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Arthropod Assemblages in a Montane Wetland Complex: Influences of Adjoining Lotic and Lentic Habitat and Temporal Variability

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Abstract

Our objective was to gain an understanding of the influences of habitat context and seasonal and interannual factors on arthropod assemblage structure in a wetland environment. We hypothesized that river and pond riparian habitats in the wetland would have greater diversity and abundance than core wetland habitat, and that these differences would be driven by aquatic subsidy via emerging aquatic insects. We also hypothesized that diversity and abundance of terrestrial fauna would decline through the dry summer. We sampled the study wetland, in Yosemite National Park, California, USA, through the growing seasons of 2013 and 2014; a large wildfire (> 100,000 ha) burned the entire study site during late summer of 2013. Assemblage structure was strongly influenced by habitat context, season, and year. Diversity and abundance were high at the river riparian sites, but these results were driven by a diverse and abundant terrestrial fauna, rather than by large numbers of emerging aquatic insects. Faunal assemblages became increasingly depauperate through the summer, likely due to drying of wetland habitat in this hot Mediterranean-type climate. Fire probably had a strong influence on faunal assemblages and vegetation structure, but we cannot rule out interannual variability independent of the fire.

Keywords

Arthropod assemblages, Montane wetland, Habitat context, Temporal variability, Wildfire, Aquatic subsidy

Introduction

Faunal assemblage structure in wetlands can be influenced by a number of factors, including landscape configuration and context (Armitage et al. 2013; Holmquist et al. 2014). There is high faunal richness and abundance at habitat edges in many environments (Forman 1995), often because faunal components from two adjoining habitat elements are present (Polis and Hurd 1996; Puth and Wilson 2001). Arthropod richness and abundance in forested riparian habitat can be directly increased by immigration of emerging aquatic insects (Murikami and Nakano 2002; Kato et al. 2004; Baxter et al. 2005; Jackson et al. 2015) which, in turn, can attract invertebrate predators, further increasing complexity of assemblage structure (Henschel et al. 2001; Jackson and Sullivan 2018). Although wetlands are periodically saturated or inundated, nearby lotic and lentic habitats have the potential to be important influences on the structure of wetland faunal assemblages via such direct and indirect influences.

Faunal assemblage structure in low-canopy, vegetated habitats can vary across months in a variety of tropical and temperate environments (e.g., Denlinger 1980; Holmquist et al. 2013a), and infusion of emerging aquatic insects from streams can vary seasonally in terrestrial habitats bordering streams (Puth and Wilson 2001; Kato et al. 2004; Baxter et al. 2005; Jackson and Sullivan 2018). The assemblage structure of seasonal ponds also changes throughout the year (Bischof et al. 2013) and may also drive assemblage changes in adjoining wetland habitats via aquatic insect emergence. Montane wetland fauna in drier Mediterranean climates might be expected to be influenced by both climate-driven changes in vegetation structure and temporal patterns in emergence of aquatic fauna through the short growing season. Differences in faunal assemblage structure between wetland edge and core habitats could thus shift through the growing season and across years, i.e., habitat-time interactions may be present.

We investigated spatial and temporal influences on arthropod assemblages in a montane wetland complex (Yosemite National Park, California, USA) with portions that border lotic or lentic habitat. Poopenaut Valley represents the largest montane wetland along the Tuolumne River, which has been designated as a U.S. Wild and Scenic River and is important both ecologically and as a major source of water for the San Francisco Bay Area. This wetland complex is spatially isolated from other wetland habitats (see Study Area, below).

Although response of wetland fauna to fire was not part of the study design, the wetland was completely burned by the 2013 Rim Fire, which was the largest fire (104,131 ha) recorded in the extensive mountain range of the Sierra Nevada (Lydersen et al. 2014). The fire occurred during late summer, after the first season of sampling. Such late-season fires have the potential to cause additional mortality, because some species are already in less motile and thus more vulnerable states, such as eggs, pupae, or other overwintering stages (Swengel 2001). We sampled sites immediately before the fire and during the growing season subsequent to the fire (nine months post-fire), but there was no unburned habitat in the wetland, or nearby, that could be used as a post-fire reference (see also Bess et al. 2002). The mid-study occurrence of the Rim Fire has the potential to provide some coarse insights into response of wetland fauna to fire (see also Panzer 2002), but conclusions regarding apparent effects must be limited, particularly given the nuanced responses to fire that have been observed for arthropods (Panzer and Schwarz 2000; Andersen et al. 2014; Moranz et al. 2014; Jackson and Sullivan 2015; Rose and Goebel 2015).

We addressed several central questions in this study. 1) How does assemblage structure vary as a function of wetland context? We compared a) core wetland versus edge wetland near b) river or c) pond. Based on previous work at stream-upland interfaces (Henschel et al. 2001; Murikami and Nakano 2002; Kato et al. 2004; Baxter et al. 2005), we anticipated that emerging aquatic insects would drive higher richness and abundance at river and pond edges, relative to core habitat. Wetlands are, however, productive habitats, and thus such allochthonous subsidy might be proportionally less influential than in uplands. 2) Are there strong seasonal trends for the wetland faunal assemblage, and are there interactions with habitat context? Emerging aquatic insects have been shown to decrease in abundance in near-stream forest through the growing season, whereas terrestrial arthropods can increase during the same period (Kato et al. 2003). Given the dry Mediterranean summers in this montane wetland, with vegetation senescence by July, we hypothesized that abundances of terrestrial, as well as emerging aquatic, insects would decrease, rather than increase, through the growing season. We anticipated that changes in assemblage structure through the growing season would be strongest at wetland-aquatic edges, because of the potential influence of neighboring river and pond habitat and associated fauna (Baxter et al. 2005). Our overall aim was to gain an understanding of several factors that might influence wetland faunal assemblages; we found that all study factors did have strong influences, though not necessarily as anticipated.

Materials and Methods

Study Area and Design

Poopenaut Valley is isolated by the steep granitic walls that line much of the Tuolumne River along the mid-elevation reaches, and no wetlands of the same size (26 ha) are found within 50 river km up- or downstream of the study area. The Valley is rarely visited by people, despite being only 1.75 km by trail from a road in heavily-visited Yosemite National Park, probably because the trail loses 400 m rapidly before reaching the Valley at 1,017 m. Poopenaut Valley has been little-studied until recently (Russo et al. 2012). The area receives 89 cm/y of precipitation, three-quarters of which falls between November and March, primarily as snow (Russo et al. 2012), with an ensuing three-month growing season.

The studied wetland habitat is wet meadow that is seasonally-saturated but generally not inundated. Dominant vegetation in sampled areas included beardless wildrye *Leymus triticoides* (Buckley) Pilger, Mugwort *Artemisia douglasiana* Besser, grass-leaved goldenrod *Euthamia occidentalis* Nutt., inflated sedge *Carex vesicaria* L., and Kentucky bluegrass *Poa pratensis* L. Although found in the other habitats, *Poa* was most common in core habitat, *Carex* was most common near the pond, and tule *Scirpus acutus* (S. Watson) Beetle was found exclusively near the pond. The Valley wetland is bisected by the Tuolumne River, which, at this elevation, is a fourth-order, perennial stream with a 1% gradient that is characterized by riffle-pool habitat. A three-hectare, seasonal pond lies 150m from the north bank of the river and varies in depth and length of inundation. The pond sediment was saturated, but not flooded, during 2013 but was inundated to a depth of ~0.6 m between February and April of 2014. When only saturated, the wetted pond habitat continues to support semi-terrestrial taxa and midge and mosquito larvae not found in wet meadow habitat. The Rim Fire burned the wetland at low to moderate intensity (0-50% basal area; CalFire 2013) during August of 2013. The Valley had burned previously during the 1996 Ackerson Fire.

We sampled three wetland habitats during 2013 and 2014: 1) core wetland habitat that was at least 70 m from the closest upland or aquatic habitat, 2) wetland habitat directly adjoining the river, and 3) wetland habitat directly adjoining the pond. We sampled fauna and associated vegetation structure through the growing season, i.e., starting after snow was completely melted (May) and ending just before high temperatures (mean during sampling hours = 34.3 ^{o}C, maximum > 40 ^{o}C) drove complete senescence of wetland vegetation (late July; see also Fukui et al. 2006). Most major emergences of aquatic insects also occur during these months on the west slope of the Sierra Nevada (Schalla 2015). We thus used a 3 x 3 x 2 design: Habitat (Core, River, Pond) x Month (May, June, July) x Year (2013, 2014). There were four randomly-located samples for each of the Habitat x Month x Year combinations, yielding a total of 72 faunal samples. There were two randomly-selected subsample locations within each sampling location for fauna, and there were two additional randomly-selected vegetation subsamples nested within each of the first pair of subsamples. There were thus two subsampling locations for fauna and four subsampling locations for vegetation at each sampling site. A Scientific Research and Collecting permit was obtained from the US National Park Service for work in Yosemite National Park for each year of the study. No protected species were sampled.

Faunal and Vegetation Methodology

Each sample represented 50 standard sweep net sweeps (New 1998; Henderson and Southwood 2016), evenly divided between each pair of subsampling locations and covering a total of 400 m^2. The sweep net had a mesh size of 0.5 x 0.75 mm and a 30.5 cm aperture. Sweeping was done before vegetation data collection at each sampling location so as to minimize disturbance (see Holmquist et al. 2010; 2011; 2013a for additional faunal sampling details). The same individual collected all faunal samples and vegetation data for consistency. All samples were collected between 0800 and 1800 in full sun and when wind speed was less than 12 km/h; a Kestrel 3000 meter was used to record air and ground temperature and wind speed. All arthropod fauna were identified in the laboratory to species or morphospecies (particularly for immature individuals, Kremen et al. 1993; Oliver and Beattie 1996; Gerlach et al. 2013). Arthropods from all taxa were identified, rather than only those from a single order or other taxonomic group. Analysis across all arthropod groups facilitates detection of responses to habitat characteristics and other drivers that structure ecosystems (Fahrig and Jonsen 1998; Koricheva et al. 2000; Pocock et al. 2012).

We measured percent bare ground, percent green vegetation cover, percent standing brown (senescent) vegetation cover, and percent litter cover using a 10 m point-intercept transect (20 points) centered and randomly-oriented at each subsample location. We measured stem density, canopy height, litter depth, and structural complexity (pole-touch method, Bestelmeyer and Wiens 2001) at two random locations along each of the two transects for each faunal collection. We estimated plant species richness by counting taxa that were contacted anywhere along the full length of the transect.

Analysis

Univariate analyses were primarily 3 x 3 x 2 ANOVAs (Habitat x Month x Year), which were followed by Tukey's multiple comparison tests, both using SYSTAT 12. Vegetation and physical response variables were as outlined above. Faunal response variables included total arthropod abundance, family and species richness, Margalef's index (Magurran and McGill 2011), dominance (percent of total sample abundance represented by the most abundant species in each sample), number and percentage of aquatic and terrestrial arthropods, percentage of herbivores and predators, and individual order, family, and species abundances. Proportional variables were square-root transformed, and all other variables were log-transformed. We adjusted multiple comparisons to per-family error rate with the sequential Bonferroni correction (Holm 1979; Jaccard and Guilamo-Ramos 2002) with MacBonferroni 1.6.

Multivariate analyses included multi-response permutation procedures (MRPP) and nonmetric multidimensional scaling (NMS, McCune and Grace 2002; Peck 2010) using PC-ORD 6, as well as analyses of dispersion using PERMDISP2 (Anderson 2004). Data from all factors and samples were included in the response matrices. There were two explanatory matrices; both included habitat variables and a coding variable for Year, but one matrix included a coding variable for Habitat, and the other included a coding variable for Month. The response matrices of faunal species included only taxa that were collected in at least three sites so as to reduce sparsity (Peck 2010) but not discard excessive information (Poos and Jackson 2012). Response matrices were relativized by maximum abundance for each species. The final response matrix contained 162 species/morphospecies, with a moderate (McCune and Grace 2002) coefficient of variation of 63%. The Sørensen distance measure was used for all analyses.

We assessed dimensionality of data via stress tests and construction of scree plots as part of the NMS analyses. After assessing multiple levels of dimensionality, the best balance of stress level and dimensionality was achieved at three dimensions. We then used three dimensions as an initial configuration for 250 runs with real data. Final stress was moderately high at 18, but was less than expected by chance (p = 0.0040; Monte Carlo test, 249 runs). There were 82 runs for the final solution, and stress stabilized at 51 iterations in stress versus iteration plots. Eight complete additional NMS analyses confirmed consistency of results. The permutational analyses of dispersion were based on 9,999 permutations, used the same datasets and distance measure used for MRPP, and results were derived from deviations from spatial medians and ANOVA tables. We supplemented these analyses with sign tests and rank abundance plots to provide additional perspectives on diversity, richness, and evenness (Magurran and McGill 2011;

Underwood and Fisher 2006; Savage et al. 2011). The datasets generated and/or analyzed during the current study are freely available from the corresponding author upon request.

Results

Main effects differences for the twelve vegetation and physical variables were common, and arthropod habitat quality was generally highest in May (early-season), in Pond and Core, and in 2013 (Fig. 1, Online Resource 1). Ten variables differed by Habitat, eight by Year, and six by Month, although three-quarters of the variables also indicated one or more interactions. Canopy height was lowest in May and highest in Pond habitat during 2014 (Habitat x Year). Structural complexity was halved from 2013 to 2014, and was highest in Pond habitat during July (Habitat x Month). Shoot density was lowest in River habitat, during July, and in 2014 (all main effects). Litter depth was similarly lowest for River and was reduced by a factor of two in 2014 (main effects only). There was essentially no bare ground for Pond and Core, and only ~1% for River, in 2013, but bare ground increased to ~10% for all habitats in 2014 (Fig. 1, Online Resource 1). Green cover was lowest in River, during July, and in 2013 (main effects); a Month x Year interaction was apparent (stronger monthly trends in 2014). Thus both percent bare ground and green cover were higher during 2014, and standing senescent vegetation and litter were reduced during 2014 (Fig. 1, Online Resource 1). Plant species richness was highest at River and did not differ by month or year. Air temperature was lowest in River habitat; temperatures exceeded 30 ^{o}C by July at all sites (Online Resource 1). Soil surface temperature was also lowest at the River sites. Wind speed was higher at River and Core than at Pond sites (Online Resource 1).

Vegetation metrics suggested poorer habitat structure in River, but faunal abundance, richness, diversity, and % aquatic taxa were all higher in this habitat zone (Fig. 2, Online

Resource 2). Faunal assemblage variables also generally had higher values earlier in the summer and in 2013. Richness and Margalef's diversity both followed these trends for main effects, particularly for Habitat (River was two-fold higher), and interactions were absent (Fig. 2, Online Resource 2). Abundance results were similar, but there was also a Month x Year interaction. In accord with the trends for richness and diversity, dominance was low at River. The percent of adult taxa that had aquatic juvenile stages (% aquatic) was low for all months and habitats in 2013; aquatics represented only 0.46 – 2.71% of the fauna at River, but these animals were absent or essentially absent at Pond and Core. In 2014, these values increased slightly for Pond and Core, and % aquatic at River increased to a range of 3.68 to 9.71% (Fig. 2, Online Resource 2). Trends were similar for number of aquatics collected in the wetlands. Abundance of terrestrials was also greatest in River, but numbers were higher in 2013 than in 2014. The percent of the assemblage represented by predators was greatest in late summer, as was the predator:herbivore ratio; % herbivores was conversely highest in early summer (Fig. 2, Online Resource 2). Predator:herbivore ratio was greatest in 2014; this ratio was never greater than one during 2013 at any sites. Month x Year interactions were present for a number of variables, particularly for variables relating to the relative abundance of aquatics and terrestrials and for predators and herbivores. There was only a single, relatively weak, Habitat x Month interaction (species dominance).

The 7,372 individuals collected during the study yielded representatives of seventeen orders, 127 families, and 310 species/morphospecies. Hemiptera was the most abundant order overall (60.1 individuals/50 sweeps, SE= 6.0, Fig. 3, Online Resource 3), followed by Coleoptera ($\bar{x}$ = 10.8, SE= 1.6), Araneae ($\bar{x}$ = 9.6, SE = 0.80), Diptera ($\bar{x}$ = 9.1, SE = 1.1), and Hymenoptera ($\bar{x}$ = 5.9, SE = 0.82). The most abundant species were all hemipterans (Fig. 4, Online Resource 3): the aphid *Sitobion avenae* (Fabricius) (overall $\bar{x}$ = 6.9, SE = 2.0), the mirid plant bug *Europiella artemisiae* (Becker) ($\bar{x}$ = 4.7, SE = 2.2) the delphacid leafhopper *Nothodelphax consimilis* (Van Duzee) ($\bar{x}$ = 4.7, SE = 1.2), and the cicadellid leafhoppers *Hebacephalus discessus* (Van Duzee) ($\bar{x}$ = 6.0, SE = 1.1), *Mesamia* sp. ($\bar{x}$ = 3.9, SE = 1.7), and *Dikraneura carneola* (Stål) ($\bar{x}$ =3.3, SE = 0.7). Overall family richness was highest for Diptera (32), Hymenoptera (26), and Coleoptera (20); species/morphospecies richness was greatest for Diptera and Hemiptera (both 71) and Hymenoptera (65). The most speciose families were cicadellid leafhoppers (25 species/morphospecies), braconid and pteromalid wasps (13 and 12, respectively), and aphids (12).

Abundances of dominant orders reflected many of the patterns observed at the assemblage level, but there was also variability by order (Fig. 3, Online Resource 3). Hemiptera and Coleoptera were most abundant early in the season, near the river, and in 2013. Diptera were most abundant along the river but did not have lower abundances in 2014. Diptera decreased in abundance through the growing season in 2014 but not in 2013 (Fig. 3, Online Resource 3). Hymenoptera (wasps and ants) were most abundant near the river and in 2013, but monthly patterns were absent. Araneae (spiders) did not demonstrate differences as a function of habitat, and temporal differences were the opposite of those more generally observed: numbers were lowest in early season and rose thereafter. Spider abundances were much lower in 2014 than in 2013. Lepidoptera (moths and butterflies) were most abundant near the river, but abundances were low after the fire (Fig. 3, Online Resource 3). Peak lepidopteran abundances occurred in June in 2013, but there were no monthly patterns in 2014. There were no Habitat x Month interactions among the abundant orders.

Dominant species showed strong trends as a function of study factors, particularly Year. (Fig. 4, Online Resource 3). The aphid *Sitobion avenae* had low abundances throughout the study—except in May of 2014, when there was a 40-fold increase in abundance. There was also a two-fold increase in the cicadellid leafhopper *Dikraneura carneola* at this time. Conversely, a number of dominant species demonstrated the common pattern of higher abundances in River habitat, low abundances in 2014, and variable seasonal patterns: the delphacid leafhopper *Nothodelphax consimilis*, the cicadellid leafhopper *Mesamia* sp., and the plant bug *Europiella artemisiae* (Fig. 4, Online Resource 3). Yet another cicadellid, *Hebecephalus discessus*, was also virtually absent in 2014, but lacked clear patterns as a function of habitat or month. There were significant overall trends of higher abundances in River habitat ($p = 0.0015$, sign test across taxa in Online Resource 3) and in 2013 ($p = 0.019$) but not for a given month ($p > 0.063$ for all). Habitat x Month interactions were uncommon.

Rank-abundance relationships and multivariate analyses were consistent with the univariate trends of overall higher diversity near the river, in early season, and in 2013. Rank-abundance slopes were low for River, and high for Pond and July (Fig. 5). Multiple response permutation procedure results as a function of Month and Year were highly significant ($p < 0.000001$; $A > 0.53$), and all multiple comparisons were significant (all $p < 0.0064$). There were similar levels of significance for MRPP on Habitat and Year ($p < 0.000001$, $A > 0.41$; all multiple comparisons $p < 0.035$). Permutational analyses of dispersion were non-significant for the factor combinations in both MRPP analyses, indicating that the differences observed via MRPP were due to differences in assemblage structure rather than being attributable to dispersion. The overall PERMDISP result for Month x Year was $p = 0.61$, and pairwise contrasts ranged from 0.70 to 0.98. The Habitat x Year result was p = 0.54; pairwise comparisons ranged from 0.83 to 0.91.

Nonmetric multidimensional scaling showed lack of overlap between years in ordinal space (Figs. 6 and 7). Months were also somewhat disjunct (Fig. 6), but there was more overlap among habitats (Fig. 7). Cumulative R^2 was 0.66 for both ordinations. Important explanatory variables in the Month-Year ordination included complexity ($R^2 = 0.34$), litter depth (0.22), green cover (0.22), and litter cover (0.21), which were most strongly associated with Axis 2 (Fig. 6). Results were similar for the Habitat-Year ordination, but percent cover by senescent vegetation ($R^2 = 0.20$) also met the threshold for variable-axis correlation for inclusion in the joint plot (Fig. 7). Explanatory variables were again most closely associated with Axis 2 (Fig. 7).

Discussion

We found a high diversity and abundance of fauna in riparian edge habitat, relative to core wetland, as we had hypothesized, but this relationship only held for the river riparian sites. Contrary to expectations, the pond riparian fauna was similar to that of core habitat that was distant from water. Further, the trends observed at River sites were driven by terrestrial fauna, rather than by emerging aquatic insects as had been anticipated on the basis of previous work (Murakami and Nakano 2002; Kato et al. 2004; Baxter et al. 2005; Fukui et al. 2006). It seems unlikely that the dearth of aquatic taxa near the river was the result of low lotic abundance. Limited sampling of the river near the wetland, coincident with each wetland sample (Holmquist and Schmidt unpublished data; Online Resource 4) yielded a faunal assemblage that was analogous to that of other montane river habitat (Holmquist and Waddle 2013) and should have provided a source pool of emerging lotic fauna.

If there were few aquatic fauna sampled in river riparian habitat, and habitat structure was relatively poor near the river, why were wetland fauna so diverse and abundant at the River sites? There are several non-mutually exclusive possibilities. a) Summer microclimate may have been more favorable for arthropods near the river. River sites had lower air and ground temperatures than were recorded from the other sites. Wind speeds were higher at River than Pond, which may have also contributed to the cooling effect. Humidity was not recorded but may have been higher near the river as well, particularly after the wetlands dried later in the season. b) Vegetation structure can have important influences on wetland arthropods, particularly in mountain environments with short growing seasons (Holmquist et al. 2013b; 2014). Structure was unlikely to have been responsible for the rich faunal assemblage of the river riparian wetland, given that structure metrics indicated poorer habitat quality near the river than in Core and Pond habitat. It is possible that unknown factors associated with *Scirpus acutus* and *Carex* near the pond and *Poa* in core habitat were unfavorable for arthropods, but taller plants, such as *Carex vesicaria* and *Scirpus acutus*, are known to provide good habitat for wetland arthropods (Cunha et al. 2012; Holmquist et al. 2011; 2013b). The River habitat did have higher plant species richness, which should have a positive influence on fauna (Schaffers et al. 2008), though plant species richness can be less important than vegetation structure in driving wetland arthropod richness (Cunha et al. 2012; Holmquist et al. 2013b). c) Many terrestrial insects undertake long, active flights or are carried passively by winds, and rivers are flyways (Forman 1995; Puth and Wilson 2001). Many of the taxa found in the study wetland are strong fliers or are small enough to be transported passively by wind. There may be a settlement shadow (Gaines and Roughgarden 1985; Lewin 1986) that increases diversity and abundance near the river. There is little wetland habitat along the montane portion of the river, which is largely bordered by steep canyon walls, and insects flying along the river corridor may settle in the first portion of acceptable habitat that is encountered after a long flight, i.e., river riparian habitat. d) Many of the terrestrial taxa may be “multi-habitat” species (Forman 1995) that, though lacking an aquatic life stage, make use of the river bank for puddling (drinking), cooling, or egg laying in sand. e) We may have largely missed the emergences of aquatic insects in either time or space, if the emergences of the variety of aquatic taxa had been devoured or otherwise perished before these animals could be sampled or if the emerging individuals largely avoid wetland vegetation. Some combination of these phenomena, or others, apparently yields substantial edge effects resulting in high diversity and abundance (Polis and Hurd 1996; Fukui et al. 2006) at the river-wetland ecotone. In contrast, the pond riparian fauna may have been as depauperate as core wetland because of distance from the river flyway and because of low water levels during the study.

