PLANT-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Leaf litter quality affects aquatic insect emergence: contrasting patterns from two foundation trees

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Abstract Reciprocal subsidies between rivers and terrestrial habitats are common where terrestrial leaf litter provides energy to aquatic invertebrates while emerging aquatic insects provide energy to terrestrial predators (e.g., birds, lizards, spiders). We examined how aquatic insect emergence changed seasonally with litter from two foundation riparian trees, whose litter often dominates riparian streams of the southwestern United States: Fremont (*Populus fremontii*) and narrowleaf (*Populus angustifolia*) cottonwood. *P. fremontii* litter is fast-decomposing and lower in defensive phytochemicals (i.e., condensed tannins, lignin) relative to *P. angustifolia*. We experimentally manipulated leaf litter from these two species by placing them in leaf enclosures with emergence traps attached in order to determine how leaf type influenced insect emergence. Contrary to our initial predictions, we found that packs with slow-decomposing leaves tended to support more emergent insects relative to packs with fast-decomposing leaves. Three findings emerged. Firstly, abundance (number of emerging insects m^{-2} day^{-1}) was 25 % higher on narrowleaf compared to Fremont leaves for the spring but did not differ in the fall, demonstrating that leaf quality from two dominant trees of the same genus yielded different emergence patterns and that these patterns changed seasonally. Secondly, functional feeding groups of emerging insects differed between treatments and seasons. Specifically, in the spring collector-gatherer abundance and biomass were higher on narrowleaf leaves, whereas collector-filterer abundance and biomass were higher on Fremont leaves. Shredder abundance and biomass were higher on narrowleaf leaves in the fall. Thirdly, diversity (Shannon's H') was higher on Fremont leaves in the spring, but no differences were found in the fall, showing that fast-decomposing leaves can support a more diverse, complex emergent insect assemblage during certain times of the year. Collectively, these results challenge the notion that leaf quality is a simple function of decomposition, suggesting instead that aquatic insects benefit differentially from different leaf types, such that some use slow-decomposing litter for habitat and its temporal longevity and others utilize fast-decomposing litter with more immediate nutrient release.

Communicated by Robert Hall.

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Introduction

Streams and their surrounding terrestrial environments are trophically linked (Baxter et al. 2005). Riparian leaves

provide energy for aquatic invertebrates (Petersen and Cummins 1974; Vannote et al. 1980) while emerging aquatic insects provide energy for terrestrial animals, including birds (Gray 1993; McIntosh 2000), bats (Barclay 1991; de Jong and Ahlén 1991; Sullivan et al. 1993), lizards (Sabo and Power 2002) and spiders (Sanzone et al. 2003; Paetzold et al. 2005). Stream subsidies to terrestrial predators can be particularly important when they coincide with periods of low terrestrial productivity (Nakano and Murakami 2001). These subsidies can exert bottom-up control by feeding riparian predators. For example, horizontal orb weaver (Tetragnathidae) abundance was reduced by 57 and 65 % in emergent insect exclusion vs. control reaches in a coastal temperate rainforest (Marczak and Richardson 2007) and a temperate forest in northern Japan (Baxter et al. 2004), respectively. Additionally, 25.6 % of the annual energy budget of an insectivorous riparian bird community in northern Japan came from emergent aquatic insects (Nakano and Murakami 2001). Aquatic insect subsidies can also impact predator growth rates, as a 55–65 % decrease in emergence resulted in a sevenfold decrease in the growth of a riparian lizard (Sabo and Power 2002). Additionally, emergent dragonflies exert top-down controls on the terrestrial environment via predation on terrestrial plant pollinators (Knight et al. 2005). Even slight differences in animal populations in the riparian zone, then, could have major consequences for ecosystem function, especially at the landscape level and over long temporal periods.

Many studies have compared leaf litter decomposition rates and insect abundances on aquatic invertebrates in their larval stages. Leaf litter quality is often defined in the context of microbial decomposition (see Fogel and Cromack 1977; Melillo et al. 1982) because decomposition correlates so well to other leaf quality variables (e.g., defensive compounds or nutrient content); thus decomposition can be viewed as a holistic, comprehensive metric for leaf quality. In streams, defensive compounds in leaves (e.g., condensed tannins and salicortin) are thought to lower leaf quality by slowing decomposition and nutrient concentration, resulting in lower shredder abundance (Davies and Boulton 2009) and preference (Irons et al. 1988; Rincón and Martínez 2006). Because differences among leaf types can affect the abundance (Hieber and Gessner 2002; Yanoviak 1999), biomass (Hieber and Gessner 2002) or community structure (Cummins et al. 1989; LeRoy and Marks 2006; LeRoy et al. 2006) of aquatic insects, leaf quality likely also affects the quantity and timing of emerging insects. Aquatic insects often discriminate among leaves of different species, on the basis of toughness, nutrient content and secondary compounds (Webster and Benfield 1986; Graça 2001). Insects can occur in higher abundances on

fast-decomposing leaves (e.g., Basaguren and Pozo 1994; Malmqvist and Oberle 1995; Webster and Benfield 1986); however, slow-decomposing leaves can increase abundance (Grubbs and Cummins 1994) and biomass (Stout et al. 1993) of some shredder taxa at larger, reach-level scales, presumably because they stay in the stream long enough to allow for the establishment of spring and summer shredder fauna (Grubbs and Cummins 1994).

