	Terrestrial		Aquatic				Terrestrial		Aquatic			
			No flow		Flow				No flow		Flow	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Linyphiidae	0.70	0.19					0.66	0.17				
Lycosidae	0.42	0.20					0.21	0.08				
Oxyopidae	0.03	0.03					0.04	0.03				
Philodromidae	0.12	0.07					0.43	0.28				
Tetragnathidae	0.76	0.18					0.45	0.10				
Thomisidae	14.18	2.96					9.79	1.70				
Salticidae	0.12	0.07					0.45	0.27				
Acari	0.33	0.19	1.33	0.92	5.85	2.66	0.26	0.14	0.82	0.38	2.44	1.06
Arrenuridae					0.15	0.15					0.06	0.06
Erythraeidae	0.15	0.15										
Hydrachnidae			0.08	0.08	1.62	0.98			0.27	0.20	0.94	0.47
Hydryphantidae			0.25	0.25	2.31	1.61			0.45	0.28	0.81	0.56
Oxidae					0.39	0.27			0.09	0.09		
Sperchontidae					1.15	0.69						
Gastropoda					0.15	0.10					0.41	0.35
Hydrobiidae					0.08	0.08					0.12	0.08
Lymnaeidae					0.08	0.08					0.29	0.29
Veneroida			15.25	4.91	163.46	71.48			32.09	17.67	85.75	42.48
Sphaeriidae			15.25	4.91	163.46	71.48			32.09	17.67	85.75	42.48
Tricladida					2.08	1.39					6.94	4.43
Planariidae					2.08	1.39					6.94	4.43

APPENDIX 2.

Agglomerative cluster analysis of terrestrial sites with overlay by habitat type.
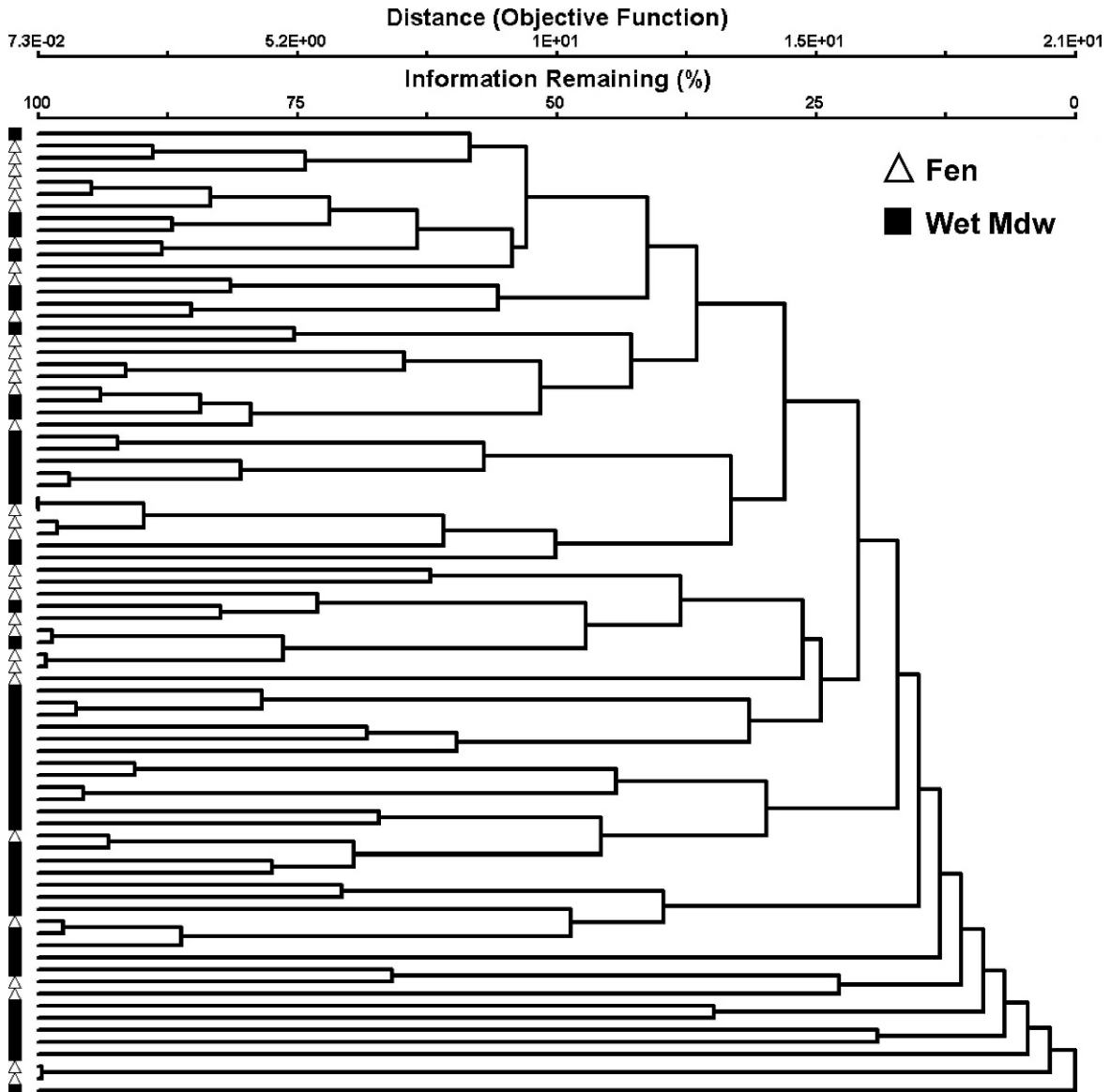
APPENDIX 3.

Agglomerative cluster analysis of aquatic sites with overlay by habitat type.