We had hypothesized that both terrestrial fauna and aquatic adults would decrease in abundance through the growing season in this Mediterranean climate, and this pattern was indeed evident. The congruent directionality for terrestrials and aquatics contrasted with previously observed opposing trends through the growing season in other locations: decreasing aquatic abundance but increasing terrestrial abundance through the growing season (Kato et al. 2003; Nakano and Murakami 2001). Summer in the montane Sierra Nevada is a stressful period after early season, in contrast with wetter environments. In these Sierrran wetlands, soils dry and plant productivity slows or ceases before temperatures cool, (Online Resource 1, % senescent vegetation; Holmquist et al. 2013a), and faunal diversity and abundance appear to also decline well before the end of summer. Terrestrial arthropods are generally in diapause-- variously as eggs, larvae, nymphs, pupae, or adults— during times of the year in which photoperiod, temperature, and food resources are not optimal (Wolda 1988; Cardoso et al. 2007). In the Sierra Nevada, the optimal period between the wet winter and dry summer is short indeed. These seasonal faunal declines at our montane study sites were more precipitous than previously observed in subalpine wetlands (Holmquist et al. 2013a), likely because of less snow accumulation, less soil saturation, and warmer summer temperatures at these lower elevations. Neither the terrestrial or aquatic seasonal decreases are likely to be supply-side in nature, as a function of decreasing aquatic subsidy; lotic densities tend to be highest in mid- to late season (Online Resource 4; Holmquist et al. 2015). There were few Habitat x Month interactions, indicating that differences among habitats were, contrary to our hypothesis, consistent through the growing season.

Predators, particularly spiders, were an exception to the trend of decreasing arthropod abundances through the growing season. The high early-season abundances of herbivores, particularly leafhoppers and beetles, may have fueled spider abundances that remained high after seasonal reductions in herbivore densities (Henschel et al. 2001; but see Denlinger 1980), although seasonal drying and senescence are likely to have caused at least as much of the observed herbivore decrease as predation (Holmquist et al. 2013a).

Interannual effects for fauna were common and strong and indicated an overall negative trend from 2013 to 2014. We cannot unequivocally claim that these trends were caused by fire, due to lack of available reference habitat (see also Rose and Goebel 2015), but trends for both vegetation and fauna were consistent with frequently-reported fire effects. Fire in grass and sedge-dominated habitats burns away litter and standing senescent vegetation, increases the proportion of bare ground, and increases green cover within a year (Kato et al. 2003; Vogel et al. 2010; Little et al. 2013, Masunga et al. 2013; see also Hosoishi et al. 2014). We observed identical directionality for these metrics at our sites following the Rim Fire. Faunal assemblages can be strongly influenced by indirect fire effects, via these shifts in vegetation structure, and by direct effects (Vogel et al. 2010; Little et al. 2013), though responses can vary among environments and taxa (Warren et al. 1987; Siemann et al. 1997; Swengel 2001; Panzer 2002; Hanula and Wade 2003; Doamba et al. 2014). Affected fauna may be killed directly by wildfire (Bock and Bock 1991; Swengel 2001) or may emigrate during or after the fire (Swengel 2001; Doamba et al. 2014). Direct mortality is most likely for species that are in immobile stages just prior to the coming fall and winter (Swengel 2001; Malmström et al. 2009). Leafhoppers and Lepidoptera are univoltine, and eggs and dormant juveniles are likely to be sequestered in litter in late season (Panzer and Schwartz 2000). These groups may be particularly susceptible to fire and other disturbances (Armitage et al. 2013), and leafhoppers and Lepidoptera had much lower abundances on our sites in 2014 than in 2013. There were also major 2014 decreases in Coleoptera, Hymenoptera, and Araneae, as well as decreases in overall abundance, species richness, and diversity. Similar trends were common at the species level, but the aphid *Sitobion avenae* and the leafhopper *Dikraneura carneola* were exceptions. Both taxa can produce outbreaks under certain conditions, and may have been able to respond rapidly to the additional food resources present during greenup in 2014. In contrast, fire-sensitive taxa may be slow to recover (Vogel et al. 2010), particularly if source habitat is limited and/or distant (Anderson et al. 1989; Swengel 2001; Panzer 2002). There were no unburned portions of the study wetland, and source wetlands were distant and at higher elevation; this level of isolation may have contributed to the low diversity and abundance present in the study wetlands in 2014. The decreases that we observed in 2014 may or may not have been due to fire effects, but were unlikely to have been a proximate result of reduced aquatic subsidy, though fire and stream productivity can demonstrate complex interactions (Malison and Baxter 2010; Jackson et al. 2012; Jackson and Sullivan 2018). Abundance and richness of emergent lotic fauna were nominally greater in 2014 than in 2013, and pond inundation occurred in 2014 and likely increased the supply of emerging lentic fauna. Emerging aquatics nonetheless represented a small proportion of the wetland fauna in either year.

Conclusions

Wetland arthropods were strongly influenced by habitat context and seasonal and interannual factors, but emerging aquatic insects had little proximate influence on these patterns, which was an unexpected result, and powerful aquatic subsidies to riparian habitats should not be assumed to be a universal phenomenon. Faunal diversity and abundance were markedly reduced through the summer, likely due to drying of wetland habitat. Differences among habitats were consistent through the growing season and did not shift as a function of changes in aquatic subsidy or increasing wetland senescence. Fire probably had a strong influence on faunal assemblages and vegetation, though we cannot rule out stochastic change between 2013 and 2014.

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Figure Captions

Fig 1

Vegetation means (SE) as a function of Habitat (H), Month (M), and Year (Y). Letters indicate ANOVA contrasts for main effects and interactions that were significant at $p < 0.01$; see Online Resource 1 for additional parameters and detailed test results

Fig 2

Faunal assemblage means (SE) as a function of Habitat (H), Month (M), and Year (Y). All metrics were based on 50-sweep samples. Capital letters indicate ANOVA contrasts for main effects and interactions that were significant at $p<0.01$, and lower case letters indicate significance at $p<0.05$; see Online Resource 2 for additional parameters and detailed test results

Fig 3

Mean (SE) abundances of most abundant faunal orders as a function of Habitat (H), Month (M), and Year (Y). All metrics were based on 50-sweep samples. Note differing y-axes. Capital letters indicate ANOVA contrasts for main effects and interactions that were significant at $p<0.01$, and lower case letters indicate significance at $p<0.05$; see Online Resource 3 for additional orders and detailed test results

Fig 4

Mean (SE) abundances of abundant species as a function of Habitat (H), Month (M), and Year (Y). All metrics were based on 50-sweep samples. Note differing y-axes. Capital letters indicate ANOVA contrasts for main effects and interactions that were significant at $p<0.01$, and lower case letters indicate significance at $p<0.05$; see Online Resource 3 for additional species and detailed test results

Fig 5

Rank-abundance plots, from total study abundances, for Habitat and Year (top), and Month and Year (bottom). Thick and thin lines reference 2013 and 2014, respectively

Fig 6

Ordination of faunal assemblages by Month and Year across samples using nonmetric multidimensional scaling. Distance between site icons increases with dissimilarity among samples; convex hulls surround all samples of a given Month-Year combination. White and black symbols indicate 2013 and 2014 samples, respectively. Squares indicate May, triangles June, and diamonds July. Plots were scaled by proportion of maximum; orthogonality was 100% for each axis pair. Axis labels note R^2 values estimating post-hoc percent of variation within the distance matrix that is explained by each axis. Cumulative R^2 was 0.66. Explanatory variables in joint plot: Co = Complexity, LC = Litter Cover, GC = Green Cover, LD = Litter Depth. Minimum explanatory variable-axis correlation for inclusion in the joint plot was $R^2 = 0.20$

Fig 7

Ordination of faunal assemblages by Habitat and Year across samples using nonmetric multidimensional scaling. Distance between site icons increases with dissimilarity among samples; convex hulls surround all samples of a given Habitat-Year combination. White and black symbols indicate 2013 and 2014 samples, respectively. Squares indicate Pond, triangles

River, and diamonds Core. Plots were scaled by proportion of maximum; orthogonality was 100% for each axis pair. Axis labels note R^2 values estimating post-hoc percent of variation within the distance matrix that is explained by each axis. Cumulative R^2 was 0.66. Explanatory variables in joint plot: Co = Complexity, LC = Litter Cover, GC = Green Cover, BC = Brown (standing senescent) Cover, LD = Litter Depth. Minimum explanatory variable-axis correlation for inclusion in the joint plot was $R^2 = 0.20$

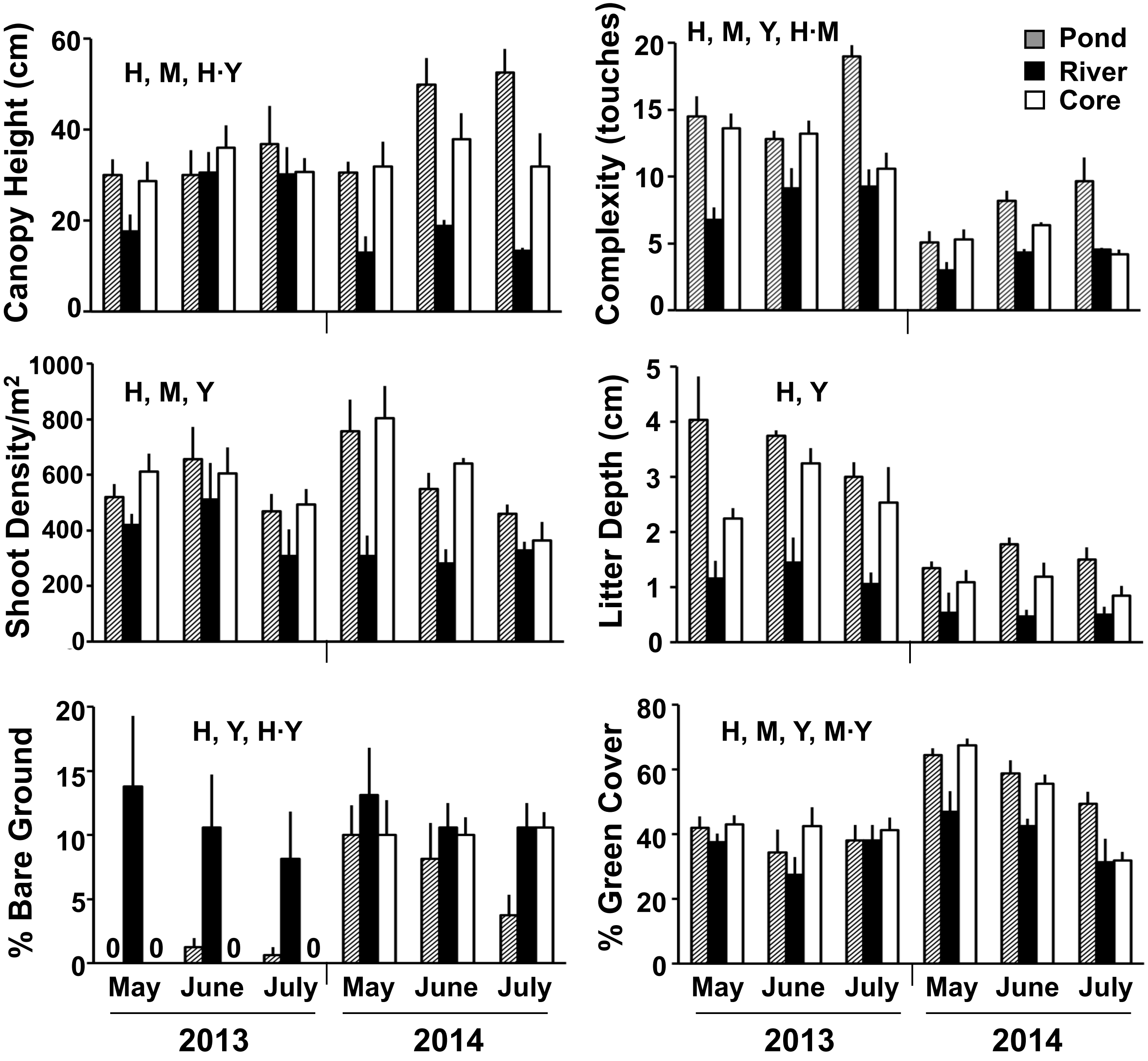
Online Resource Captions

Online Resource 1. Vegetation and physical parameters. Means (standard errors) for vegetation and physical parameters and ANOVA results for main effects and two-way interactions. (pdf)

Online Resource 2. **Faunal assemblage parameters.** Means (standard errors) for faunal assemblage parameters (all based upon 50 sweeps) and ANOVA results for main effects and two-way interactions. (pdf)

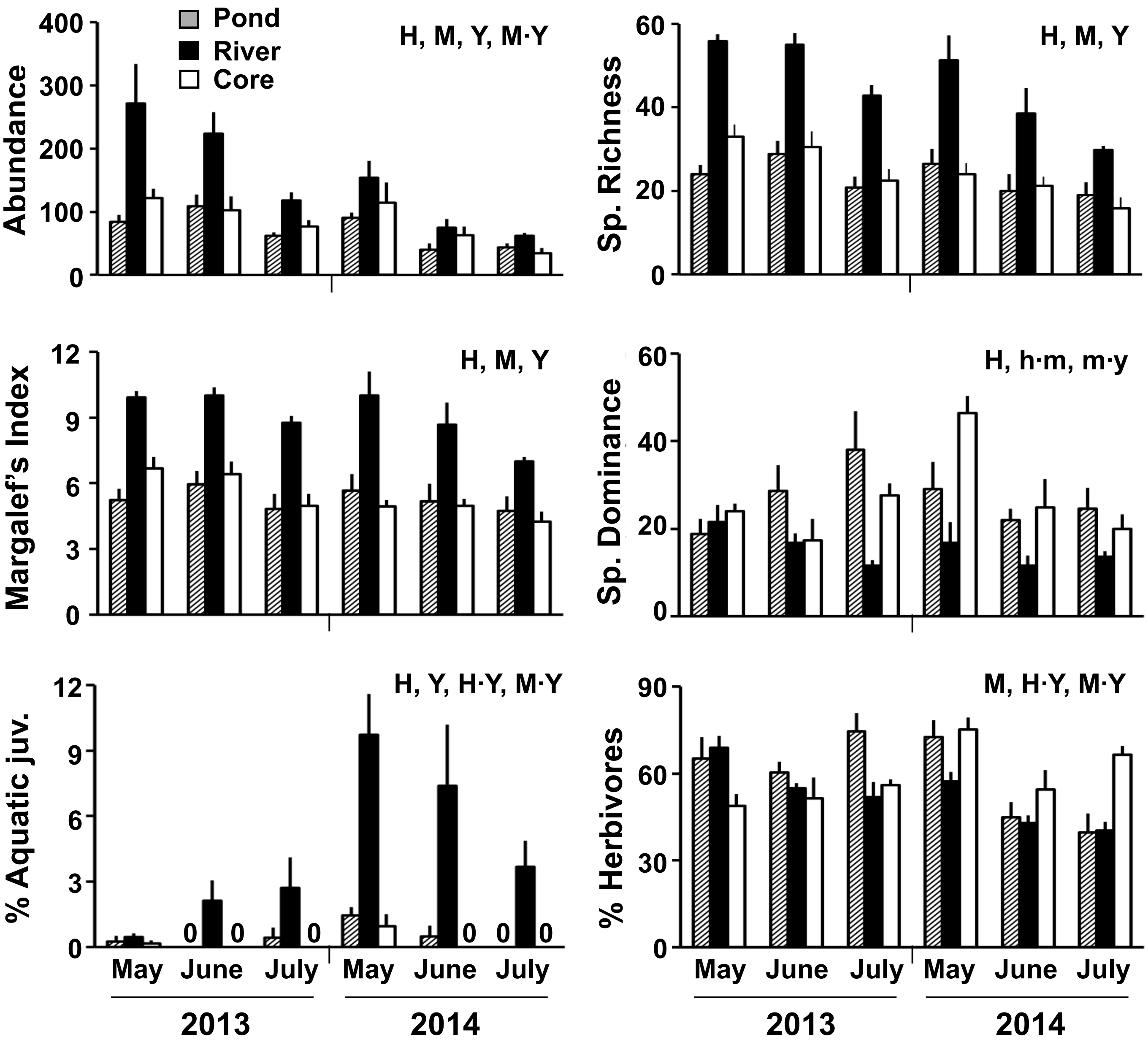
Online Resource 3. **Faunal orders and most abundant families and species**. Mean number of individuals (standard errors) for faunal orders and ten most abundant families and species (all based upon 50 sweeps) and ANOVA results for main effects and two-way interactions. (pdf)

Online Resource 4. **Lotic fauna near wetland.** Raw data, means, and standard errors for Tuolumne River lotic fauna near wetland sites. Results are from 1 m^2 kick net samples from cobble habitat. (xlsx)



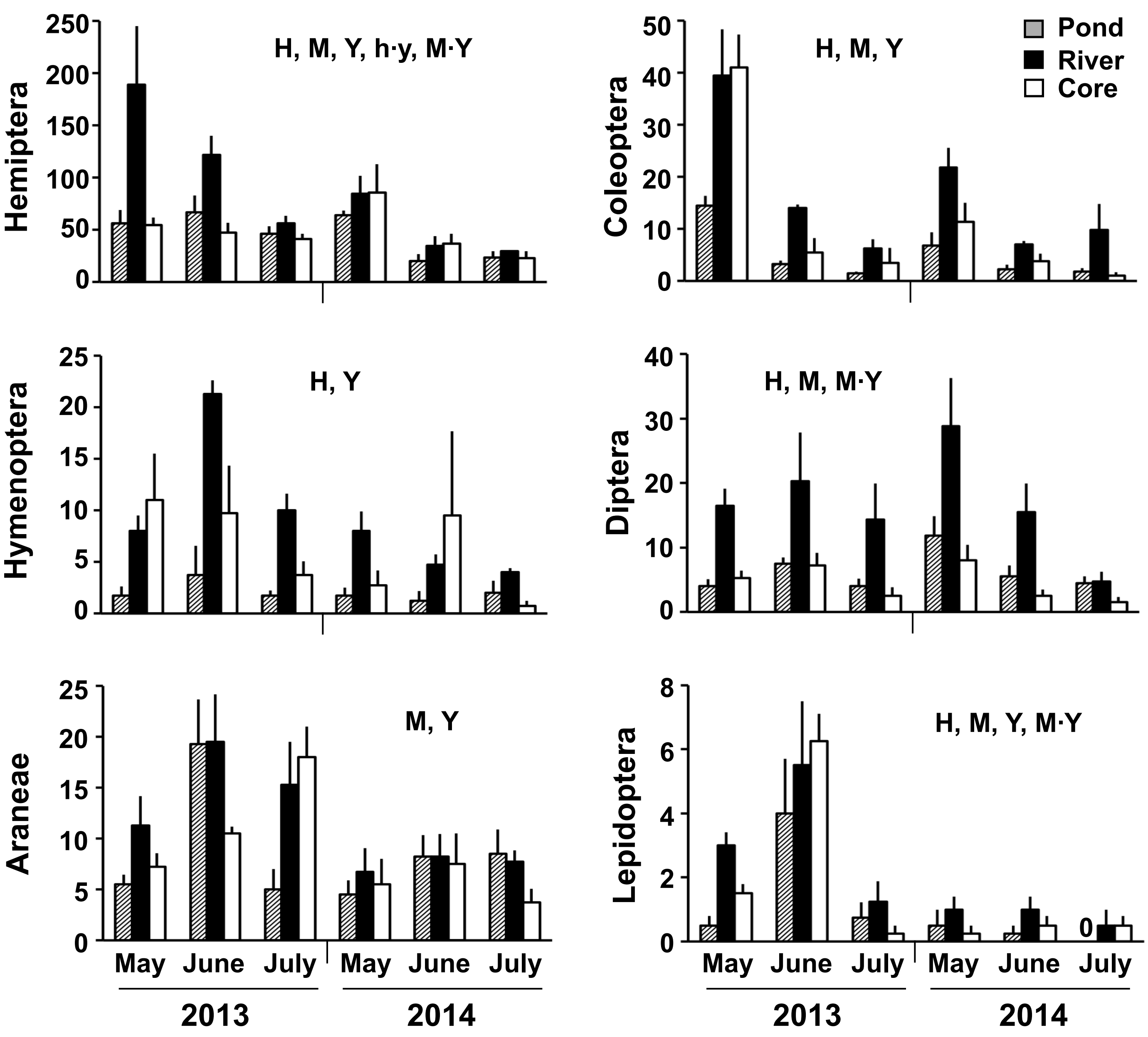
Canopy Height (cm)
60
40
20
0
H, M, H·Y
Complexity (touches)
20
15
10
5
0
H, M, Y, H·M
Pond
River
Core
Shoot Density/m^2
1000
800
600
400
200
0
H, M, Y
Litter Depth (cm)
5
4
3
2
1
0
H, Y
% Bare Ground
20
15
10
5
0
H, Y, H·Y
0
0
0
0
% Green Cover
80
60
40
20
0
H, M, Y, M·Y
May
June
July
May
June
July
2013
2014
May
June
July
May
June
July
2013
2014

Fig. 1



Pond
River
Core
Abundance
H, M, Y, M·Y
Sp. Richness
H, M, Y
Margalef's Index
H, M, Y
Sp. Dominance
H, h·m, m·y
% Aquatic juv.
H, Y, H·Y, M·Y
0
% Herbivores
M, H·Y, M·Y
May
June
July
2013
2014

Fig. 2



Hemiptera
H, M, Y, h·y, M·Y
250
200
150
100
50
0
Coleoptera
H, M, Y
50
40
30
20
10
0
Pond
River
Core
Hymenoptera
H, Y
25
20
15
10
5
0
Diptera
H, M, M·Y
40
30
20
10
0
Araneae
M, Y
25
20
15
10
5
0
Lepidoptera
H, M, Y, M·Y
8
6
4
2
0
May
June
July
May
June
July
2013
2014