The aim of this study was to determine how much leaf litter of varying decomposition rates and phytochemistry (e.g., condensed tannins, lignin) influences aquatic insect emergence. We hypothesized that leaf quality for emerging insects is not a simple function of decomposition rate and likely varies across insect taxa. If leaf defenses and structural compounds primarily inhibit nutrient transfer, then we would expect more insects to emerge on fast- versus slow-decomposing litter. Slow-decomposing leaves, however, may be advantageous to some invertebrates for two reasons. First, persistence in the river may provide more stable food resources and better protection against predators. Second, the microbial assemblages, if dominated by fungi over bacteria, may provide a better food source for invertebrates feeding on slowly decomposing substrates (see Findlay et al. 1986). We experimentally manipulated leaf litter of two cottonwood species: *Populus fremontii* (Fremont) and *Populus angustifolia* (narrowleaf). These species have predictable differences in chemical composition and decomposition rates (see Whitham et al. 2006 for review). *P. fremontii* leaves have lower levels of condensed tannins and lignin (Rehill et al. 2006; LeRoy et al. 2007) and decompose more quickly relative to *P. angustifolia* leaves (LeRoy and Marks 2006).

We made three a priori predictions:

(a) Fast-decomposing Fremont leaves would yield more total emergent insects than slow-decomposing narrowleaf leaves.

(b) Community composition of emergent insects would differ (in terms of taxa abundances and presence-absence) between leaf types, such that Fremont litter would have higher abundances of taxa directly associated with the litter (i.e., shredders and detrital scrappers).

(c) Diversity would be higher on narrowleaf relative to Fremont leaves.

The rationale behind the first prediction is that leaves with lower carbon:nitrogen ratios would provide a better food resource for most insects emerging from experimental enclosures. The rationale behind our second prediction is that we expected taxa would respond differently to leaf quality, generating different community assemblages (i.e., communities with differing abundances and

presence-absence of different taxa) across treatments, as seen with benthic insects (LeRoy and Marks 2006; LeRoy et al. 2006). Specifically, we expect taxa abundances to be higher on fast-decomposing Fremont compared to narrowleaf litter, and that Fremont litter will support more taxa directly associated with the litter (i.e., shredders, detrital scrappers) compared to narrowleaf litter because of the lower contents of defensive compounds found in Fremont litter. We also examined the community in terms of functional feeding groups, expecting that functional feeding groups most closely associated with leaf litter (i.e., shredders) would yield more emergence abundance and biomass from fast-decomposing Fremont litter compared to slow-decomposing narrowleaf litter due to relatively lower contents of defensive compounds associated with this litter. In addition to overall community composition and functional feeding groups, we chose to examine how Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa responded to leaf-quality treatments because of known relationships in EPT taxa richness and water quality (Weber 1973) and of the relevance of these taxa to conservation and restoration. Specifically, we expected EPT emergence abundance and biomass to be lower on narrowleaf compared to Fremont litter due to relatively high amounts of defensive compounds. The rationale behind our third prediction is that emergent insect diversity would follow similar patterns found with microbial assemblages, where bacterial and fungal diversity were higher on narrowleaf compared to Fremont leaves (Marks et al. 2009).

Materials and methods

Study site

This study took place in Wet Beaver Creek, in north central Arizona, USA, located east of Arizona state road 179 (34°41′N, 111°41′W) at an elevation of $\sim$1,400 (m a.s.l.). Wet Beaver Creek is a headwater desert stream (Strahler stream order 4 for our study sites) that is part of the Verde River catchment and drains off the southwestern edge of the Colorado Plateau. The riparian vegetation is dominated by Fremont cottonwood (*Populus fremontii* S. Wats.), narrowleaf cottonwood (*Populus angustifolia* James), Arizona alder (*Alnus oblongifolia* Torr.), box elder (*Acer negundo* L.), Gambel oak (*Quercus gambelii* Nutt.), Arizona sycamore (*Platanus wrightii* S. Wats), velvet ash (*Fraxinus velutina* Torr.), coyote willow (*Salix exigua* Nutt.), and Goodding's willow (*Salix gooddingii* Ball) (see LeRoy and Marks 2006). The average annual flow of Wet Beaver Creek is 340 L s^{-1}, and the geomorphology consists of Palaeozoic sandstones and Tertiary igneous

formations, giving it a relatively high alkalinity (LeRoy and Marks 2006).