Fig. 3

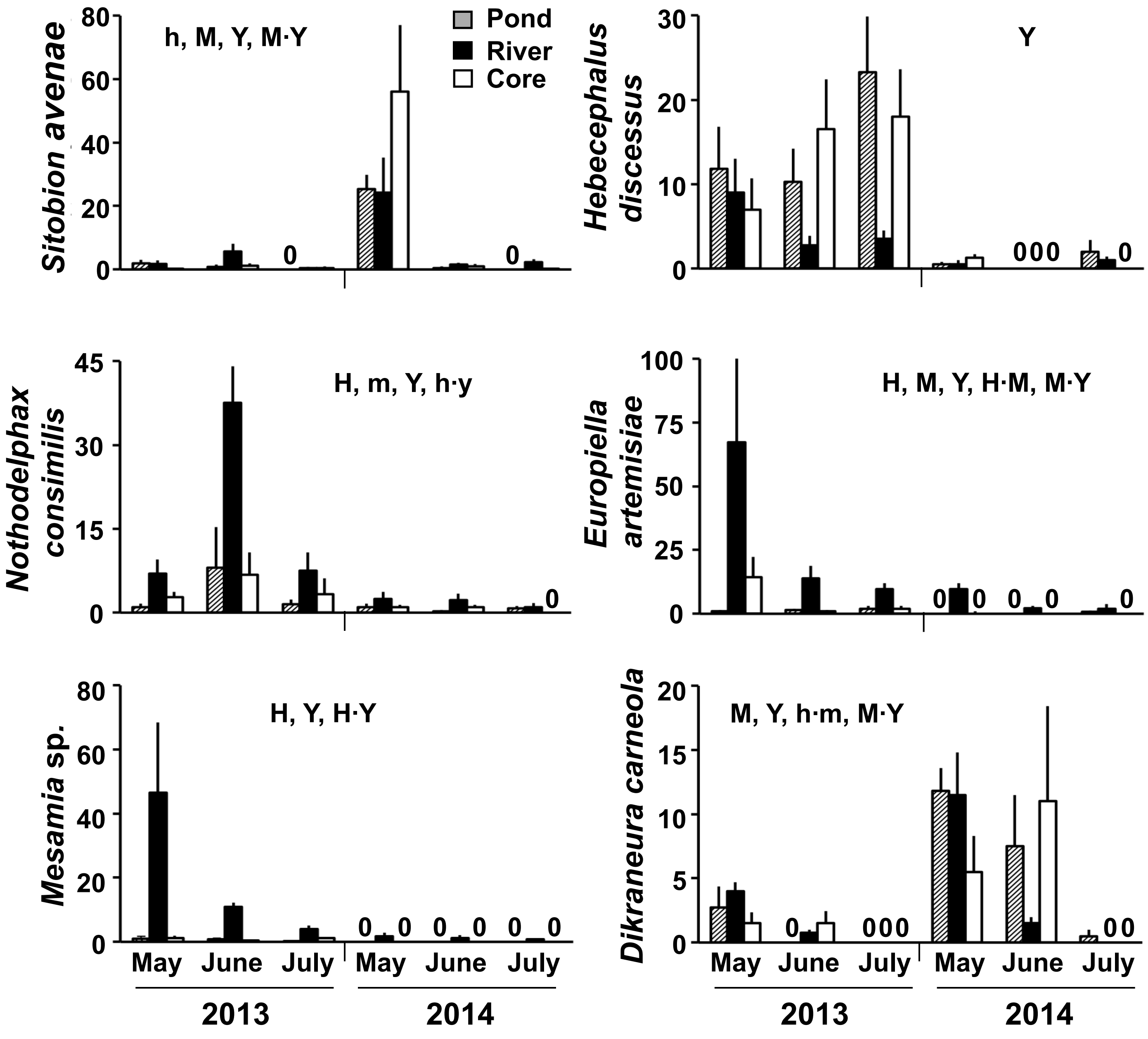
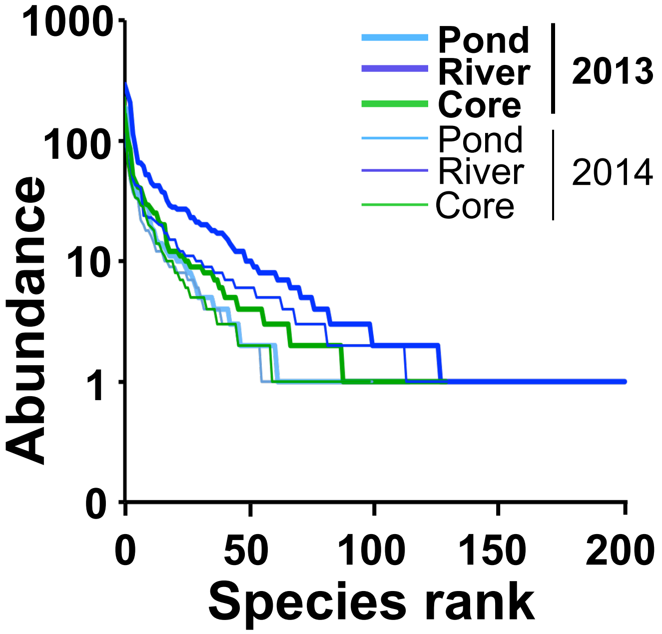

Sitobion avenae
h, M, Y, M·Y
Pond
River
Core
Hebecephalus discessus
Y
Nothodelphax consimilis
H, m, Y, h·y
Europiella artemisiae
H, M, Y, H·M, M·Y
Mesamia sp.
H, Y, H·Y
Dikraneura carneola
M, Y, h·m, M·Y
0
80
60
40
20
30
10
45
15
100
75
50
25
5
May
June
July
2013
2014

Fig. 4


1000
100
10
1
0
Abundance
0
50
100
150
200
Species rank
Pond
River
Core
2013
Pond
River
Core
2014

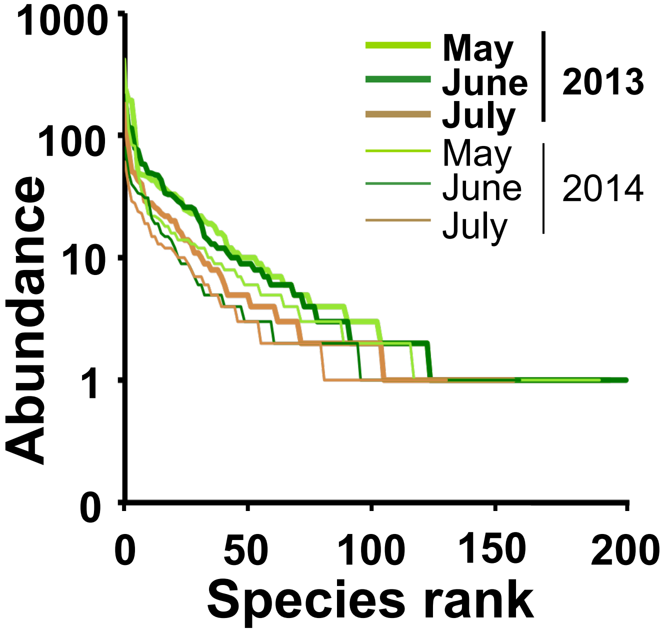

1000
100
10
1
0
Abundance
0
50
100
150
200
Species rank
May
June
July
2013
May
June
July
2014

Fig. 5

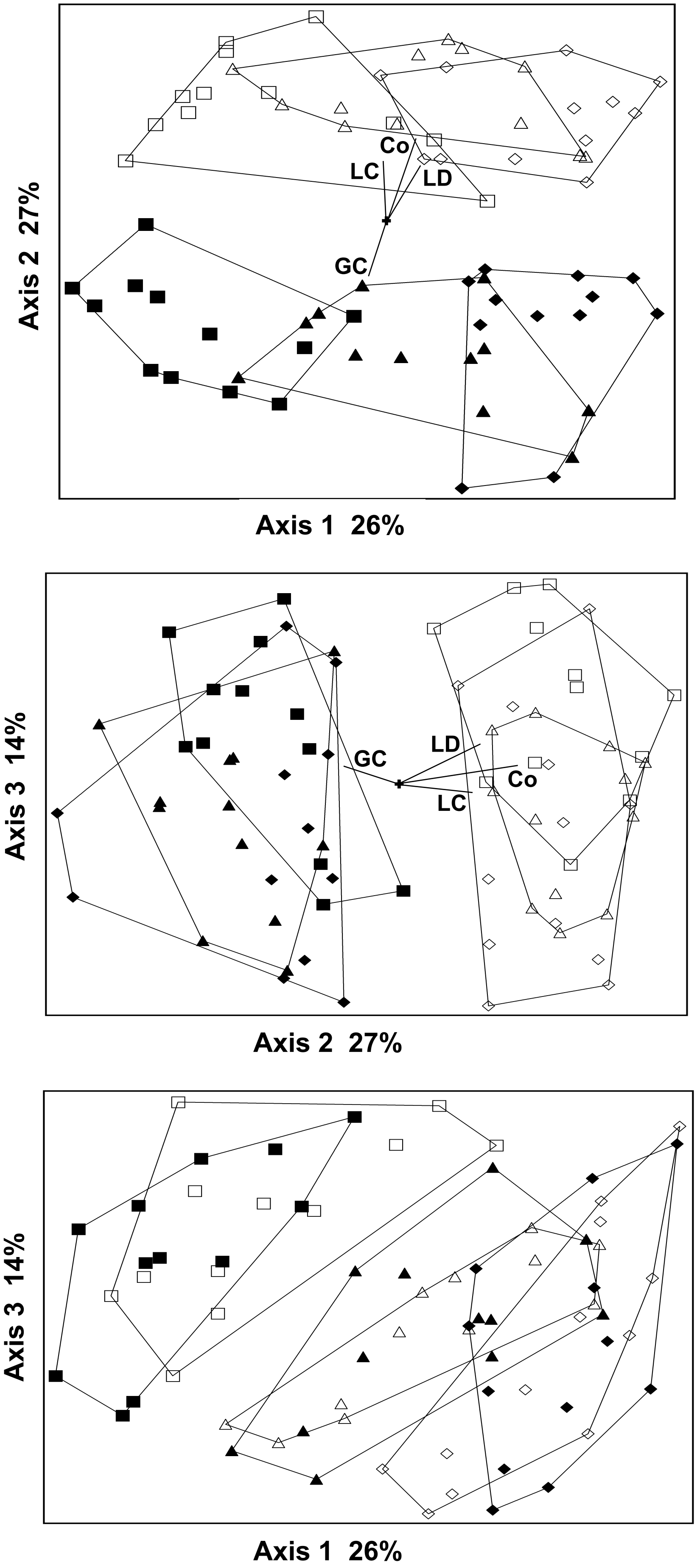

Co
LC
LD
GC
Axis 2 27%
Axis 1 26%
GC
LD
Co
LC
Axis 3 14%
Axis 2 27%
Axis 3 14%
Axis 1 26%

Fig. 6

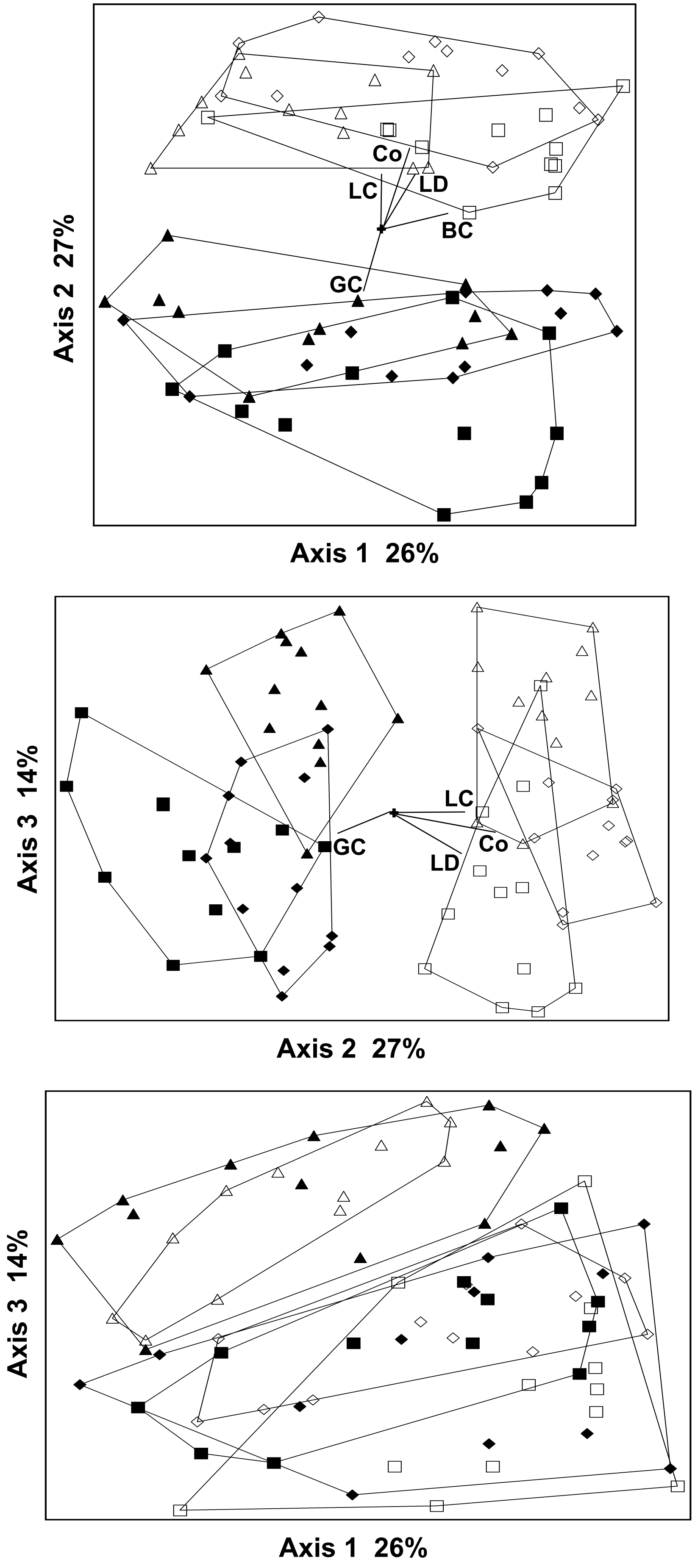

Co
LC
LD
BC
GC
Axis 2 27%
Axis 1 26%
LC
GC
Co
LD
Axis 3 14%
Axis 2 27%
Axis 3 14%
Axis 1 26%

Fig. 7

Supplementary material: Arthropod Assemblages in a Montane Wetland Complex: Influences of Adjoining Lotic and Lentic Habitat and Temporal Variability, *Wetlands*, Jeffrey G Holmquist and Jutta Schmidt-Gengenbach, UCLA, jholmquist@ucla.edu

Online Resource 1 Vegetation and physical parameters. Means (standard errors) and ANOVA results for main effects and two-way interactions

		2013			2014			ANOVA results					
		May	June	July	May	June	July	H^a	M^b	Y^c	HxM	HxY	MxY
Canopy ht. (cm)	Pond	30.0 (3.5)	30.0 (5.5)	36.8 (8.4)	30.5 (2.4)	49.9 (5.9)	52.6 (5.2)	** P^{d}C^e>R^f	** 6^{g}7^h>5^i			**	
	River	17.6 (3.8)	30.6 (4.5)	30.2 (6.0)	13.0 (3.5)	18.8 (1.3)	13.3 (0.75)						
	Core	28.7 (4.3)	36.0 (5.0)	30.7 (3.0)	31.9 (5.5)	37.9 (5.7)	31.9 (7.3)						
Complexity (touches)	Pond	14.5 (1.5)	12.8 (0.62)	19.0 (0.84)	5.06 (0.84)	8.19 (0.74)	9.63 (1.8)	** P>C>R	** 67>5	** 13^j>14^k	**		
	River	6.75 (0.94)	9.13 (1.5)	9.25 (1.3)	3.00 (0.60)	4.31 (0.28)	4.56 (0.11)						
	Core	13.6 (1.1)	13.2 (1.0)	10.6 (1.2)	5.31 (0.74)	6.38 (0.22)	4.19 (0.36)						
Shoot dens. per m^2	Pond	520 (46)	656 (117)	468 (64)	756 (115)	548 (58)	460 (32)	** PC>R	** 56>7	** 13>14			
	River	420 (40)	512 (130)	308 (96)	308 (73)	280 (53)	328 (31)						
	Core	612 (64)	604 (95)	492 (56)	804 (115)	640 (20)	364 (66)						
Litter depth (cm)	Pond	4.03 (0.79)	3.75 (0.09)	3.00 (0.27)	1.34 (0.13)	1.78 (0.12)	1.50 (0.22)	** P>C>R		** 13>14			
	River	1.16 (0.32)	1.44 (0.46)	1.06 (0.21)	0.53 (0.37)	0.47 (0.12)	0.50 (0.15)						
	Core	2.25 (0.18)	3.25 (0.27)	2.53 (0.65)	1.09 (0.22)	1.19 (0.26)	0.84 (0.18)						
% Bare	Pond	0 (0)	1.25 (0.72)	0.63 (0.63)	10.0 (2.3)	8.13 (2.8)	3.75 (1.6)	** R>PC		** 14>13		**	
	River	13.8 (5.5)	10.6 (4.1)	8.13 (3.7)	13.1 (3.7)	10.6 (1.9)	10.6 (1.9)						
	Core	0 (0)	0 (0)	0 (0)	10.0 (2.7)	10.0 (1.4)	10.6 (1.2)						

% Green	Pond	41.9 (3.6)	34.4 (7.0)	38.1 (4.8)	64.4 (2.1)	58.8 (4.1)	49.4 (3.7)	** PC>R	** 5>67	** 14>13			**
	River	37.5 (2.7)	27.5 (5.4)	38.1 (4.8)	46.9 (6.4)	42.5 (2.3)	31.3 (7.3)						
	Core	43.1 (2.8)	42.5 (5.8)	41.3 (3.9)	67.5 (2.0)	55.6 (2.8)	31.9 (2.6)						
% Brown	Pond	21.9 (2.6)	31.3 (6.5)	33.1 (3.6)	9.38 (1.6)	21.9 (4.1)	37.5 (4.4)		** 7>6>5	** 13>14			**
	River	26.9 (2.6)	40.0 (2.7)	32.5 (2.3)	16.9 (2.8)	16.9 (5.1)	44.4 (10)						
	Core	32.5 (12.5)	33.1 (3.7)	31.9 (4.5)	10.0 (1.8)	21.9 (3.1)	44.4 (4.0)						
% Litter	Pond	36.3 (5.1)	32.5 (4.0)	28.1 (1.2)	16.3 (1.6)	11.3 (1.6)	9.38 (2.6)			** 13>14		**	
	River	21.9 (2.8)	21.9 (1.9)	21.3 (3.0)	24.4 (6.8)	30.0 (6.7)	13.8 (2.4)						
	Core	24.4 (13)	24.4 (4.3)	26.9 (0.63)	12.5 (2.7)	13.1 (1.2)	13.1 (2.6)						
Species richness	Pond	2.88 (0.38)	2.63 (0.24)	3.00 (0.20)	2.63 (0.24)	2.63 (0.32)	2.50 (0.35)	** R>PC					
	River	4.13 (0.13)	3.63 (0.24)	3.50 (0.35)	3.63 (0.24)	3.63 (0.24)	3.75 (0.43)						
	Core	2.63 (0.38)	2.63 (0.43)	3.00 (0.54)	2.75 (0.88)	3.75 (1.1)	2.88 (0.32)						
Air temp (^{o}C)	Pond	28.3 (0.95)	28.3 (0.72)	32.7 (0.52)	26.9 (0.29)	29.7 (0.98)	36.9 (1.9)	** PC>R	** 7>6>5			*	**
	River	25.4 (1.6)	26.3 (0.64)	30.7 (0.58)	25.1 (0.78)	27.4 (0.67)	34.5 (0.29)						
	Core	29.4 (0.14)	29.5 (0.52)	34.8 (0.61)	27.1 (0.55)	27.9 (1.0)	36.3 (0.52)						
Soil surface temp (^{o}C)[1]	Pond	35.5 (0.79)	35.1 (2.4)	36.3 (1.6)				** PC>R					
	River	30.4 (2.5)	27.8 (3.1)	30.6 (2.2)									
	Core	32.5 (0.67)	33.7 (2.2)	39.8 (0.65)									

Wind speed	Pond	1.45 (0.20)	1.50 (0.06)	2.30 (0.0)	2.70 (0.06)	4.45 (1.1)	4.35 (0.26)	** RC>P	** 14>13	*
(km/hr)	River	2.55 (0.32)	2.05 (0.14)	2.60 (0.12)	7.80 (2.1)	7.45 (0.99)	7.70 (2.4)			
	Core	3.10 (0.40)	0.70 (0.40)	2.80 (0.81)	6.25 (0.78)	6.65 (1.3)	5.75 (1.9)			

Inequalities below asterisks reference multiple comparisons that were significant via Tukey's tests at $p<0.05$ following the sequential Bonferroni correction of multiple comparison to family-wise error rate. Levels on either side of the inequality differed. Multiple comparison tests were not necessary for Year, but an inequality is provided to summarize test results.

[a] Habitat.

[b] Month.

[c] Year.

[d] Pond.

[e] Core.

[f] River.

[g] June.

[h] July.

[i] May.

[j] 2013.

[k] 2014.

[l] Only 2013 data for soil surface temperature.

*$p<0.05$ for main effect or interaction.

**$p<0.01$ for main effect or interaction.

Supplementary material: Arthropod Assemblages in a Montane Wetland Complex: Influences of Adjoining Lotic and Lentic Habitat and Temporal Variability, *Wetlands*, Jeffrey G Holmquist and Jutta Schmidt-Gengenbach, UCLA, jholmquist@ucla.edu

Online Resource 2 Faunal assemblage parameters. Means (standard errors) for faunal assemblage parameters (all based upon 50 sweeps) and ANOVA results for main effects and two-way interactions.

		2013			2014			ANOVA results					
		May	June	July	May	June	July	H^{a}	M^{b}	Y^{c}	HxM	HxY	MxY
Total individuals	Pond	83.8 (11)	109 (18)	61.8 (6.0)	90.3 (8.2)	40.0 (9.8)	44.0 (6.2)	** R^{d}>P^{e}C^{f}	** 5^{g}>6^{h}>7^{i}	** 13^{j}>14^{k}			**
	River	271 (63)	224 (34)	118 (13)	154 (26)	74.5 (14)	61.5 (5.4)						
	Core	122 (14)	102 (22)	76.8 (10)	114 (32)	63.3 (13)	34.0 (8.5)						
Species richness	Pond	24.0 (2.2)	28.8 (3.3)	20.8 (2.7)	26.5 (3.6)	20.0 (4.0)	19.0 (3.0)	** R>PC	** 56>7	** 13>14			
	River	55.8 (1.7)	55.0 (2.8)	42.8 (2.5)	51.3 (6.0)	38.5 (6.2)	29.8 (1.0)						
	Core	33.0 (2.9)	30.5 (3.7)	22.5 (2.8)	24.0 (2.7)	21.3 (2.2)	15.8 (2.7)						
Family richness	Pond	16.0 (1.8)	21.0 (2.9)	15.0 (1.5)	16.8 (3.4)	14.0 (2.8)	13.8 (2.2)	** R>PC	** 56>7	** 13>14			
	River	34.0 (1.6)	33.3 (2.1)	29.0 (1.6)	30.0 (2.9)	22.5 (2.9)	19.8 (1.7)						
	Core	21.5 (2.9)	21.0 (3.1)	14.0 (2.3)	14.3 (1.5)	14.5 (0.96)	11.0 (2.0)						
% species dominance	Pond	18.8 (3.4)	28.6 (6.0)	38.0 (8.8)	29.1 (6.2)	22.0 (2.5)	24.6 (4.7)	** PC>R			*		*
	River	21.5 (4.0)	16.8 (2.1)	11.5 (1.4)	16.7 (4.8)	11.5 (2.3)	13.6 (1.2)						
	Core	24.0 (1.7)	17.4 (4.8)	27.6 (2.8)	46.4 (3.9)	24.9 (6.5)	19.9 (3.3)						
Margalef's sp. richness	Pond	5.24 (0.52)	5.95 (0.60)	4.83 (0.70)	5.66 (0.77)	5.16 (0.81)	4.74 (0.67)	** R>PC	**	** 13>14			
	River	9.92 (0.28)	10.0 (0.39)	8.77 (0.32)	10.0 (1.1)	8.68 (1.0)	7.00 (0.20)						
	Core	6.67 (0.54)	6.42 (0.58)	4.96 (0.56)	4.93 (0.30)	4.96 (0.32)	4.24 (0.48)						

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Arthropod Assemblages in a Montane Wetland Complex: Influences of Adjoining Lotic and Lentic Habitat and Temporal Variability

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Abstract

Our objective was to gain an understanding of the influences of habitat context and seasonal and interannual factors on arthropod assemblage structure in a wetland environment. We hypothesized that river and pond riparian habitats in the wetland would have greater diversity and abundance than core wetland habitat, and that these differences would be driven by aquatic subsidy via emerging aquatic insects. We also hypothesized that diversity and abundance of terrestrial fauna would decline through the dry summer. We sampled the study wetland, in Yosemite National Park, California, USA, through the growing seasons of 2013 and 2014; a large wildfire (> 100,000 ha) burned the entire study site during late summer of 2013. Assemblage structure was strongly influenced by habitat context, season, and year. Diversity and abundance were high at the river riparian sites, but these results were driven by a diverse and abundant terrestrial fauna, rather than by large numbers of emerging aquatic insects. Faunal assemblages became increasingly depauperate through the summer, likely due to drying of wetland habitat in this hot Mediterranean-type climate. Fire probably had a strong influence on faunal assemblages and vegetation structure, but we cannot rule out interannual variability independent of the fire.

Keywords

Arthropod assemblages, Montane wetland, Habitat context, Temporal variability, Wildfire, Aquatic subsidy

Introduction

Faunal assemblage structure in wetlands can be influenced by a number of factors, including landscape configuration and context (Armitage et al. 2013; Holmquist et al. 2014). There is high faunal richness and abundance at habitat edges in many environments (Forman 1995), often because faunal components from two adjoining habitat elements are present (Polis and Hurd 1996; Puth and Wilson 2001). Arthropod richness and abundance in forested riparian habitat can be directly increased by immigration of emerging aquatic insects (Murikami and Nakano 2002; Kato et al. 2004; Baxter et al. 2005; Jackson et al. 2015) which, in turn, can attract invertebrate predators, further increasing complexity of assemblage structure (Henschel et al. 2001; Jackson and Sullivan 2018). Although wetlands are periodically saturated or inundated, nearby lotic and lentic habitats have the potential to be important influences on the structure of wetland faunal assemblages via such direct and indirect influences.

Faunal assemblage structure in low-canopy, vegetated habitats can vary across months in a variety of tropical and temperate environments (e.g., Denlinger 1980; Holmquist et al. 2013a), and infusion of emerging aquatic insects from streams can vary seasonally in terrestrial habitats bordering streams (Puth and Wilson 2001; Kato et al. 2004; Baxter et al. 2005; Jackson and Sullivan 2018). The assemblage structure of seasonal ponds also changes throughout the year (Bischof et al. 2013) and may also drive assemblage changes in adjoining wetland habitats via aquatic insect emergence. Montane wetland fauna in drier Mediterranean climates might be expected to be influenced by both climate-driven changes in vegetation structure and temporal patterns in emergence of aquatic fauna through the short growing season. Differences in faunal assemblage structure between wetland edge and core habitats could thus shift through the growing season and across years, i.e., habitat-time interactions may be present.

We investigated spatial and temporal influences on arthropod assemblages in a montane wetland complex (Yosemite National Park, California, USA) with portions that border lotic or lentic habitat. Poopenaut Valley represents the largest montane wetland along the Tuolumne River, which has been designated as a U.S. Wild and Scenic River and is important both ecologically and as a major source of water for the San Francisco Bay Area. This wetland complex is spatially isolated from other wetland habitats (see Study Area, below).

Although response of wetland fauna to fire was not part of the study design, the wetland was completely burned by the 2013 Rim Fire, which was the largest fire (104,131 ha) recorded in the extensive mountain range of the Sierra Nevada (Lydersen et al. 2014). The fire occurred during late summer, after the first season of sampling. Such late-season fires have the potential to cause additional mortality, because some species are already in less motile and thus more vulnerable states, such as eggs, pupae, or other overwintering stages (Swengel 2001). We sampled sites immediately before the fire and during the growing season subsequent to the fire (nine months post-fire), but there was no unburned habitat in the wetland, or nearby, that could be used as a post-fire reference (see also Bess et al. 2002). The mid-study occurrence of the Rim Fire has the potential to provide some coarse insights into response of wetland fauna to fire (see also Panzer 2002), but conclusions regarding apparent effects must be limited, particularly given the nuanced responses to fire that have been observed for arthropods (Panzer and Schwarz 2000; Andersen et al. 2014; Moranz et al. 2014; Jackson and Sullivan 2015; Rose and Goebel 2015).

We addressed several central questions in this study. 1) How does assemblage structure vary as a function of wetland context? We compared a) core wetland versus edge wetland near b) river or c) pond. Based on previous work at stream-upland interfaces (Henschel et al. 2001; Murikami and Nakano 2002; Kato et al. 2004; Baxter et al. 2005), we anticipated that emerging aquatic insects would drive higher richness and abundance at river and pond edges, relative to core habitat. Wetlands are, however, productive habitats, and thus such allochthonous subsidy might be proportionally less influential than in uplands. 2) Are there strong seasonal trends for the wetland faunal assemblage, and are there interactions with habitat context? Emerging aquatic insects have been shown to decrease in abundance in near-stream forest through the growing season, whereas terrestrial arthropods can increase during the same period (Kato et al. 2003). Given the dry Mediterranean summers in this montane wetland, with vegetation senescence by July, we hypothesized that abundances of terrestrial, as well as emerging aquatic, insects would decrease, rather than increase, through the growing season. We anticipated that changes in assemblage structure through the growing season would be strongest at wetland-aquatic edges, because of the potential influence of neighboring river and pond habitat and associated fauna (Baxter et al. 2005). Our overall aim was to gain an understanding of several factors that might influence wetland faunal assemblages; we found that all study factors did have strong influences, though not necessarily as anticipated.

Materials and Methods

Study Area and Design

Poopenaut Valley is isolated by the steep granitic walls that line much of the Tuolumne River along the mid-elevation reaches, and no wetlands of the same size (26 ha) are found within 50 river km up- or downstream of the study area. The Valley is rarely visited by people, despite being only 1.75 km by trail from a road in heavily-visited Yosemite National Park, probably because the trail loses 400 m rapidly before reaching the Valley at 1,017 m. Poopenaut Valley has been little-studied until recently (Russo et al. 2012). The area receives 89 cm/y of precipitation, three-quarters of which falls between November and March, primarily as snow (Russo et al. 2012), with an ensuing three-month growing season.

The studied wetland habitat is wet meadow that is seasonally-saturated but generally not inundated. Dominant vegetation in sampled areas included beardless wildrye *Leymus triticoides* (Buckley) Pilger, Mugwort *Artemisia douglasiana* Besser, grass-leaved goldenrod *Euthamia occidentalis* Nutt., inflated sedge *Carex vesicaria* L., and Kentucky bluegrass *Poa pratensis* L. Although found in the other habitats, *Poa* was most common in core habitat, *Carex* was most common near the pond, and tule *Scirpus acutus* (S. Watson) Beetle was found exclusively near the pond. The Valley wetland is bisected by the Tuolumne River, which, at this elevation, is a fourth-order, perennial stream with a 1% gradient that is characterized by riffle-pool habitat. A three-hectare, seasonal pond lies 150m from the north bank of the river and varies in depth and length of inundation. The pond sediment was saturated, but not flooded, during 2013 but was inundated to a depth of ~0.6 m between February and April of 2014. When only saturated, the wetted pond habitat continues to support semi-terrestrial taxa and midge and mosquito larvae not found in wet meadow habitat. The Rim Fire burned the wetland at low to moderate intensity (0-50% basal area; CalFire 2013) during August of 2013. The Valley had burned previously during the 1996 Ackerson Fire.

We sampled three wetland habitats during 2013 and 2014: 1) core wetland habitat that was at least 70 m from the closest upland or aquatic habitat, 2) wetland habitat directly adjoining the river, and 3) wetland habitat directly adjoining the pond. We sampled fauna and associated vegetation structure through the growing season, i.e., starting after snow was completely melted (May) and ending just before high temperatures (mean during sampling hours = 34.3 ^{o}C, maximum > 40 ^{o}C) drove complete senescence of wetland vegetation (late July; see also Fukui et al. 2006). Most major emergences of aquatic insects also occur during these months on the west slope of the Sierra Nevada (Schalla 2015). We thus used a 3 x 3 x 2 design: Habitat (Core, River, Pond) x Month (May, June, July) x Year (2013, 2014). There were four randomly-located samples for each of the Habitat x Month x Year combinations, yielding a total of 72 faunal samples. There were two randomly-selected subsample locations within each sampling location for fauna, and there were two additional randomly-selected vegetation subsamples nested within each of the first pair of subsamples. There were thus two subsampling locations for fauna and four subsampling locations for vegetation at each sampling site. A Scientific Research and Collecting permit was obtained from the US National Park Service for work in Yosemite National Park for each year of the study. No protected species were sampled.

Faunal and Vegetation Methodology

Each sample represented 50 standard sweep net sweeps (New 1998; Henderson and Southwood 2016), evenly divided between each pair of subsampling locations and covering a total of 400 m^2. The sweep net had a mesh size of 0.5 x 0.75 mm and a 30.5 cm aperture. Sweeping was done before vegetation data collection at each sampling location so as to minimize disturbance (see Holmquist et al. 2010; 2011; 2013a for additional faunal sampling details). The same individual collected all faunal samples and vegetation data for consistency. All samples were collected between 0800 and 1800 in full sun and when wind speed was less than 12 km/h; a Kestrel 3000 meter was used to record air and ground temperature and wind speed. All arthropod fauna were identified in the laboratory to species or morphospecies (particularly for immature individuals, Kremen et al. 1993; Oliver and Beattie 1996; Gerlach et al. 2013). Arthropods from all taxa were identified, rather than only those from a single order or other taxonomic group. Analysis across all arthropod groups facilitates detection of responses to habitat characteristics and other drivers that structure ecosystems (Fahrig and Jonsen 1998; Koricheva et al. 2000; Pocock et al. 2012).

We measured percent bare ground, percent green vegetation cover, percent standing brown (senescent) vegetation cover, and percent litter cover using a 10 m point-intercept transect (20 points) centered and randomly-oriented at each subsample location. We measured stem density, canopy height, litter depth, and structural complexity (pole-touch method, Bestelmeyer and Wiens 2001) at two random locations along each of the two transects for each faunal collection. We estimated plant species richness by counting taxa that were contacted anywhere along the full length of the transect.

Analysis

Univariate analyses were primarily 3 x 3 x 2 ANOVAs (Habitat x Month x Year), which were followed by Tukey's multiple comparison tests, both using SYSTAT 12. Vegetation and physical response variables were as outlined above. Faunal response variables included total arthropod abundance, family and species richness, Margalef's index (Magurran and McGill 2011), dominance (percent of total sample abundance represented by the most abundant species in each sample), number and percentage of aquatic and terrestrial arthropods, percentage of herbivores and predators, and individual order, family, and species abundances. Proportional variables were square-root transformed, and all other variables were log-transformed. We adjusted multiple comparisons to per-family error rate with the sequential Bonferroni correction (Holm 1979; Jaccard and Guilamo-Ramos 2002) with MacBonferroni 1.6.

Multivariate analyses included multi-response permutation procedures (MRPP) and nonmetric multidimensional scaling (NMS, McCune and Grace 2002; Peck 2010) using PC-ORD 6, as well as analyses of dispersion using PERMDISP2 (Anderson 2004). Data from all factors and samples were included in the response matrices. There were two explanatory matrices; both included habitat variables and a coding variable for Year, but one matrix included a coding variable for Habitat, and the other included a coding variable for Month. The response matrices of faunal species included only taxa that were collected in at least three sites so as to reduce sparsity (Peck 2010) but not discard excessive information (Poos and Jackson 2012). Response matrices were relativized by maximum abundance for each species. The final response matrix contained 162 species/morphospecies, with a moderate (McCune and Grace 2002) coefficient of variation of 63%. The Sørensen distance measure was used for all analyses.

We assessed dimensionality of data via stress tests and construction of scree plots as part of the NMS analyses. After assessing multiple levels of dimensionality, the best balance of stress level and dimensionality was achieved at three dimensions. We then used three dimensions as an initial configuration for 250 runs with real data. Final stress was moderately high at 18, but was less than expected by chance (p = 0.0040; Monte Carlo test, 249 runs). There were 82 runs for the final solution, and stress stabilized at 51 iterations in stress versus iteration plots. Eight complete additional NMS analyses confirmed consistency of results. The permutational analyses of dispersion were based on 9,999 permutations, used the same datasets and distance measure used for MRPP, and results were derived from deviations from spatial medians and ANOVA tables. We supplemented these analyses with sign tests and rank abundance plots to provide additional perspectives on diversity, richness, and evenness (Magurran and McGill 2011;

Underwood and Fisher 2006; Savage et al. 2011). The datasets generated and/or analyzed during the current study are freely available from the corresponding author upon request.

Results

Main effects differences for the twelve vegetation and physical variables were common, and arthropod habitat quality was generally highest in May (early-season), in Pond and Core, and in 2013 (Fig. 1, Online Resource 1). Ten variables differed by Habitat, eight by Year, and six by Month, although three-quarters of the variables also indicated one or more interactions. Canopy height was lowest in May and highest in Pond habitat during 2014 (Habitat x Year). Structural complexity was halved from 2013 to 2014, and was highest in Pond habitat during July (Habitat x Month). Shoot density was lowest in River habitat, during July, and in 2014 (all main effects). Litter depth was similarly lowest for River and was reduced by a factor of two in 2014 (main effects only). There was essentially no bare ground for Pond and Core, and only ~1% for River, in 2013, but bare ground increased to ~10% for all habitats in 2014 (Fig. 1, Online Resource 1). Green cover was lowest in River, during July, and in 2013 (main effects); a Month x Year interaction was apparent (stronger monthly trends in 2014). Thus both percent bare ground and green cover were higher during 2014, and standing senescent vegetation and litter were reduced during 2014 (Fig. 1, Online Resource 1). Plant species richness was highest at River and did not differ by month or year. Air temperature was lowest in River habitat; temperatures exceeded 30 ^{o}C by July at all sites (Online Resource 1). Soil surface temperature was also lowest at the River sites. Wind speed was higher at River and Core than at Pond sites (Online Resource 1).

Vegetation metrics suggested poorer habitat structure in River, but faunal abundance, richness, diversity, and % aquatic taxa were all higher in this habitat zone (Fig. 2, Online

Resource 2). Faunal assemblage variables also generally had higher values earlier in the summer and in 2013. Richness and Margalef's diversity both followed these trends for main effects, particularly for Habitat (River was two-fold higher), and interactions were absent (Fig. 2, Online Resource 2). Abundance results were similar, but there was also a Month x Year interaction. In accord with the trends for richness and diversity, dominance was low at River. The percent of adult taxa that had aquatic juvenile stages (% aquatic) was low for all months and habitats in 2013; aquatics represented only 0.46 – 2.71% of the fauna at River, but these animals were absent or essentially absent at Pond and Core. In 2014, these values increased slightly for Pond and Core, and % aquatic at River increased to a range of 3.68 to 9.71% (Fig. 2, Online Resource 2). Trends were similar for number of aquatics collected in the wetlands. Abundance of terrestrials was also greatest in River, but numbers were higher in 2013 than in 2014. The percent of the assemblage represented by predators was greatest in late summer, as was the predator:herbivore ratio; % herbivores was conversely highest in early summer (Fig. 2, Online Resource 2). Predator:herbivore ratio was greatest in 2014; this ratio was never greater than one during 2013 at any sites. Month x Year interactions were present for a number of variables, particularly for variables relating to the relative abundance of aquatics and terrestrials and for predators and herbivores. There was only a single, relatively weak, Habitat x Month interaction (species dominance).

The 7,372 individuals collected during the study yielded representatives of seventeen orders, 127 families, and 310 species/morphospecies. Hemiptera was the most abundant order overall (60.1 individuals/50 sweeps, SE= 6.0, Fig. 3, Online Resource 3), followed by Coleoptera ($\overline{x}$ = 10.8, SE= 1.6), Araneae ($\overline{x}$ = 9.6, SE = 0.80), Diptera ($\overline{x}$ = 9.1, SE = 1.1), and Hymenoptera ($\overline{x}$ = 5.9, SE = 0.82). The most abundant species were all hemipterans (Fig. 4, Online Resource 3): the aphid *Sitobion avenae* (Fabricius) (overall $\bar{x}$ = 6.9, SE = 2.0), the mirid plant bug *Europiella artemisiae* (Becker) ($\bar{x}$ = 4.7, SE = 2.2) the delphacid leafhopper *Nothodelphax consimilis* (Van Duzee) ($\bar{x}$ = 4.7, SE = 1.2), and the cicadellid leafhoppers *Hebacephalus discessus* (Van Duzee) ($\bar{x}$ = 6.0, SE = 1.1), *Mesamia* sp. ($\bar{x}$ = 3.9, SE = 1.7), and *Dikraneura carneola* (Stål) ($\bar{x}$ =3.3, SE = 0.7). Overall family richness was highest for Diptera (32), Hymenoptera (26), and Coleoptera (20); species/morphospecies richness was greatest for Diptera and Hemiptera (both 71) and Hymenoptera (65). The most speciose families were cicadellid leafhoppers (25 species/morphospecies), braconid and pteromalid wasps (13 and 12, respectively), and aphids (12).

Abundances of dominant orders reflected many of the patterns observed at the assemblage level, but there was also variability by order (Fig. 3, Online Resource 3). Hemiptera and Coleoptera were most abundant early in the season, near the river, and in 2013. Diptera were most abundant along the river but did not have lower abundances in 2014. Diptera decreased in abundance through the growing season in 2014 but not in 2013 (Fig. 3, Online Resource 3). Hymenoptera (wasps and ants) were most abundant near the river and in 2013, but monthly patterns were absent. Araneae (spiders) did not demonstrate differences as a function of habitat, and temporal differences were the opposite of those more generally observed: numbers were lowest in early season and rose thereafter. Spider abundances were much lower in 2014 than in 2013. Lepidoptera (moths and butterflies) were most abundant near the river, but abundances were low after the fire (Fig. 3, Online Resource 3). Peak lepidopteran abundances occurred in June in 2013, but there were no monthly patterns in 2014. There were no Habitat x Month interactions among the abundant orders.

Dominant species showed strong trends as a function of study factors, particularly Year. (Fig. 4, Online Resource 3). The aphid *Sitobion avenae* had low abundances throughout the study—except in May of 2014, when there was a 40-fold increase in abundance. There was also a two-fold increase in the cicadellid leafhopper *Dikraneura carneola* at this time. Conversely, a number of dominant species demonstrated the common pattern of higher abundances in River habitat, low abundances in 2014, and variable seasonal patterns: the delphacid leafhopper *Nothodelphax consimilis*, the cicadellid leafhopper *Mesamia* sp., and the plant bug *Europiella artemisiae* (Fig. 4, Online Resource 3). Yet another cicadellid, *Hebecephalus discessus*, was also virtually absent in 2014, but lacked clear patterns as a function of habitat or month. There were significant overall trends of higher abundances in River habitat ($p = 0.0015$, sign test across taxa in Online Resource 3) and in 2013 ($p = 0.019$) but not for a given month ($p > 0.063$ for all). Habitat x Month interactions were uncommon.

Rank-abundance relationships and multivariate analyses were consistent with the univariate trends of overall higher diversity near the river, in early season, and in 2013. Rank-abundance slopes were low for River, and high for Pond and July (Fig. 5). Multiple response permutation procedure results as a function of Month and Year were highly significant ($p < 0.000001$; $A > 0.53$), and all multiple comparisons were significant (all $p < 0.0064$). There were similar levels of significance for MRPP on Habitat and Year ($p < 0.000001$, $A > 0.41$; all multiple comparisons $p < 0.035$). Permutational analyses of dispersion were non-significant for the factor combinations in both MRPP analyses, indicating that the differences observed via MRPP were due to differences in assemblage structure rather than being attributable to dispersion. The overall PERMDISP result for Month x Year was $p = 0.61$, and pairwise contrasts ranged from 0.70 to 0.98. The Habitat x Year result was p = 0.54; pairwise comparisons ranged from 0.83 to 0.91.

Nonmetric multidimensional scaling showed lack of overlap between years in ordinal space (Figs. 6 and 7). Months were also somewhat disjunct (Fig. 6), but there was more overlap among habitats (Fig. 7). Cumulative R^2 was 0.66 for both ordinations. Important explanatory variables in the Month-Year ordination included complexity ($R^2 = 0.34$), litter depth (0.22), green cover (0.22), and litter cover (0.21), which were most strongly associated with Axis 2 (Fig. 6). Results were similar for the Habitat-Year ordination, but percent cover by senescent vegetation ($R^2 = 0.20$) also met the threshold for variable-axis correlation for inclusion in the joint plot (Fig. 7). Explanatory variables were again most closely associated with Axis 2 (Fig. 7).

Discussion

We found a high diversity and abundance of fauna in riparian edge habitat, relative to core wetland, as we had hypothesized, but this relationship only held for the river riparian sites. Contrary to expectations, the pond riparian fauna was similar to that of core habitat that was distant from water. Further, the trends observed at River sites were driven by terrestrial fauna, rather than by emerging aquatic insects as had been anticipated on the basis of previous work (Murakami and Nakano 2002; Kato et al. 2004; Baxter et al. 2005; Fukui et al. 2006). It seems unlikely that the dearth of aquatic taxa near the river was the result of low lotic abundance. Limited sampling of the river near the wetland, coincident with each wetland sample (Holmquist and Schmidt unpublished data; Online Resource 4) yielded a faunal assemblage that was analogous to that of other montane river habitat (Holmquist and Waddle 2013) and should have provided a source pool of emerging lotic fauna.

If there were few aquatic fauna sampled in river riparian habitat, and habitat structure was relatively poor near the river, why were wetland fauna so diverse and abundant at the River sites? There are several non-mutually exclusive possibilities. a) Summer microclimate may have been more favorable for arthropods near the river. River sites had lower air and ground temperatures than were recorded from the other sites. Wind speeds were higher at River than Pond, which may have also contributed to the cooling effect. Humidity was not recorded but may have been higher near the river as well, particularly after the wetlands dried later in the season. b) Vegetation structure can have important influences on wetland arthropods, particularly in mountain environments with short growing seasons (Holmquist et al. 2013b; 2014). Structure was unlikely to have been responsible for the rich faunal assemblage of the river riparian wetland, given that structure metrics indicated poorer habitat quality near the river than in Core and Pond habitat. It is possible that unknown factors associated with *Scirpus acutus* and *Carex* near the pond and *Poa* in core habitat were unfavorable for arthropods, but taller plants, such as *Carex vesicaria* and *Scirpus acutus*, are known to provide good habitat for wetland arthropods (Cunha et al. 2012; Holmquist et al. 2011; 2013b). The River habitat did have higher plant species richness, which should have a positive influence on fauna (Schaffers et al. 2008), though plant species richness can be less important than vegetation structure in driving wetland arthropod richness (Cunha et al. 2012; Holmquist et al. 2013b). c) Many terrestrial insects undertake long, active flights or are carried passively by winds, and rivers are flyways (Forman 1995; Puth and Wilson 2001). Many of the taxa found in the study wetland are strong fliers or are small enough to be transported passively by wind. There may be a settlement shadow (Gaines and Roughgarden 1985; Lewin 1986) that increases diversity and abundance near the river. There is little wetland habitat along the montane portion of the river, which is largely bordered by steep canyon walls, and insects flying along the river corridor may settle in the first portion of acceptable habitat that is encountered after a long flight, i.e., river riparian habitat. d) Many of the terrestrial taxa may be “multi-habitat” species (Forman 1995) that, though lacking an aquatic life stage, make use of the river bank for puddling (drinking), cooling, or egg laying in sand. e) We may have largely missed the emergences of aquatic insects in either time or space, if the emergences of the variety of aquatic taxa had been devoured or otherwise perished before these animals could be sampled or if the emerging individuals largely avoid wetland vegetation. Some combination of these phenomena, or others, apparently yields substantial edge effects resulting in high diversity and abundance (Polis and Hurd 1996; Fukui et al. 2006) at the river-wetland ecotone. In contrast, the pond riparian fauna may have been as depauperate as core wetland because of distance from the river flyway and because of low water levels during the study.

We had hypothesized that both terrestrial fauna and aquatic adults would decrease in abundance through the growing season in this Mediterranean climate, and this pattern was indeed evident. The congruent directionality for terrestrials and aquatics contrasted with previously observed opposing trends through the growing season in other locations: decreasing aquatic abundance but increasing terrestrial abundance through the growing season (Kato et al. 2003; Nakano and Murakami 2001). Summer in the montane Sierra Nevada is a stressful period after early season, in contrast with wetter environments. In these Sierrran wetlands, soils dry and plant productivity slows or ceases before temperatures cool, (Online Resource 1, % senescent vegetation; Holmquist et al. 2013a), and faunal diversity and abundance appear to also decline well before the end of summer. Terrestrial arthropods are generally in diapause-- variously as eggs, larvae, nymphs, pupae, or adults— during times of the year in which photoperiod, temperature, and food resources are not optimal (Wolda 1988; Cardoso et al. 2007). In the Sierra Nevada, the optimal period between the wet winter and dry summer is short indeed. These seasonal faunal declines at our montane study sites were more precipitous than previously observed in subalpine wetlands (Holmquist et al. 2013a), likely because of less snow accumulation, less soil saturation, and warmer summer temperatures at these lower elevations. Neither the terrestrial or aquatic seasonal decreases are likely to be supply-side in nature, as a function of decreasing aquatic subsidy; lotic densities tend to be highest in mid- to late season (Online Resource 4; Holmquist et al. 2015). There were few Habitat x Month interactions, indicating that differences among habitats were, contrary to our hypothesis, consistent through the growing season.

Predators, particularly spiders, were an exception to the trend of decreasing arthropod abundances through the growing season. The high early-season abundances of herbivores, particularly leafhoppers and beetles, may have fueled spider abundances that remained high after seasonal reductions in herbivore densities (Henschel et al. 2001; but see Denlinger 1980), although seasonal drying and senescence are likely to have caused at least as much of the observed herbivore decrease as predation (Holmquist et al. 2013a).

Interannual effects for fauna were common and strong and indicated an overall negative trend from 2013 to 2014. We cannot unequivocally claim that these trends were caused by fire, due to lack of available reference habitat (see also Rose and Goebel 2015), but trends for both vegetation and fauna were consistent with frequently-reported fire effects. Fire in grass and sedge-dominated habitats burns away litter and standing senescent vegetation, increases the proportion of bare ground, and increases green cover within a year (Kato et al. 2003; Vogel et al. 2010; Little et al. 2013, Masunga et al. 2013; see also Hosoishi et al. 2014). We observed identical directionality for these metrics at our sites following the Rim Fire. Faunal assemblages can be strongly influenced by indirect fire effects, via these shifts in vegetation structure, and by direct effects (Vogel et al. 2010; Little et al. 2013), though responses can vary among environments and taxa (Warren et al. 1987; Siemann et al. 1997; Swengel 2001; Panzer 2002; Hanula and Wade 2003; Doamba et al. 2014). Affected fauna may be killed directly by wildfire (Bock and Bock 1991; Swengel 2001) or may emigrate during or after the fire (Swengel 2001; Doamba et al. 2014). Direct mortality is most likely for species that are in immobile stages just prior to the coming fall and winter (Swengel 2001; Malmström et al. 2009). Leafhoppers and Lepidoptera are univoltine, and eggs and dormant juveniles are likely to be sequestered in litter in late season (Panzer and Schwartz 2000). These groups may be particularly susceptible to fire and other disturbances (Armitage et al. 2013), and leafhoppers and Lepidoptera had much lower abundances on our sites in 2014 than in 2013. There were also major 2014 decreases in Coleoptera, Hymenoptera, and Araneae, as well as decreases in overall abundance, species richness, and diversity. Similar trends were common at the species level, but the aphid *Sitobion avenae* and the leafhopper *Dikraneura carneola* were exceptions. Both taxa can produce outbreaks under certain conditions, and may have been able to respond rapidly to the additional food resources present during greenup in 2014. In contrast, fire-sensitive taxa may be slow to recover (Vogel et al. 2010), particularly if source habitat is limited and/or distant (Anderson et al. 1989; Swengel 2001; Panzer 2002). There were no unburned portions of the study wetland, and source wetlands were distant and at higher elevation; this level of isolation may have contributed to the low diversity and abundance present in the study wetlands in 2014. The decreases that we observed in 2014 may or may not have been due to fire effects, but were unlikely to have been a proximate result of reduced aquatic subsidy, though fire and stream productivity can demonstrate complex interactions (Malison and Baxter 2010; Jackson et al. 2012; Jackson and Sullivan 2018). Abundance and richness of emergent lotic fauna were nominally greater in 2014 than in 2013, and pond inundation occurred in 2014 and likely increased the supply of emerging lentic fauna. Emerging aquatics nonetheless represented a small proportion of the wetland fauna in either year.

Conclusions

Wetland arthropods were strongly influenced by habitat context and seasonal and interannual factors, but emerging aquatic insects had little proximate influence on these patterns, which was an unexpected result, and powerful aquatic subsidies to riparian habitats should not be assumed to be a universal phenomenon. Faunal diversity and abundance were markedly reduced through the summer, likely due to drying of wetland habitat. Differences among habitats were consistent through the growing season and did not shift as a function of changes in aquatic subsidy or increasing wetland senescence. Fire probably had a strong influence on faunal assemblages and vegetation, though we cannot rule out stochastic change between 2013 and 2014.

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Figure Captions

Fig 1

Vegetation means (SE) as a function of Habitat (H), Month (M), and Year (Y). Letters indicate ANOVA contrasts for main effects and interactions that were significant at $p < 0.01$; see Online Resource 1 for additional parameters and detailed test results

Fig 2

Faunal assemblage means (SE) as a function of Habitat (H), Month (M), and Year (Y). All metrics were based on 50-sweep samples. Capital letters indicate ANOVA contrasts for main effects and interactions that were significant at $p<0.01$, and lower case letters indicate significance at $p<0.05$; see Online Resource 2 for additional parameters and detailed test results

Fig 3

Mean (SE) abundances of most abundant faunal orders as a function of Habitat (H), Month (M), and Year (Y). All metrics were based on 50-sweep samples. Note differing y-axes. Capital letters indicate ANOVA contrasts for main effects and interactions that were significant at $p<0.01$, and lower case letters indicate significance at $p<0.05$; see Online Resource 3 for additional orders and detailed test results

Fig 4

Mean (SE) abundances of abundant species as a function of Habitat (H), Month (M), and Year (Y). All metrics were based on 50-sweep samples. Note differing y-axes. Capital letters indicate ANOVA contrasts for main effects and interactions that were significant at $p<0.01$, and lower case letters indicate significance at $p<0.05$; see Online Resource 3 for additional species and detailed test results

Fig 5

Rank-abundance plots, from total study abundances, for Habitat and Year (top), and Month and Year (bottom). Thick and thin lines reference 2013 and 2014, respectively

Fig 6

Ordination of faunal assemblages by Month and Year across samples using nonmetric multidimensional scaling. Distance between site icons increases with dissimilarity among samples; convex hulls surround all samples of a given Month-Year combination. White and black symbols indicate 2013 and 2014 samples, respectively. Squares indicate May, triangles June, and diamonds July. Plots were scaled by proportion of maximum; orthogonality was 100% for each axis pair. Axis labels note R^2 values estimating post-hoc percent of variation within the distance matrix that is explained by each axis. Cumulative R^2 was 0.66. Explanatory variables in joint plot: Co = Complexity, LC = Litter Cover, GC = Green Cover, LD = Litter Depth. Minimum explanatory variable-axis correlation for inclusion in the joint plot was $R^2 = 0.20$

Fig 7

Ordination of faunal assemblages by Habitat and Year across samples using nonmetric multidimensional scaling. Distance between site icons increases with dissimilarity among samples; convex hulls surround all samples of a given Habitat-Year combination. White and black symbols indicate 2013 and 2014 samples, respectively. Squares indicate Pond, triangles

River, and diamonds Core. Plots were scaled by proportion of maximum; orthogonality was 100% for each axis pair. Axis labels note R^2 values estimating post-hoc percent of variation within the distance matrix that is explained by each axis. Cumulative R^2 was 0.66. Explanatory variables in joint plot: Co = Complexity, LC = Litter Cover, GC = Green Cover, BC = Brown (standing senescent) Cover, LD = Litter Depth. Minimum explanatory variable-axis correlation for inclusion in the joint plot was $R^2 = 0.20$

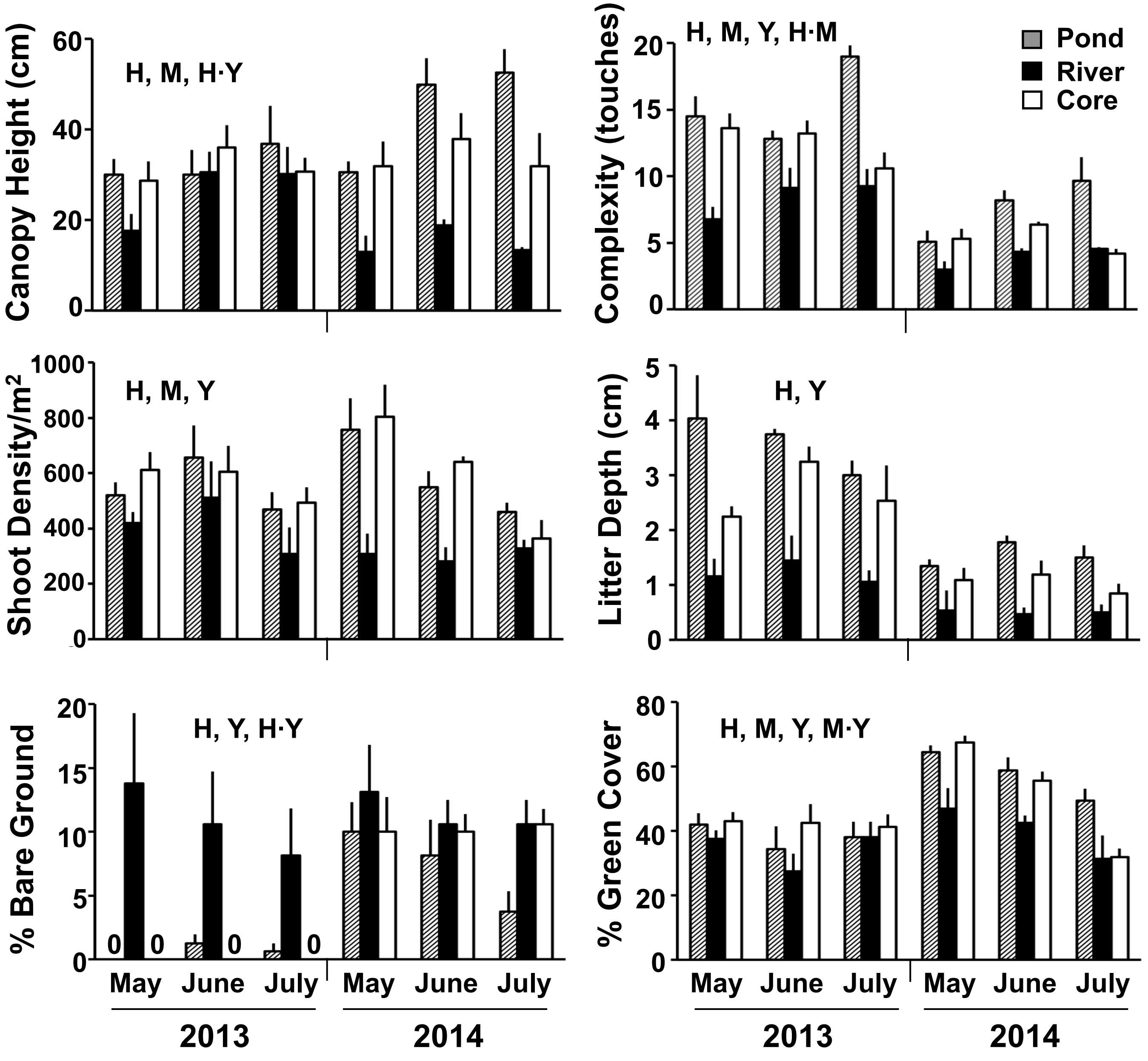
Online Resource Captions

Online Resource 1. Vegetation and physical parameters. Means (standard errors) for vegetation and physical parameters and ANOVA results for main effects and two-way interactions. (pdf)

Online Resource 2. **Faunal assemblage parameters.** Means (standard errors) for faunal assemblage parameters (all based upon 50 sweeps) and ANOVA results for main effects and two-way interactions. (pdf)

Online Resource 3. **Faunal orders and most abundant families and species**. Mean number of individuals (standard errors) for faunal orders and ten most abundant families and species (all based upon 50 sweeps) and ANOVA results for main effects and two-way interactions. (pdf)

Online Resource 4. **Lotic fauna near wetland.** Raw data, means, and standard errors for Tuolumne River lotic fauna near wetland sites. Results are from 1 m^2 kick net samples from cobble habitat. (xlsx)



Canopy Height (cm)
0
20
40
60
H, M, H·Y
Complexity (touches)
0
5
10
15
20
H, M, Y, H·M
Pond
River
Core
Shoot Density/m^2
0
200
400
600
800
1000
H, M, Y
Litter Depth (cm)
0
1
2
3
4
5
H, Y
% Bare Ground
0
5
10
15
20
H, Y, H·Y
0
0
0
0
% Green Cover
0
20
40
60
80
H, M, Y, M·Y
May
June
July
May
June
July
2013
2014

Fig. 1

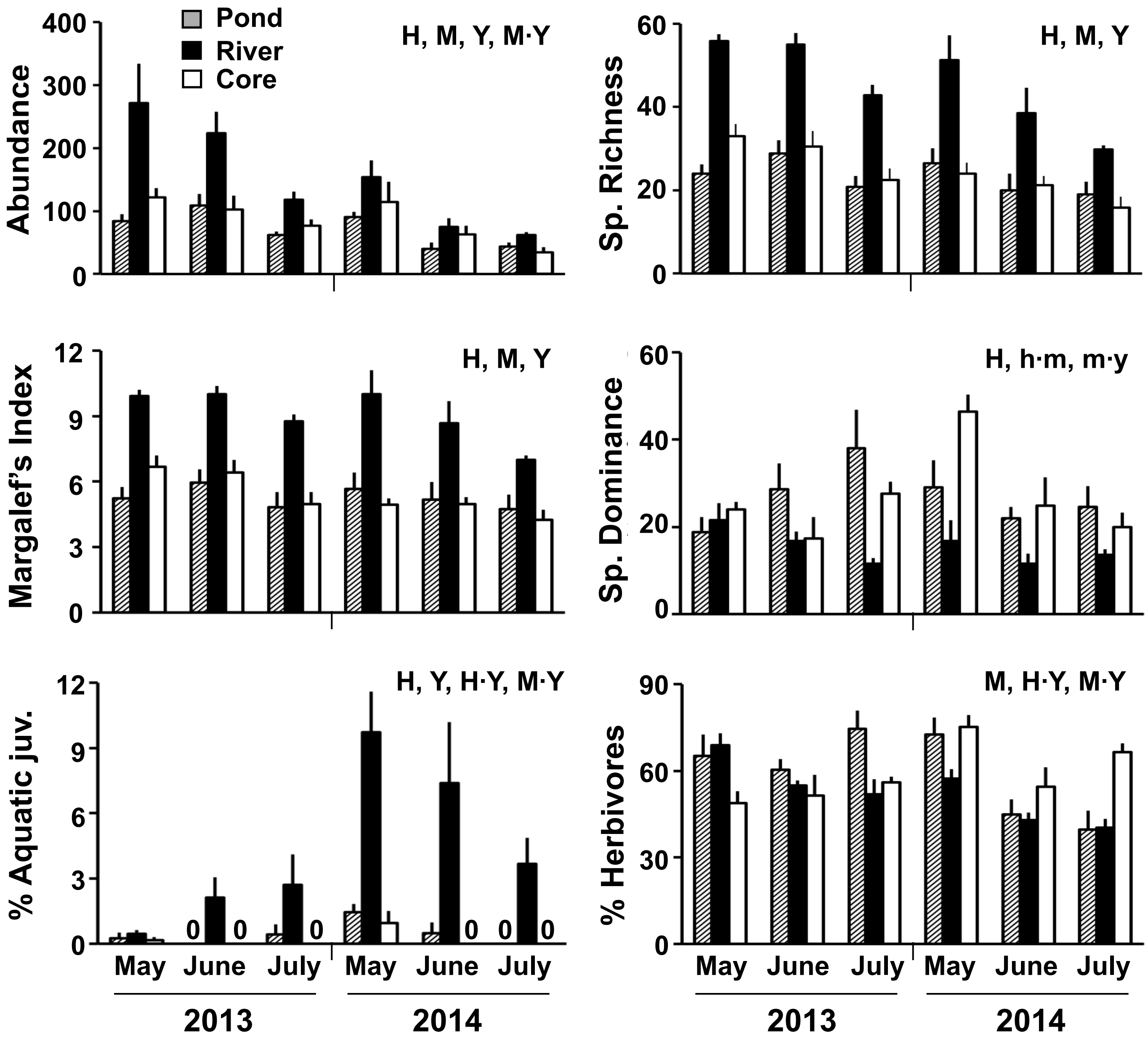

Pond
River
Core
Abundance
400
300
200
100
0
H, M, Y, M·Y
Sp. Richness
60
40
20
0
H, M, Y
Margalef's Index
12
9
6
3
0
H, M, Y
Sp. Dominance
60
40
20
0
H, h·m, m·y
% Aquatic juv.
12
9
6
3
0
H, Y, H·Y, M·Y
0
0
0
0
0
0
% Herbivores
90
60
30
0
M, H·Y, M·Y
May
June
July
May
June
July
2013
2014
May
June
July
May
June
July
2013
2014

Fig. 2

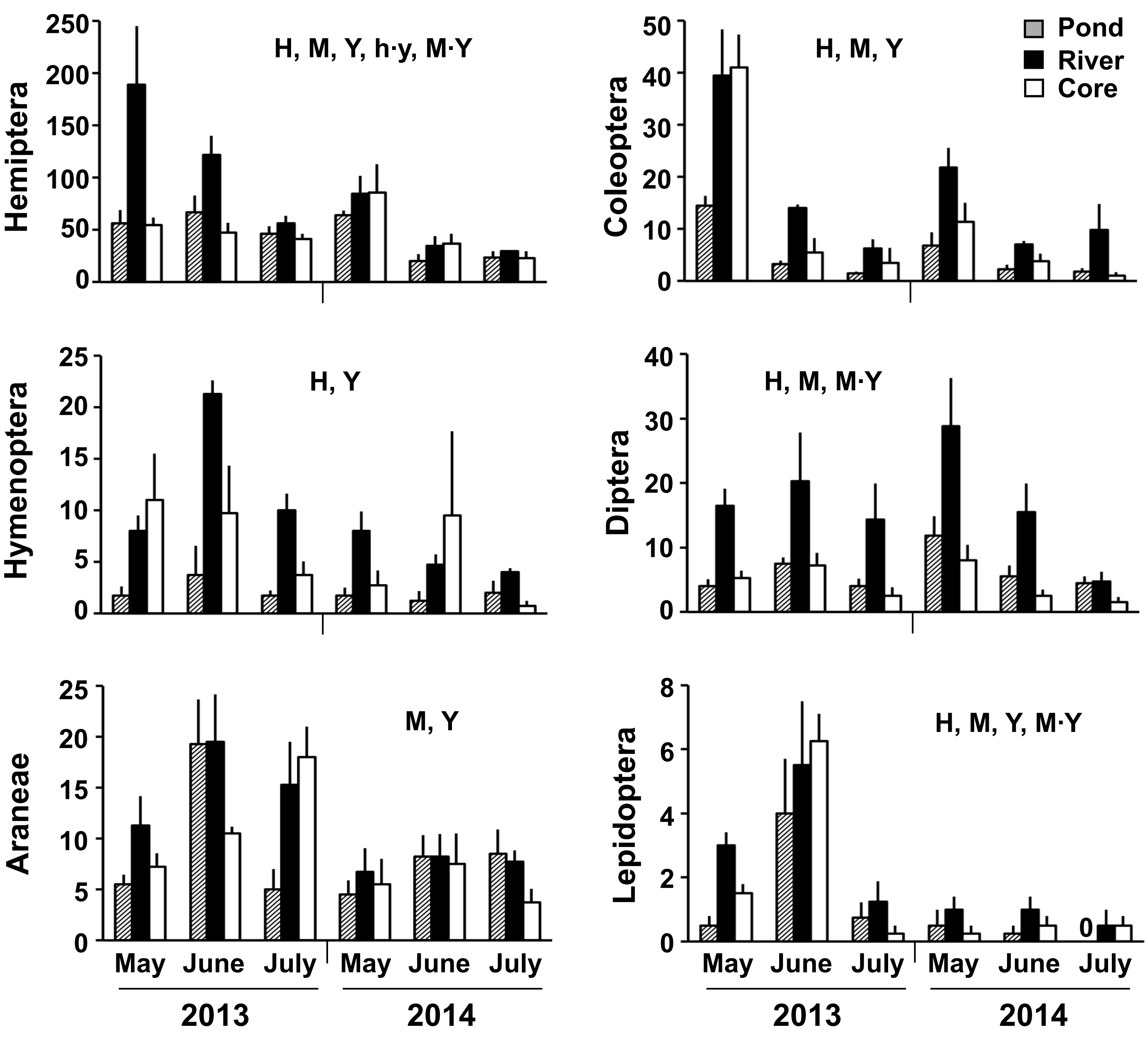
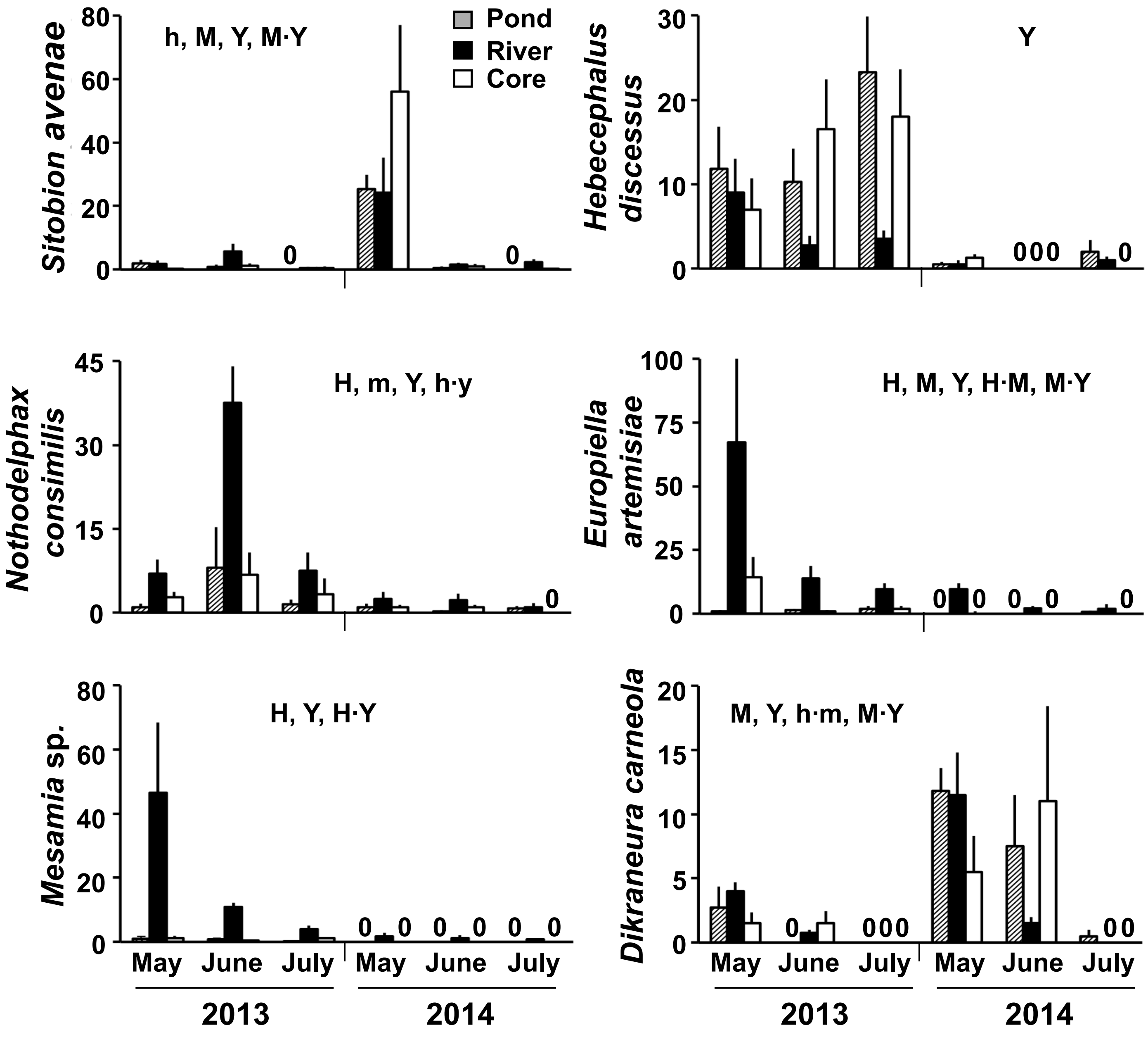
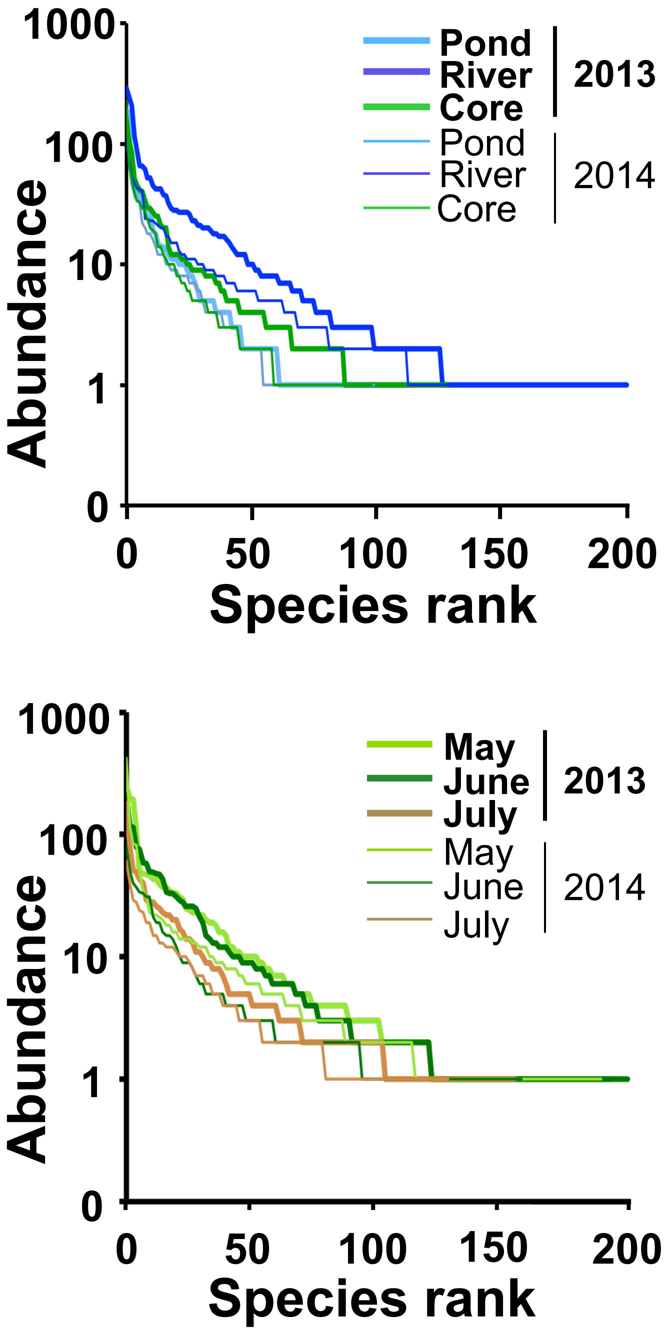

Hemiptera
H, M, Y, h·y, M·Y
0
50
100
150
200
250
Coleoptera
H, M, Y
0
10
20
30
40
50
Pond
River
Core
Hymenoptera
H, Y
0
5
10
15
20
25
Diptera
H, M, M·Y
0
10
20
30
40
Araneae
M, Y
0
5
10
15
20
25
Lepidoptera
H, M, Y, M·Y
0
2
4
6
8
0
May
June
July
May
June
July
2013
2014
May
June
July
May
June
July
2013
2014

Fig. 3



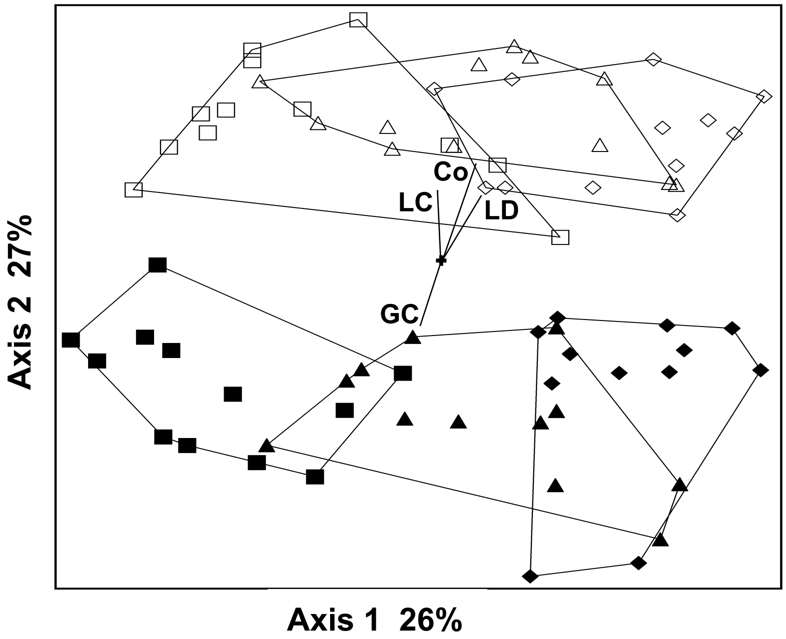
Sitobion avenae
h, M, Y, M·Y
Pond
River
Core
Hebecephalus discessus
Y
Nothodelphax consimilis
H, m, Y, h·y
Europiella artemisiae
H, M, Y, H·M, M·Y
Mesamia sp.
H, Y, H·Y
Dikraneura carneola
M, Y, h·m, M·Y
0
80
60
40
20
30
10
45
15
100
75
50
25
5
May
June
July
2013
2014

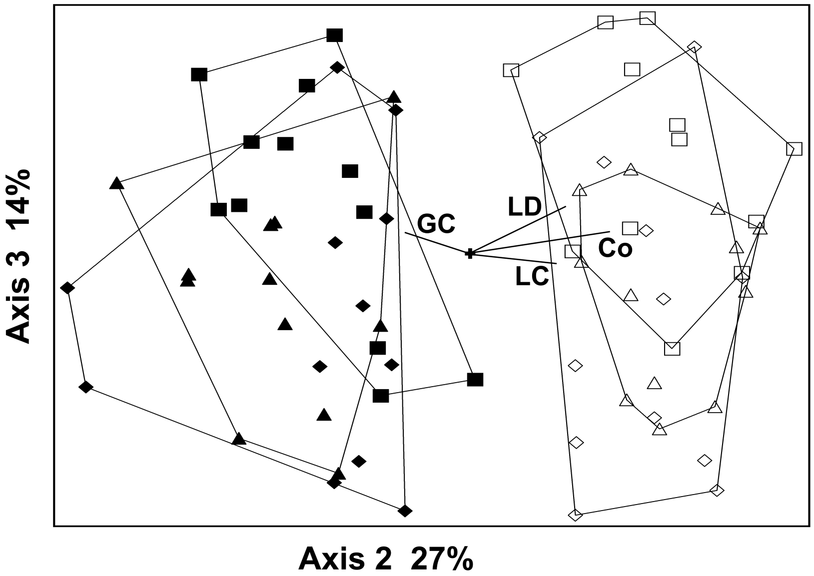
Fig. 4



1000
100
10
1
0
Abundance
0
50
100
150
200
Species rank
Pond
River
Core
2013
Pond
River
Core
2014
1000
100
10
1
0
Abundance
0
50
100
150
200
Species rank
May
June
July
2013
May
June
July
2014

Fig. 5


Axis 2 27%
Axis 1 26%
Co
LC
LD
GC


Axis 3 14%
Axis 2 27%
GC
LD
Co
LC

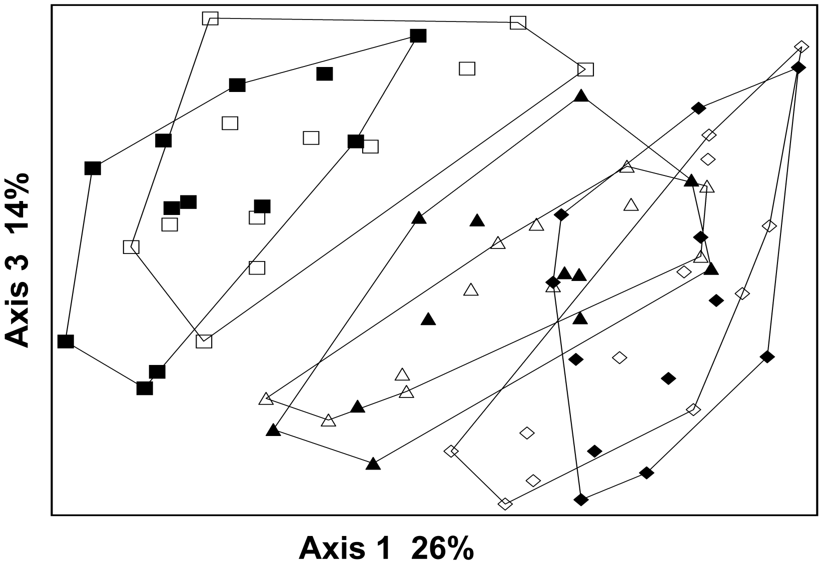

Axis 3 14%
Axis 1 26%

Fig. 6

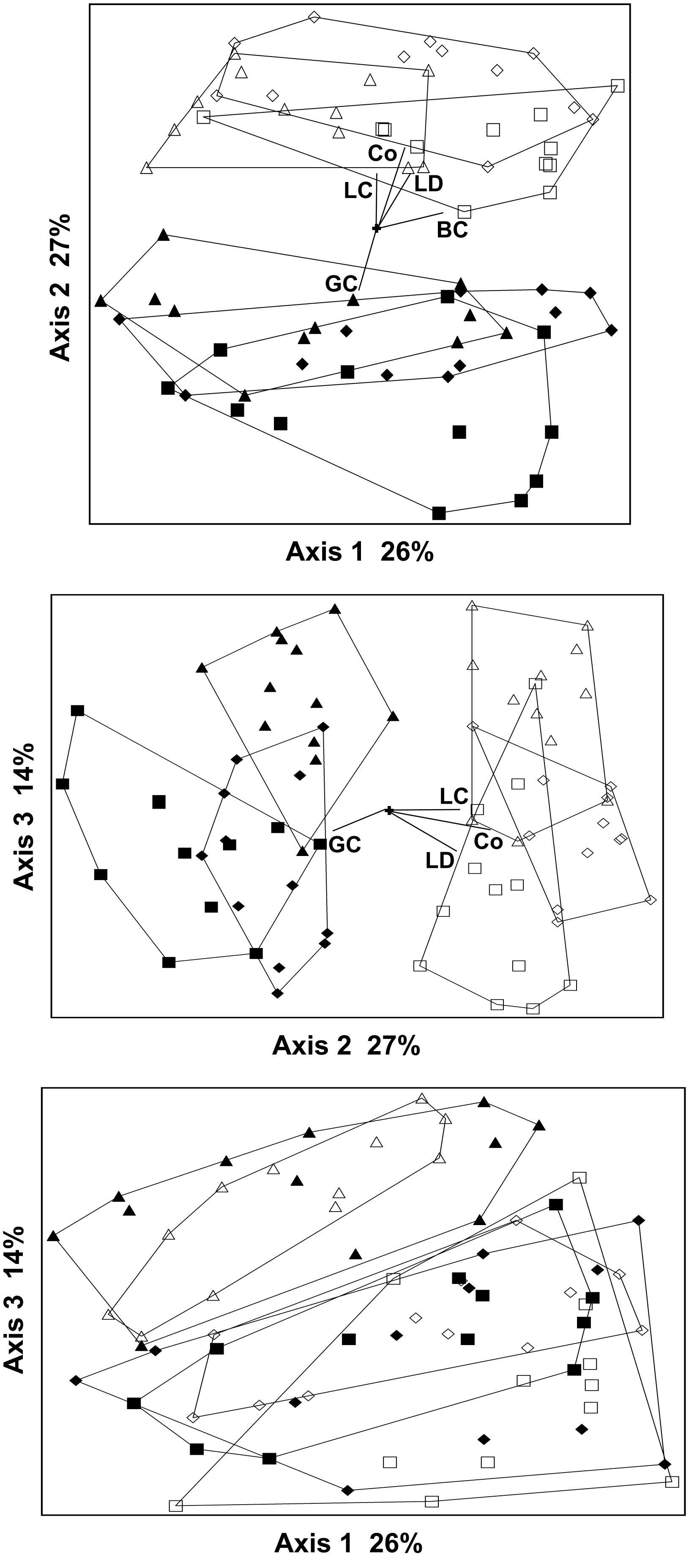

Co
LC
LD
BC
GC
Axis 2 27%
Axis 1 26%
LC
GC
Co
LD
Axis 3 14%
Axis 2 27%
Axis 3 14%
Axis 1 26%

Fig. 7

Supplementary material: Arthropod Assemblages in a Montane Wetland Complex: Influences of Adjoining Lotic and Lentic Habitat and Temporal Variability, *Wetlands*, Jeffrey G Holmquist and Jutta Schmidt-Gengenbach, UCLA, jholmquist@ucla.edu

Online Resource 1 Vegetation and physical parameters. Means (standard errors) and ANOVA results for main effects and two-way interactions

		2013			2014			ANOVA results					
		May	June	July	May	June	July	H[a]	M[b]	Y[c]	HxM	HxY	MxY
Canopy ht. (cm)	Pond	30.0 (3.5)	30.0 (5.5)	36.8 (8.4)	30.5 (2.4)	49.9 (5.9)	52.6 (5.2)	** P[d]C[e]>R[f]	** 6[g]7[h]>5[i]			**	
	River	17.6 (3.8)	30.6 (4.5)	30.2 (6.0)	13.0 (3.5)	18.8 (1.3)	13.3 (0.75)						
	Core	28.7 (4.3)	36.0 (5.0)	30.7 (3.0)	31.9 (5.5)	37.9 (5.7)	31.9 (7.3)						
Complexity (touches)	Pond	14.5 (1.5)	12.8 (0.62)	19.0 (0.84)	5.06 (0.84)	8.19 (0.74)	9.63 (1.8)	** P>C>R	** 67>5	** 13[j]>14[k]	**		
	River	6.75 (0.94)	9.13 (1.5)	9.25 (1.3)	3.00 (0.60)	4.31 (0.28)	4.56 (0.11)						
	Core	13.6 (1.1)	13.2 (1.0)	10.6 (1.2)	5.31 (0.74)	6.38 (0.22)	4.19 (0.36)						
Shoot dens. per m^2	Pond	520 (46)	656 (117)	468 (64)	756 (115)	548 (58)	460 (32)	** PC>R	** 56>7	** 13>14			
	River	420 (40)	512 (130)	308 (96)	308 (73)	280 (53)	328 (31)						
	Core	612 (64)	604 (95)	492 (56)	804 (115)	640 (20)	364 (66)						
Litter depth (cm)	Pond	4.03 (0.79)	3.75 (0.09)	3.00 (0.27)	1.34 (0.13)	1.78 (0.12)	1.50 (0.22)	** P>C>R		** 13>14			
	River	1.16 (0.32)	1.44 (0.46)	1.06 (0.21)	0.53 (0.37)	0.47 (0.12)	0.50 (0.15)						
	Core	2.25 (0.18)	3.25 (0.27)	2.53 (0.65)	1.09 (0.22)	1.19 (0.26)	0.84 (0.18)						
% Bare	Pond	0 (0)	1.25 (0.72)	0.63 (0.63)	10.0 (2.3)	8.13 (2.8)	3.75 (1.6)	** R>PC		** 14>13		**	
	River	13.8 (5.5)	10.6 (4.1)	8.13 (3.7)	13.1 (3.7)	10.6 (1.9)	10.6 (1.9)						
	Core	0 (0)	0 (0)	0 (0)	10.0 (2.7)	10.0 (1.4)	10.6 (1.2)						

% Green	Pond	41.9 (3.6)	34.4 (7.0)	38.1 (4.8)	64.4 (2.1)	58.8 (4.1)	49.4 (3.7)	** PC>R	** 5>67	** 14>13			**
	River	37.5 (2.7)	27.5 (5.4)	38.1 (4.8)	46.9 (6.4)	42.5 (2.3)	31.3 (7.3)						
	Core	43.1 (2.8)	42.5 (5.8)	41.3 (3.9)	67.5 (2.0)	55.6 (2.8)	31.9 (2.6)						
% Brown	Pond	21.9 (2.6)	31.3 (6.5)	33.1 (3.6)	9.38 (1.6)	21.9 (4.1)	37.5 (4.4)		** 7>6>5	** 13>14			**
	River	26.9 (2.6)	40.0 (2.7)	32.5 (2.3)	16.9 (2.8)	16.9 (5.1)	44.4 (10)						
	Core	32.5 (12.5)	33.1 (3.7)	31.9 (4.5)	10.0 (1.8)	21.9 (3.1)	44.4 (4.0)						
% Litter	Pond	36.3 (5.1)	32.5 (4.0)	28.1 (1.2)	16.3 (1.6)	11.3 (1.6)	9.38 (2.6)			** 13>14		**	
	River	21.9 (2.8)	21.9 (1.9)	21.3 (3.0)	24.4 (6.8)	30.0 (6.7)	13.8 (2.4)						
	Core	24.4 (13)	24.4 (4.3)	26.9 (0.63)	12.5 (2.7)	13.1 (1.2)	13.1 (2.6)						
Species	Pond	2.88 (0.38)	2.63 (0.24)	3.00 (0.20)	2.63 (0.24)	2.63 (0.32)	2.50 (0.35)	** R>PC					
richness	River	4.13 (0.13)	3.63 (0.24)	3.50 (0.35)	3.63 (0.24)	3.63 (0.24)	3.75 (0.43)						
	Core	2.63 (0.38)	2.63 (0.43)	3.00 (0.54)	2.75 (0.88)	3.75 (1.1)	2.88 (0.32)						
Air temp	Pond	28.3 (0.95)	28.3 (0.72)	32.7 (0.52)	26.9 (0.29)	29.7 (0.98)	36.9 (1.9)	** PC>R	** 7>6>5			*	**
(°C)	River	25.4 (1.6)	26.3 (0.64)	30.7 (0.58)	25.1 (0.78)	27.4 (0.67)	34.5 (0.29)						
	Core	29.4 (0.14)	29.5 (0.52)	34.8 (0.61)	27.1 (0.55)	27.9 (1.0)	36.3 (0.52)						
Soil surface	Pond	35.5 (0.79)	35.1 (2.4)	36.3 (1.6)				** PC>R					
temp (°C)[1]	River	30.4 (2.5)	27.8 (3.1)	30.6 (2.2)									
	Core	32.5 (0.67)	33.7 (2.2)	39.8 (0.65)									

Wind speed	Pond	1.45 (0.20)	1.50 (0.06)	2.30 (0.0)	2.70 (0.06)	4.45 (1.1)	4.35 (0.26)	** RC>P	** 14>13	*
(km/hr)	River	2.55 (0.32)	2.05 (0.14)	2.60 (0.12)	7.80 (2.1)	7.45 (0.99)	7.70 (2.4)			
	Core	3.10 (0.40)	0.70 (0.40)	2.80 (0.81)	6.25 (0.78)	6.65 (1.3)	5.75 (1.9)			

Inequalities below asterisks reference multiple comparisons that were significant via Tukey's tests at $p<0.05$ following the sequential Bonferroni correction of multiple comparison to family-wise error rate. Levels on either side of the inequality differed. Multiple comparison tests were not necessary for Year, but an inequality is provided to summarize test results.

[a] Habitat.
[b] Month.
[c] Year.
[d] Pond.
[e] Core.
[f] River.
[g] June.
[h] July.
[i] May.
[j] 2013.
[k] 2014.
[l] Only 2013 data for soil surface temperature.
*$p<0.05$ for main effect or interaction.
**$p<0.01$ for main effect or interaction.

Supplementary material: Arthropod Assemblages in a Montane Wetland Complex: Influences of Adjoining Lotic and Lentic Habitat and Temporal Variability, *Wetlands*, Jeffrey G Holmquist and Jutta Schmidt-Gengenbach, UCLA, jholmquist@ucla.edu

Online Resource 2 Faunal assemblage parameters. Means (standard errors) for faunal assemblage parameters (all based upon 50 sweeps) and ANOVA results for main effects and two-way interactions.

		2013			2014			ANOVA results					
		May	June	July	May	June	July	H^a	M^b	Y^c	HxM	HxY	MxY
Total individuals	Pond	83.8 (11)	109 (18)	61.8 (6.0)	90.3 (8.2)	40.0 (9.8)	44.0 (6.2)	** $R^d>P^eC^f$	** $5^g>6^h>7^i$	** $13^j>14^k$			**
	River	271 (63)	224 (34)	118 (13)	154 (26)	74.5 (14)	61.5 (5.4)						
	Core	122 (14)	102 (22)	76.8 (10)	114 (32)	63.3 (13)	34.0 (8.5)						
Species richness	Pond	24.0 (2.2)	28.8 (3.3)	20.8 (2.7)	26.5 (3.6)	20.0 (4.0)	19.0 (3.0)	** R>PC	** 56>7	** 13>14			
	River	55.8 (1.7)	55.0 (2.8)	42.8 (2.5)	51.3 (6.0)	38.5 (6.2)	29.8 (1.0)						
	Core	33.0 (2.9)	30.5 (3.7)	22.5 (2.8)	24.0 (2.7)	21.3 (2.2)	15.8 (2.7)						
Family richness	Pond	16.0 (1.8)	21.0 (2.9)	15.0 (1.5)	16.8 (3.4)	14.0 (2.8)	13.8 (2.2)	** R>PC	** 56>7	** 13>14			
	River	34.0 (1.6)	33.3 (2.1)	29.0 (1.6)	30.0 (2.9)	22.5 (2.9)	19.8 (1.7)						
	Core	21.5 (2.9)	21.0 (3.1)	14.0 (2.3)	14.3 (1.5)	14.5 (0.96)	11.0 (2.0)						
% species dominance	Pond	18.8 (3.4)	28.6 (6.0)	38.0 (8.8)	29.1 (6.2)	22.0 (2.5)	24.6 (4.7)	** PC>R			*		*
	River	21.5 (4.0)	16.8 (2.1)	11.5 (1.4)	16.7 (4.8)	11.5 (2.3)	13.6 (1.2)						
	Core	24.0 (1.7)	17.4 (4.8)	27.6 (2.8)	46.4 (3.9)	24.9 (6.5)	19.9 (3.3)						
Margalef's sp. richness	Pond	5.24 (0.52)	5.95 (0.60)	4.83 (0.70)	5.66 (0.77)	5.16 (0.81)	4.74 (0.67)	** R>PC	**	** 13>14			
	River	9.92 (0.28)	10.0 (0.39)	8.77 (0.32)	10.0 (1.1)	8.68 (1.0)	7.00 (0.20)						
	Core	6.67 (0.54)	6.42 (0.58)	4.96 (0.56)	4.93 (0.30)	4.96 (0.32)	4.24 (0.48)						

% Aquatic	Pond	0.26 (0.26)	0 (0)	0.44 (0.44)	1.45 (0.38)	0.49 (0.49)	0 (0)	** R>PC		** 14>13	**	**
	River	0.46 (0.16)	2.12 (0.94)	2.71 (1.4)	9.71 (1.9)	7.38 (2.8)	3.68 (1.2)					
	Core	0.16 (0.16)	0 (0)	0 (0)	0.96 (0.55)	0 (0)	0 (0)					
Number aquatic	Pond	0.25 (0.25)	0 (0)	0.25 (0.25)	1.25 (0.25)	0.25 (0.25)	0 (0)	** R>PC	** 5>6	** 14>13	**	**
	River	1.00 (0.41)	4.50 (1.8)	3.00 (1.5)	15.5 (5.3)	5.75 (2.3)	2.25 (0.75)					
	Core	0.25 (0.25)	0 (0)	0 (0)	1.50 (0.96)	0 (0)	0 (0)					
Number terrestrial	Pond	83.5 (11)	109 (18)	61.5 (6.1)	89.0 (8.3)	39.8 (9.8)	44.0 (6.2)	** R>PC	**	** 13>14		*
	River	270 (63)	220 (34)	115 (14)	139 (22)	68.8 (13)	59.3 (5.3)					
	Core	122 (14)	102 (22)	76.8 (10)	113 (31)	63.3 (13)	34.0 (8.5)					
% Predators	Pond	28.8 (5.4)	29.1 (4.4)	19.1 (7.3)	14.0 (3.3)	40.8 (6.8)	45.4 (5.4)		** 7>5		*	**
	River	18.9 (3.2)	21.5 (2.9)	20.4 (2.0)	18.5 (2.8)	27.0 (3.5)	41.6 (3.3)					
	Core	39.0 (4.3)	25.0 (2.9)	31.5 (2.8)	15.8 (3.4)	31.5 (12)	29.4 (3.5)					
% Herbivores	Pond	65.2 (7.3)	60.4 (3.7)	74.5 (6.3)	72.6 (5.9)	44.8 (5.4)	39.7 (6.4)		** 5>67		**	**
	River	68.9 (4.1)	55.0 (1.7)	51.8 (5.4)	57.4 (3.2)	42.9 (2.6)	40.2 (3.2)					
	Core	48.7 (4.2)	51.4 (7.3)	56.0 (2.0)	75.3 (4.0)	54.5 (6.8)	66.4 (3.2)					
Predator: Herbivore	Pond	0.50 (0.16)	0.50 (0.10)	0.29 (0.14)	0.21 (0.06)	1.01 (0.28)	1.33 (0.40)		** 67>5	* 14>13	**	**
	River	0.28 (0.06)	0.40 (0.07)	0.40 (0.04)	0.33 (0.07)	0.64 (0.11)	1.07 (0.15)					
	Core	0.84 (0.05)	0.50 (0.05)	0.57 (0.06)	0.22 (0.06)	0.62 (0.25)	0.45 (0.07)					

Inequalities below asterisks reference multiple comparisons that were significant via Tukey's tests at $p<0.05$ following the sequential Bonferroni correction of multiple comparison to family-wise error rate. Only factor levels on either side of the inequality differed. Multiple comparison tests were not necessary for Year, but an inequality is provided to summarize test results.

[a] Habitat.
[b] Month.
[c] Year.
[d] River.
[e] Pond.
[f] Core.
[g] May.
[h] June.
[i] July.
[j] 2013.
[k] 2014.
*p<0.05 for main effect or interaction.
**p<0.01 for main effect or interaction.

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Online Resource 3 **Faunal orders and most abundant families and species**. Mean number of individuals (standard errors) for faunal orders and ten most abundant families and species (all based upon 50 sweeps) and ANOVA results for main effects and two-way interactions.
(PDF)

		2013			2014			GLM results					
		May	June	July	May	June	July	H[a]	M[b]	Y[c]	HxM	HxY	MxY
Microcoryphia	Pond	0 (0)	0.75 (0.48)	0.25 (0.25)	0 (0)	0 (0)	0 (0)	** R[d]>P[e]C[f]	** 5[g]>6[h]7[i]	** 13[j]>14[k]	**	**	*
	River	0 (0)	19.0 (10)	9.50 (3.1)	0.25 (0.25)	1.00 (1.0)	0.25 (0.25)						
	Core	0.25 (0.25)	0 (0)	1.00 (0.41)	0 (0)	0.25 (0.25)	0.25 (0.25)						
Odonata	Pond	0 (0)	0 (0)	0.25 (0.25)	0 (0)	0 (0)	0 (0)		* 7>56				
	River	0 (0)	0 (0)	0.25 (0.25)	0 (0)	0 (0)	0.75 (0.48)						
	Core	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)						
Orthoptera	Pond	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	** R>PC					
	River	0 (0)	0.25 (0.25)	2.00 (0.71)	0 (0)	0.50 (0.50)	0 (0)						
	Core	0.25 (0.25)	0.25 (0.25)	0 (0)	0 (0)	0 (0)	0.25 (0.25)						
Plecoptera	Pond	0.25 (0.25)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)						
	River	0.25 (0.25)	0.25 (0.25)	0 (0)	0 (0)	0 (0)	0 (0)						
	Core	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)						
Mantodea	Pond	0 (0)	0.25 (0.25)	0 (0)	0 (0)	0 (0)	0 (0)						
	River	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.25 (0.25)						

	Core	0 (0)	0 (0)	0.75 (0.48)	0 (0)	0 (0)	0 (0)						
Hemiptera	Pond	56.0 (13)	67.0 (16)	46.0 (7.3)	64.0 (4.4)	20.3 (6.7)	23.5 (6.1)	** R>PC	** 5>67	** 13>14		*	**
	River	189 (56)	122 (18)	56.3 (7.4)	84.8 (17)	34.5 (9.6)	29.3 (1.1)						
	Core	54.8 (7.2)	47.3 (9.6)	41.0 (5.0)	85.8 (27)	36.8 (9.6)	23.0 (6.6)						
Miridae	Pond	1.00 (0.56)	1.50 (0.50)	2.00 (1.1)	0 (0)	0 (0)	0.75 (0.48)	** R>PC	** 5>67	** 13>14	**		
	River	67.3 (34)	13.8 (5.0)	9.75 (2.3)	9.75 (2.3)	2.25 (0.85)	2.00 (1.7)						
	Core	14.3 (8.0)	1.00 (0.41)	2.00 (1.1)	0 (0)	0 (0)	0 (0)						
Europiella artemisiae	Pond	0.50 (0.29)	1.00 (0.71)	1.50 (0.96)	0 (0)	0 (0)	0 (0)	** R>PC	** 5>67	** 13>14	**		**
	River	60.0 (30)	5.25 (1.9)	8.25 (1.4)	3.50 (1.8)	0 (0)	0.75 (0.48)						
	Core	3.00 (2.0)	0.25 (0.25)	0.25 (0.25)	0 (0)	0 (0)	0 (0)						
Cicadellidae	Pond	34.5 (6.7)	21.5 (2.6)	32.0 (6.3)	24.8 (4.4)	16.0 (6.1)	11.8 (1.5)	** R>PC	** 5>7	** 13>14			
	River	107 (26)	50.5 (6.2)	35.0 (6.4)	31.8 (5.6)	19.8 (5.5)	15.3 (2.3)						
	Core	34.0 (8.4)	28.0 (6.1)	31.8 (5.4)	15.8 (2.3)	27.5 (8.4)	11.8 (2.7)						
Hebecephalus discessus	Pond	11.8 (5.0)	10.3 (3.9)	23.3 (6.6)	0.50 (0.29)	0 (0)	2.00 (1.4)			** 13>14			
	River	9.00 (4.0)	2.75 (1.1)	3.50 (1.0)	0.50 (0.50)	0 (0)	1.00 (0.41)						
	Core	7.00 (3.7)	16.5 (5.9)	18.0 (5.6)	1.25 (0.48)	0 (0)	0 (0)						
Mesamia sp.	Pond	1.00 (0.71)	0.75 (0.48)	0.25 (0.25)	0 (0)	0 (0)	0 (0)	** R>PC		** 13>14		**	
	River	46.5 (22)	11.0 (1.3)	4.00 (1.1)	1.75 (1.1)	1.25 (0.95)	0.75 (0.48)						
	Core	1.25 (0.75)	0.50 (0.29)	1.25 (0.25)	0 (0)	0 (0)	0 (0)						
Dikraneura carneola	Pond	2.75 (1.6)	0 (0)	0 (0)	11.8 (1.8)	7.50 (4.0)	0.50 (0.50)		** 5>6>7	** 14>13	*		**

	River	4.00 (0.71)	0.75 (0.25)	0 (0)	11.5 (3.3)	1.50 (0.50)	0 (0)						
	Core	1.50 (0.87)	1.50 (0.96)	0 (0)	5.50 (2.8)	11.0 (7.4)	0 (0)						
Delphacidae	Pond	1.00 (0.58)	8.00 (7.3)	2.50 (1.8)	1.00 (0.58)	0.25 (0.25)	0.75 (0.48)	** R>PC	*	** 13>14		*	
	River	11.0 (3.8)	44.0 (8.6)	7.50 (3.3)	3.00 (1.1)	3.00 (1.2)	1.00 (0.71)						
	Core	3.50 (1.4)	8.50 (5.4)	3.25 (2.9)	1.00 (0.41)	1.00 (0.41)	0 (0)						
Nothodelphax consimilis	Pond	1.00 (0.58)	8.00 (7.3)	1.50 (0.87)	1.00 (0.58)	0.25 (0.25)	0.75 (0.48)	** R>PC	*	** 13>14		*	
	River	7.00 (2.5)	37.5 (6.6)	7.50 (3.3)	2.50 (1.2)	2.25 (1.1)	1.00 (0.71)						
	Core	2.75 (1.0)	6.75 (4.0)	3.25 (2.9)	1.00 (0.41)	1.00 (0.41)	0 (0)						
Issidae	Pond	11.8 (6.3)	28.8 (14)	7.00 (3.5)	0 (0)	0 (0)	0 (0)	** P>RC		** 13>14		**	
	River	0 (0)	0 (0)	0 (0)	0 (0)	0.50 (0.50)	0 (0)						
	Core	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)						
Aphelonema histrionica	Pond	11.8 (6.3)	28.8 (14)	7.00 (3.5)	0 (0)	0 (0)	0 (0)	** P>RC		** 13>14		**	
	River	0 (0)	0 (0)	0 (0)	0 (0)	0.50 (0.50)	0 (0)						
	Core	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)						
Aphididae	Pond	5.25 (1.8)	0.75 (0.75)	0.25 (0.25)	37.3 (4.4)	1.00 (0.41)	0.25 (0.25)	** R>P	** 5>67	** 14>13		*	**
	River	4.50 (0.87)	6.75 (2.5)	1.00 (0.41)	36.8 (11)	3.00 (1.6)	4.00 (1.8)						
	Core	0.50 (0.29)	1.75 (0.63)	0.50 (0.50)	68.8 (26)	2.50 (1.3)	3.25 (1.7)						
Sitobion avenae	Pond	2.00 (1.1)	0.75 (0.75)	0 (0)	25.3 (4.6)	0.50 (0.50)	0 (0)	*	** 5>67	** 14>13			**
	River	1.75 (1.2)	5.75 (2.3)	0.50 (0.29)	24.3 (11)	1.50 (0.65)	2.25 (1.0)						
	Core	0.25 (0.25)	1.25 (0.75)	0.50 (0.50)	56.0 (21)	1.00 (0.71)	0.25 (0.25)						

Thysanoptera	Pond	0.250 (0.25)	0.50 (0.50)	1.75 (0.48)	0.25 (0.25)	0.25 (0.25)	0.75 (0.48)	* C>PR	** 7>5			
	River	0.75 (0.25)	0.25 (0.25)	1.25 (0.63)	0.25 (0.25)	0.50 (0.29)	0.25 (0.25)					
	Core	0.50 (0.29)	2.25 (1.3)	5.75 (3.1)	0.25 (0.25)	1.25 (0.75)	2.25 (0.95)					
Psocoptera	Pond	0.25 (0.25)	2.00 (0.71)	0.25 (0.25)	0.25 (0.25)	0.50 (0.50)	0.25 (0.25)	** P>RC	*	* 13>14		*
	River	0 (0)	0.50 (0.29)	0.25 (0.25)	0 (0)	0 (0)	0 (0)					
	Core	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)					
Coleoptera	Pond	14.5 (1.9)	3.25 (0.63)	1.50 (0.29)	6.75 (2.6)	2.25 (0.85)	1.75 (0.75)	** R>PC	** 5>6>7	** 13>14		
	River	39.5 (8.8)	14.0 (0.71)	6.25 (1.8)	21.8 (3.8)	7.00 (0.71)	9.75 (5.0)					
	Core	41.0 (6.4)	5.50 (2.7)	3.50 (2.9)	11.3 (3.7)	3.75 (1.5)	1.00 (0.71)					
Melyridae	Pond	12.3 (1.2)	0.25 (0.25)	0 (0)	0.50 (0.29)	0 (0)	0 (0)	** RC>P	** 5>67	** 13>14		**
	River	17.0 (2.5)	1.50 (0.87)	0.75 (0.75)	2.25 (0.63)	0 (0)	0 (0)					
	Core	25.8 (8.1)	0.75 (0.25)	0 (0)	2.75 (0.75)	0 (0)	0 (0)					
Malachius sp.	Pond	8.00 (0.71)	0 (0)	0 (0)	0.25 (0.25)	0 (0)	0 (0)	** RC>P	** 5>67	** 13>14	**	**
	River	13.3 (3.7)	1.00 (1.0)	0 (0)	2.25 (0.63)	0 (0)	0 (0)					
	Core	25.5 (8.1)	0.75 (0.25)	0 (0)	2.50 (0.65)	0 (0)	0 (0)					
Coccinellidae	Pond	0.25 (0.25)	2.00 (0.41)	1.00 (0.41)	5.75 (2.9)	1.75 (0.85)	1.75 (0.75)	** R>PC	** 5>7	** 14>13		
	River	4.75 (2.4)	1.50 (0.65)	0.75 (0.48)	8.00 (2.4)	5.75 (0.48)	6.00 (1.8)					
	Core	1.00 (1.0)	0.75 (0.75)	0.25 (0.25)	6.75 (2.6)	1.00 (0.58)	0.50 (0.29)					
Hippodamia convergens	Pond	0 (0)	1.00 (0.0)	0.75 (0.48)	5.75 (2.9)	1.75 (0.85)	1.75 (0.75)	** R>PC	** 5>67	** 14>13		
	River	4.75 (2.4)	1.50 (0.65)	0.50 (0.29)	8.00 (2.4)	5.75 (0.48)	4.75 (1.7)					

	Core	1.00 (1.0)	0 (0)	0 (0)	6.75 (2.6)	1.00 (0.58	0.50 (0.29)				
Neuroptera	Pond	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.25 (0.63)	** R>PC			*
	River	1.75 (0.85)	1.00 (0.58)	0.50 (0.29)	0.50 (0.50)	0.25 (0.25)	1.25 (0.48)				
	Core	0 (0)	0.25 (0.25)	0 (0)	0.25 (0.25)	0.25 (0.25)	0 (0)				
Hymenoptera	Pond	1.75 (0.85)	3.75 (2.8)	1.75 (0.48)	1.75 (0.75)	1.25 (0.95)	2.00 (1.2)	** R>C>P		** 13>14	
	River	8.00 (1.5)	21.3 (1.3)	10.0 (1.6)	8.00 (1.9)	4.75 (1.0)	4.00 (0.41)				
	Core	11.0 (4.5)	9.75 (4.6)	3.75 (1.3)	2.75 (1.4)	9.50 (8.2)	0.75 (0.48)				
Formicidae	Pond	0.25 (0.25)	3.00 (2.7)	0.25 (0.25)	0.50 (0.50)	0.25 (0.25)	1.25 (0.75)				
	River	0.25 (0.25)	5.50 (3.4)	4.00 (2.3)	1.25 (0.63)	2.75 (1.0)	2.25 (0.85)				
	Core	7.50 (4.8)	3.50 (2.9)	1.50 (0.87)	2.25 (1.1)	8.25 (7.6)	0.25 (0.25)				
Trichoptera	Pond	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	**			*
	River	0 (0)	0.50 (0.50)	1.00 (0.71)	1.00 (0.41)	0 (0)	0 (0)				
	Core	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)				
Lepidoptera	Pond	0.50 (0.29)	4.00 (1.7)	0.75 (0.48)	0.50 (0.50)	0.25 (0.25)	0 (0)	** R>P	** 6>57	** 13>14	**
	River	3.00 (0.41)	5.50 (2.0)	1.25 (0.63)	1.00 (0.41)	1.00 (0.41)	0.50 (0.50)				
	Core	1.50 (0.29)	6.25 (0.85)	0.25 (0.25)	0.25 (0.25)	0.50 (0.29)	0.50 (0.29)				
Diptera	Pond	4.00 (1.1)	7.50 (0.96)	4.00 (1.2)	11.8 (3.1)	5.50 (1.7)	4.50 (1.0)	** R>PC	** 56>7		**
	River	16.5 (2.6)	20.3 (7.5)	14.3 (5.6)	28.8 (7.5)	15.5 (4.4)	4.75 (1.5)				
	Core	5.25 (1.2)	7.25 (1.9)	2.50 (1.3)	8.00 (2.4)	2.50 (1.0)	1.50 (0.87)				
Araneae	Pond	5.50 (0.96)	19.3 (4.4)	5.00 (2.0)	4.50 (1.4)	8.25 (2.1)	8.50 (2.4)		** 6>5	** 13>14	

	River	11.3 (2.9)	19.5 (4.7)	15.3 (4.2)	6.75 (2.3)	8.25 (2.2)	7.75 (1.1)					
	Core	7.25 (1.3)	10.5 (0.65)	18.0 (3.0)	5.50 (2.5)	7.50 (3.0)	3.75 (1.3)					
Philodromidae	Pond	4.25 (1.3)	3.25 (1.4)	2.25 (1.6)	0 (0)	0 (0)	0.25 (0.25)	*		** 13>14	*	
	River	4.00 (1.4)	4.50 (0.65)	4.50 (2.0)	0.25 (0.25)	0.50 (0.50)	1.50 (0.87)					
	Core	4.25 (1.4)	4.75 (0.25)	12.5 (2.3)	0 (0)	0.25 (0.25)	0 (0)					
Tibellus oblongus	Pond	4.25 (1.3)	3.25 (1.4)	2.25 (1.6)	0 (0)	0 (0)	0.25 (0.25)	*		** 13>14	*	
	River	4.00 (1.4)	4.50 (0.65)	4.50 (2.0)	0.25 (0.25)	0 (0)	1.00 (0.71)					
	Core	4.25 (1.4)	4.75 (0.25)	12.5 (2.3)	0 (0)	0.25 (0.25)	0 (0)					
Thomisidae	Pond	0.50 (0.50)	1.50 (0.65)	0.50 (0.29)	2.50 (0.96)	6.75 (2.4)	7.75 (2.4)	** R>C	** 6>57	** 14>13	**	
	River	1.25 (0.63)	8.00 (2.6)	4.25 (1.2)	1.25 (0;75)	5.50 (1.2)	2.00 (0.58)					
	Core	0.50 (0.29)	1.50 (0.50)	0.50 (0.29)	1.50 (0.65)	4.75 (1.3)	1.25 (1.3)					
Opiliones	Pond	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)					
	River	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)					
	Core	0.25 (0.25)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)					
Acari	Pond	0.75 (0.48)	0.50 (0.29)	0.25 (0.25)	0.50 (0.5)	1.50 (0.87)	1.50 (0.87)			** 14>13		*
	River	0.50 (0.50)	0 (0)	0 (0)	1.00 (1.0)	1.00 (0.71)	2.75 (1.4)					
	Core	0.25 (0.25)	0 (0)	0.25 (0.25)	0 (0)	1.00 (0.71)	0.75 (0.25)					

Inequalities below asterisks reference multiple comparisons that were significant via Tukey's tests at $p<0.05$ following the sequential Bonferroni correction of multiple comparison to family-wise error rate. Only factor levels on either side of the inequality differed. Multiple comparison tests were not necessary for Year, but an inequality is provided to summarize test results.

[a] Habitat.
[b] Month.
[c] Year.
[d] River.
[e] Pond.
[f] Core.
[g] May.
[h] June.
[i] July.
[j] 2013.
[k] 2014.
*p<0.05 for main effect or interaction.
**p<0.01 for main effect or interaction.

Supplementary material: Arthropod Assemblages in a Montane Wetland Complex: Influences of Adjoining Lotic and Lentic Habitat and Temporal Variability, *Wetlands*, Jeffrey G Holmquist and Jutta Schmidt-Gengenbach, UCLA, jholmquist@ucla.edu

Online Resource 4 Lotic fauna near wetland. Raw data, means, and standard errors for Tuolumne River lotic fauna at two sites near wetland studv area. Results are from 1 m^2 kick net samples from cobble habitat

	2013			2014		
	Total Individuals	Species Richness	Chironomid Abundance	Total Individuals	Species Richness	Chironomid Abundance
May Site 1	102	21	44	552	25	332
May Site 2	130	22	48	623	35	361
June Site 1	987	27	637	529	22	351
June Site 2	690	28	226	521	27	321
July Site 1	479	25	389	648	30	187
July Site 2	393	29	185	999	36	433
Mean	464	25.3	255	645	29.2	331
SE	138	1.3	93	74	2.3	33

% Aquatic	Pond	0.26 (0.26)	0 (0)	0.44 (0.44)	1.45 (0.38)	0.49 (0.49)	0 (0)	** R>PC		** 14>13	**	**
	River	0.46 (0.16)	2.12 (0.94)	2.71 (1.4)	9.71 (1.9)	7.38 (2.8)	3.68 (1.2)					
	Core	0.16 (0.16)	0 (0)	0 (0)	0.96 (0.55)	0 (0)	0 (0)					
Number aquatic	Pond	0.25 (0.25)	0 (0)	0.25 (0.25)	1.25 (0.25)	0.25 (0.25)	0 (0)	** R>PC	** 5>6	** 14>13	**	**
	River	1.00 (0.41)	4.50 (1.8)	3.00 (1.5)	15.5 (5.3)	5.75 (2.3)	2.25 (0.75)					
	Core	0.25 (0.25)	0 (0)	0 (0)	1.50 (0.96)	0 (0)	0 (0)					
Number terrestrial	Pond	83.5 (11)	109 (18)	61.5 (6.1)	89.0 (8.3)	39.8 (9.8)	44.0 (6.2)	** R>PC	**	** 13>14		*
	River	270 (63)	220 (34)	115 (14)	139 (22)	68.8 (13)	59.3 (5.3)					
	Core	122 (14)	102 (22)	76.8 (10)	113 (31)	63.3 (13)	34.0 (8.5)					
% Predators	Pond	28.8 (5.4)	29.1 (4.4)	19.1 (7.3)	14.0 (3.3)	40.8 (6.8)	45.4 (5.4)		** 7>5		*	**
	River	18.9 (3.2)	21.5 (2.9)	20.4 (2.0)	18.5 (2.8)	27.0 (3.5)	41.6 (3.3)					
	Core	39.0 (4.3)	25.0 (2.9)	31.5 (2.8)	15.8 (3.4)	31.5 (12)	29.4 (3.5)					
% Herbivores	Pond	65.2 (7.3)	60.4 (3.7)	74.5 (6.3)	72.6 (5.9)	44.8 (5.4)	39.7 (6.4)		** 5>67		**	**
	River	68.9 (4.1)	55.0 (1.7)	51.8 (5.4)	57.4 (3.2)	42.9 (2.6)	40.2 (3.2)					
	Core	48.7 (4.2)	51.4 (7.3)	56.0 (2.0)	75.3 (4.0)	54.5 (6.8)	66.4 (3.2)					
Predator: Herbivore	Pond	0.50 (0.16)	0.50 (0.10)	0.29 (0.14)	0.21 (0.06)	1.01 (0.28)	1.33 (0.40)		** 67>5	* 14>13	**	**
	River	0.28 (0.06)	0.40 (0.07)	0.40 (0.04)	0.33 (0.07)	0.64 (0.11)	1.07 (0.15)					
	Core	0.84 (0.05)	0.50 (0.05)	0.57 (0.06)	0.22 (0.06)	0.62 (0.25)	0.45 (0.07)					

Inequalities below asterisks reference multiple comparisons that were significant via Tukey's tests at $p<0.05$ following the sequential Bonferroni correction of multiple comparison to family-wise error rate. Only factor levels on either side of the inequality differed. Multiple comparison tests were not necessary for Year, but an inequality is provided to summarize test results.

[a] Habitat.
[b] Month.
[c] Year.
[d] River.
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[g] May.
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[j] 2013.
[k] 2014.
*$p<0.05$ for main effect or interaction.
**$p<0.01$ for main effect or interaction.

Supplementary material: Arthropod Assemblages in a Montane Wetland Complex: Influences of Adjoining Lotic and Lentic Habitat and Temporal Variability, Wetlands, Jeffrey G Holmquist and Jutta Schmidt-Gengenbach, UCLA, jholmquist@ucla.edu

Online Resource 3 **Faunal orders and most abundant families and species**. Mean number of individuals (standard errors) for faunal orders and ten most abundant families and species (all based upon 50 sweeps) and ANOVA results for main effects and two-way interactions.
(PDF)

		2013			2014			GLM results					
		May	June	July	May	June	July	H[a]	M[b]	Y[c]	HxM	HxY	MxY
Microcoryphia	Pond	0 (0)	0.75 (0.48)	0.25 (0.25)	0 (0)	0 (0)	0 (0)	** R[d]>P[e]C[f]	** 5[g]>6[h]7[i]	** 13[j]>14[k]	**	**	*
	River	0 (0)	19.0 (10)	9.50 (3.1)	0.25 (0.25)	1.00 (1.0)	0.25 (0.25)						
	Core	0.25 (0.25)	0 (0)	1.00 (0.41)	0 (0)	0.25 (0.25)	0.25 (0.25)						
Odonata	Pond	0 (0)	0 (0)	0.25 (0.25)	0 (0)	0 (0)	0 (0)		* 7>56				
	River	0 (0)	0 (0)	0.25 (0.25)	0 (0)	0 (0)	0.75 (0.48)						
	Core	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)						
Orthoptera	Pond	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	** R>PC					
	River	0 (0)	0.25 (0.25)	2.00 (0.71)	0 (0)	0.50 (0.50)	0 (0)						
	Core	0.25 (0.25)	0.25 (0.25)	0 (0)	0 (0)	0 (0)	0.25 (0.25)						
Plecoptera	Pond	0.25 (0.25)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)						
	River	0.25 (0.25)	0.25 (0.25)	0 (0)	0 (0)	0 (0)	0 (0)						
	Core	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)						
Mantodea	Pond	0 (0)	0.25 (0.25)	0 (0)	0 (0)	0 (0)	0 (0)						
	River	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.25 (0.25)						

	Core	0 (0)	0 (0)	0.75 (0.48)	0 (0)	0 (0)	0 (0)						
Hemiptera	Pond	56.0 (13)	67.0 (16)	46.0 (7.3)	64.0 (4.4)	20.3 (6.7)	23.5 (6.1)	** R>PC	** 5>67	** 13>14		*	**
	River	189 (56)	122 (18)	56.3 (7.4)	84.8 (17)	34.5 (9.6)	29.3 (1.1)						
	Core	54.8 (7.2)	47.3 (9.6)	41.0 (5.0)	85.8 (27)	36.8 (9.6)	23.0 (6.6)						
Miridae	Pond	1.00 (0.56)	1.50 (0.50)	2.00 (1.1)	0 (0)	0 (0)	0.75 (0.48)	** R>PC	** 5>67	** 13>14	**		
	River	67.3 (34)	13.8 (5.0)	9.75 (2.3)	9.75 (2.3)	2.25 (0.85)	2.00 (1.7)						
	Core	14.3 (8.0)	1.00 (0.41)	2.00 (1.1)	0 (0)	0 (0)	0 (0)						
Europiella artemisiae	Pond	0.50 (0.29)	1.00 (0.71)	1.50 (0.96)	0 (0)	0 (0)	0 (0)	** R>PC	** 5>67	** 13>14	**		**
	River	60.0 (30)	5.25 (1.9)	8.25 (1.4)	3.50 (1.8)	0 (0)	0.75 (0.48)						
	Core	3.00 (2.0)	0.25 (0.25)	0.25 (0.25)	0 (0)	0 (0)	0 (0)						
Cicadellidae	Pond	34.5 (6.7)	21.5 (2.6)	32.0 (6.3)	24.8 (4.4)	16.0 (6.1)	11.8 (1.5)	** R>PC	** 5>7	** 13>14			
	River	107 (26)	50.5 (6.2)	35.0 (6.4)	31.8 (5.6)	19.8 (5.5)	15.3 (2.3)						
	Core	34.0 (8.4)	28.0 (6.1)	31.8 (5.4)	15.8 (2.3)	27.5 (8.4)	11.8 (2.7)						
Hebecephalus discessus	Pond	11.8 (5.0)	10.3 (3.9)	23.3 (6.6)	0.50 (0.29)	0 (0)	2.00 (1.4)			** 13>14			
	River	9.00 (4.0)	2.75 (1.1)	3.50 (1.0)	0.50 (0.50)	0 (0)	1.00 (0.41)						
	Core	7.00 (3.7)	16.5 (5.9)	18.0 (5.6)	1.25 (0.48)	0 (0)	0 (0)						
Mesamia sp.	Pond	1.00 (0.71)	0.75 (0.48)	0.25 (0.25)	0 (0)	0 (0)	0 (0)	** R>PC		** 13>14		**	
	River	46.5 (22)	11.0 (1.3)	4.00 (1.1)	1.75 (1.1)	1.25 (0.95)	0.75 (0.48)						
	Core	1.25 (0.75)	0.50 (0.29)	1.25 (0.25)	0 (0)	0 (0)	0 (0)						
Dikraneura carneola	Pond	2.75 (1.6)	0 (0)	0 (0)	11.8 (1.8)	7.50 (4.0)	0.50 (0.50)		** 5>6>7	** 14>13	*		**

	River	4.00 (0.71)	0.75 (0.25)	0 (0)	11.5 (3.3)	1.50 (0.50)	0 (0)					
	Core	1.50 (0.87)	1.50 (0.96)	0 (0)	5.50 (2.8)	11.0 (7.4)	0 (0)					
Delphacidae	Pond	1.00 (0.58)	8.00 (7.3)	2.50 (1.8)	1.00 (0.58)	0.25 (0.25)	0.75 (0.48)	** R>PC	*	** 13>14	*	
	River	11.0 (3.8)	44.0 (8.6)	7.50 (3.3)	3.00 (1.1)	3.00 (1.2)	1.00 (0.71)					
	Core	3.50 (1.4)	8.50 (5.4)	3.25 (2.9)	1.00 (0.41)	1.00 (0.41)	0 (0)					
Nothodelphax consimilis	Pond	1.00 (0.58)	8.00 (7.3)	1.50 (0.87)	1.00 (0.58)	0.25 (0.25)	0.75 (0.48)	** R>PC	*	** 13>14	*	
	River	7.00 (2.5)	37.5 (6.6)	7.50 (3.3)	2.50 (1.2)	2.25 (1.1)	1.00 (0.71)					
	Core	2.75 (1.0)	6.75 (4.0)	3.25 (2.9)	1.00 (0.41)	1.00 (0.41)	0 (0)					
Issidae	Pond	11.8 (6.3)	28.8 (14)	7.00 (3.5)	0 (0)	0 (0)	0 (0)	** P>RC		** 13>14	**	
	River	0 (0)	0 (0)	0 (0)	0 (0)	0.50 (0.50)	0 (0)					
	Core	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)					
Aphelonema histrionica	Pond	11.8 (6.3)	28.8 (14)	7.00 (3.5)	0 (0)	0 (0)	0 (0)	** P>RC		** 13>14	**	
	River	0 (0)	0 (0)	0 (0)	0 (0)	0.50 (0.50)	0 (0)					
	Core	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)					
Aphididae	Pond	5.25 (1.8)	0.75 (0.75)	0.25 (0.25)	37.3 (4.4)	1.00 (0.41)	0.25 (0.25)	** R>P	** 5>67	** 14>13	*	**
	River	4.50 (0.87)	6.75 (2.5)	1.00 (0.41)	36.8 (11)	3.00 (1.6)	4.00 (1.8)					
	Core	0.50 (0.29)	1.75 (0.63)	0.50 (0.50)	68.8 (26)	2.50 (1.3)	3.25 (1.7)					
Sitobion avenae	Pond	2.00 (1.1)	0.75 (0.75)	0 (0)	25.3 (4.6)	0.50 (0.50)	0 (0)	*	** 5>67	** 14>13		**
	River	1.75 (1.2)	5.75 (2.3)	0.50 (0.29)	24.3 (11)	1.50 (0.65)	2.25 (1.0)					
	Core	0.25 (0.25)	1.25 (0.75)	0.50 (0.50)	56.0 (21)	1.00 (0.71)	0.25 (0.25)					

Thysanoptera	Pond	0.250 (0.25)	0.50 (0.50)	1.75 (0.48)	0.25 (0.25)	0.25 (0.25)	0.75 (0.48)	* C>PR	** 7>5			
	River	0.75 (0.25)	0.25 (0.25)	1.25 (0.63)	0.25 (0.25)	0.50 (0.29)	0.25 (0.25)					
	Core	0.50 (0.29)	2.25 (1.3)	5.75 (3.1)	0.25 (0.25)	1.25 (0.75)	2.25 (0.95)					
Psocoptera	Pond	0.25 (0.25)	2.00 (0.71)	0.25 (0.25)	0.25 (0.25)	0.50 (0.50)	0.25 (0.25)	** P>RC	*	* 13>14		*
	River	0 (0)	0.50 (0.29)	0.25 (0.25)	0 (0)	0 (0)	0 (0)					
	Core	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)					
Coleoptera	Pond	14.5 (1.9)	3.25 (0.63)	1.50 (0.29)	6.75 (2.6)	2.25 (0.85)	1.75 (0.75)	** R>PC	** 5>6>7	** 13>14		
	River	39.5 (8.8)	14.0 (0.71)	6.25 (1.8)	21.8 (3.8)	7.00 (0.71)	9.75 (5.0)					
	Core	41.0 (6.4)	5.50 (2.7)	3.50 (2.9)	11.3 (3.7)	3.75 (1.5)	1.00 (0.71)					
Melyridae	Pond	12.3 (1.2)	0.25 (0.25)	0 (0)	0.50 (0.29)	0 (0)	0 (0)	** RC>P	** 5>67	** 13>14		**
	River	17.0 (2.5)	1.50 (0.87)	0.75 (0.75)	2.25 (0.63)	0 (0)	0 (0)					
	Core	25.8 (8.1)	0.75 (0.25)	0 (0)	2.75 (0.75)	0 (0)	0 (0)					
Malachius sp.	Pond	8.00 (0.71)	0 (0)	0 (0)	0.25 (0.25)	0 (0)	0 (0)	** RC>P	** 5>67	** 13>14	**	**
	River	13.3 (3.7)	1.00 (1.0)	0 (0)	2.25 (0.63)	0 (0)	0 (0)					
	Core	25.5 (8.1)	0.75 (0.25)	0 (0)	2.50 (0.65)	0 (0)	0 (0)					
Coccinellidae	Pond	0.25 (0.25)	2.00 (0.41)	1.00 (0.41)	5.75 (2.9)	1.75 (0.85)	1.75 (0.75)	** R>PC	** 5>7	** 14>13		
	River	4.75 (2.4)	1.50 (0.65)	0.75 (0.48)	8.00 (2.4)	5.75 (0.48)	6.00 (1.8)					
	Core	1.00 (1.0)	0.75 (0.75)	0.25 (0.25)	6.75 (2.6)	1.00 (0.58)	0.50 (0.29)					
Hippodamia convergens	Pond	0 (0)	1.00 (0.0)	0.75 (0.48)	5.75 (2.9)	1.75 (0.85)	1.75 (0.75)	** R>PC	** 5>67	** 14>13		
	River	4.75 (2.4)	1.50 (0.65)	0.50 (0.29)	8.00 (2.4)	5.75 (0.48)	4.75 (1.7)					

	Core	1.00 (1.0)	0 (0)	0 (0)	6.75 (2.6)	1.00 (0.58	0.50 (0.29)				
Neuroptera	Pond	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.25 (0.63)	** R>PC			*
	River	1.75 (0.85)	1.00 (0.58)	0.50 (0.29)	0.50 (0.50)	0.25 (0.25)	1.25 (0.48)				
	Core	0 (0)	0.25 (0.25)	0 (0)	0.25 (0.25)	0.25 (0.25)	0 (0)				
Hymenoptera	Pond	1.75 (0.85)	3.75 (2.8)	1.75 (0.48)	1.75 (0.75)	1.25 (0.95)	2.00 (1.2)	** R>C>P		** 13>14	
	River	8.00 (1.5)	21.3 (1.3)	10.0 (1.6)	8.00 (1.9)	4.75 (1.0)	4.00 (0.41)				
	Core	11.0 (4.5)	9.75 (4.6)	3.75 (1.3)	2.75 (1.4)	9.50 (8.2)	0.75 (0.48)				
Formicidae	Pond	0.25 (0.25)	3.00 (2.7)	0.25 (0.25)	0.50 (0.50)	0.25 (0.25)	1.25 (0.75)				
	River	0.25 (0.25)	5.50 (3.4)	4.00 (2.3)	1.25 (0.63)	2.75 (1.0)	2.25 (0.85)				
	Core	7.50 (4.8)	3.50 (2.9)	1.50 (0.87)	2.25 (1.1)	8.25 (7.6)	0.25 (0.25)				
Trichoptera	Pond	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	**			*
	River	0 (0)	0.50 (0.50)	1.00 (0.71)	1.00 (0.41)	0 (0)	0 (0)				
	Core	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)				
Lepidoptera	Pond	0.50 (0.29)	4.00 (1.7)	0.75 (0.48)	0.50 (0.50)	0.25 (0.25)	0 (0)	** R>P	** 6>57	** 13>14	**
	River	3.00 (0.41)	5.50 (2.0)	1.25 (0.63)	1.00 (0.41)	1.00 (0.41)	0.50 (0.50)				
	Core	1.50 (0.29)	6.25 (0.85)	0.25 (0.25)	0.25 (0.25)	0.50 (0.29)	0.50 (0.29)				
Diptera	Pond	4.00 (1.1)	7.50 (0.96)	4.00 (1.2)	11.8 (3.1)	5.50 (1.7)	4.50 (1.0)	** R>PC	** 56>7		**
	River	16.5 (2.6)	20.3 (7.5)	14.3 (5.6)	28.8 (7.5)	15.5 (4.4)	4.75 (1.5)				
	Core	5.25 (1.2)	7.25 (1.9)	2.50 (1.3)	8.00 (2.4)	2.50 (1.0)	1.50 (0.87)				
Araneae	Pond	5.50 (0.96)	19.3 (4.4)	5.00 (2.0)	4.50 (1.4)	8.25 (2.1)	8.50 (2.4)		** 6>5	** 13>14	

	River	11.3 (2.9)	19.5 (4.7)	15.3 (4.2)	6.75 (2.3)	8.25 (2.2)	7.75 (1.1)					
	Core	7.25 (1.3)	10.5 (0.65)	18.0 (3.0)	5.50 (2.5)	7.50 (3.0)	3.75 (1.3)					
Philodromidae	Pond	4.25 (1.3)	3.25 (1.4)	2.25 (1.6)	0 (0)	0 (0)	0.25 (0.25)	*		** 13>14	*	
	River	4.00 (1.4)	4.50 (0.65)	4.50 (2.0)	0.25 (0.25)	0.50 (0.50)	1.50 (0.87)					
	Core	4.25 (1.4)	4.75 (0.25)	12.5 (2.3)	0 (0)	0.25 (0.25)	0 (0)					
Tibellus oblongus	Pond	4.25 (1.3)	3.25 (1.4)	2.25 (1.6)	0 (0)	0 (0)	0.25 (0.25)	*		** 13>14	*	
	River	4.00 (1.4)	4.50 (0.65)	4.50 (2.0)	0.25 (0.25)	0 (0)	1.00 (0.71)					
	Core	4.25 (1.4)	4.75 (0.25)	12.5 (2.3)	0 (0)	0.25 (0.25)	0 (0)					
Thomisidae	Pond	0.50 (0.50)	1.50 (0.65)	0.50 (0.29)	2.50 (0.96)	6.75 (2.4)	7.75 (2.4)	** R>C	** 6>57	** 14>13	**	
	River	1.25 (0.63)	8.00 (2.6)	4.25 (1.2)	1.25 (0;75)	5.50 (1.2)	2.00 (0.58)					
	Core	0.50 (0.29)	1.50 (0.50)	0.50 (0.29)	1.50 (0.65)	4.75 (1.3)	1.25 (1.3)					
Opiliones	Pond	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)					
	River	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)					
	Core	0.25 (0.25)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)					
Acari	Pond	0.75 (0.48)	0.50 (0.29)	0.25 (0.25)	0.50 (0.5)	1.50 (0.87)	1.50 (0.87)			** 14>13		*
	River	0.50 (0.50)	0 (0)	0 (0)	1.00 (1.0)	1.00 (0.71)	2.75 (1.4)					
	Core	0.25 (0.25)	0 (0)	0.25 (0.25)	0 (0)	1.00 (0.71)	0.75 (0.25)					

Inequalities below asterisks reference multiple comparisons that were significant via Tukey's tests at $p<0.05$ following the sequential Bonferroni correction of multiple comparison to family-wise error rate. Only factor levels on either side of the inequality differed. Multiple comparison tests were not necessary for Year, but an inequality is provided to summarize test results.

[a] Habitat.
[b] Month.
[c] Year.
[d] River.
[e] Pond.
[f] Core.
[g] May.
[h] June.
[i] July.
[j] 2013.
[k] 2014.
*$p<0.05$ for main effect or interaction.
**$p<0.01$ for main effect or interaction.

Supplementary material: Arthropod Assemblages in a Montane Wetland Complex: Influences of Adjoining Lotic and Lentic Habitat and Temporal Variability, *Wetlands*, Jeffrey G Holmquist and Jutta Schmidt-Gengenbach, UCLA, jholmquist@ucla.edu

Online Resource 4 Lotic fauna near wetland. Raw data, means, and standard errors for Tuolumne River lotic fauna at two sites near wetland study area. Results are from 1 m^2 kick net samples from cobble habitat

	2013			2014		
	Total Individuals	Species Richness	Chironomid Abundance	Total Individuals	Species Richness	Chironomid Abundance
May Site 1	102	21	44	552	25	332
May Site 2	130	22	48	623	35	361
June Site 1	987	27	637	529	22	351
June Site 2	690	28	226	521	27	321
July Site 1	479	25	389	648	30	187
July Site 2	393	29	185	999	36	433
Mean	464	25.3	255	645	29.2	331
SE	138	1.3	93	74	2.3	33