The spring study ran for 8 weeks from 5 May up to and including 30 June 2008, and the fall study ran for 8 weeks from 2 December 2008 up to and including 27 January 2009. During our study, the median flow was 200 L s^{-1} (25 % quartile, 190 L s^{-1}; 75 % quartile, 210 L s^{-1}) for the spring and 280 L s^{-1} (25 % quartile, 220 L s^{-1}; 75 % quartile, 420 L s^{-1}) for the fall (data from USGS gaging station). Average wetted width ($\pm$SD) of Wet Beaver Creek was 8.03 $\pm$ 2.15 m across our study sites. Water chemistry parameters (means $\pm$ SDs) were measured using a Hydrolab MS5 probe with a Surveyor 4 data logger (Hydrolab, USA). Mean water temperature (°C) was 24.23 $\pm$ 0.21 in the spring and 9.19 $\pm$ 1.03 in the fall. Dissolved oxygen (% saturation) was supersaturated throughout both seasons (>100 %). Total dissolved solids (g L^{-1}), specific conductivity (μS cm^{-1}), and salinity (p.p.t.) were 0.19 $\pm$ 0.0020 and 0.15 $\pm$ 0.00034, 289.14 $\pm$ 3.10 and 230.48 $\pm$ 2.71, and 0.14 $\pm$ 0.00 and 0.11 $\pm$ 0.00 for the spring and fall, respectively. pH was 7.59 $\pm$ 0.032 in the spring, but instrument error prevented us from obtaining pH for the fall.

Cottonwood study system

We used cottonwoods for three reasons. First, cottonwoods are a foundation species that structure riparian communities throughout the western US (Whitham et al. 2006). Second, trees have been grown in a common garden at the Ogden Nature Center in Ogden, Utah, to isolate species from environmental effects. This common garden was planted in 1991 and consists of known genotypes of both parental species (*P. fremontii* and *P. angustifolia*). Third, leaf quality differences within this system have been well documented; senescent cottonwood leaves vary at the cross type and genotype levels in phytochemistry (e.g., condensed tannins and lignin) (Schweitzer et al. 2004; LeRoy et al. 2006, 2007) and decomposition rates (LeRoy et al. 2006, 2007), with *P. fremontii* leaves demonstrating lower contents of defensive compounds and faster decomposition rates than *P. angustifolia*. Data from the literature for senescent leaf litter demonstrate these differences (Table 1). Narrowleaf leaves have higher tannin, lignin and carbon:nitrogen ratios than Fremont leaves. Nitrogen and phosphorus concentrations are lower on narrowleaf compared to Fremont leaves. Decomposition rates are also significantly lower for narrowleaf relative to Fremont leaves in terrestrial and aquatic environments. Additionally, relative species, cross type, and genotype ranks of most phytochemicals of leaves from this common garden are generally consistent across years (L. M. Holeski, personal communication).

Table 1 Defensive chemistry, nutrient content and decomposition values (k) for senescent Fremont (*Populus fremontii*) and narrowleaf (*Populus angustifolia*) cottonwood leaf litter. Values are means from two studies from different years (LeRoy et al. 2006, 2007)

Variable	*P. fremontii*	*P. angustifolia*
Soluble condensed tannins	0.222 ± 0.0683	9.58 ± 1.41
Lignin (%)	5.20 ± 0.290	20.3 ± 0.915
Carbon:nitrogen	94.7 ± 7.40	90.9 ± 4.46
% Nitrogen	0.460 ± 0.0293	0.503 ± 0.0212
% Phosphorus	0.0583 ± 0.0158	0.134 ± 0.0336
k (day^{-1})	0.0112 ± 0.000856	0.0092 ± 0.000545

Leaf collection

Leaf litter from Fremont and narrowleaf cottonwood was collected from 20 trees in the common garden at the Ogden Nature Center in Ogden during the fall of 2007. Leaves from seven Fremont genotypes ($n = 10$ trees) and ten narrowleaf genotypes ($n = 10$ trees) were collected. Genotypes within a species were mixed together. Whole-tree bridal veil nets, approximately 3.5 m in length, were stapled together as needed to cover the entire circumference of each tree. The corners of nets were tied to upper branches as close to the stem of the tree as possible to prevent leaves from interacting with the ground and to prevent leaves from other trees blowing into the nets. Nets were set in mid-October before changing color and harvested in late November after leaf senescence. No appreciable rainfall occurred during the collection event, minimizing the possibility of leaching or decomposition in nets during harvest; upon collection, leaves appeared relatively dry. Nets were taken inside and leaves were spread out to fully air dry and were stored in the laboratory.

Study design

We compared insect emergence between narrowleaf and Fremont cottonwoods along 5 km of Wet Beaver Creek in the spring and fall of 2008. The spring experiment ran for 8 weeks from April to June and the fall experiment ran for 8 weeks from November to January. Large leaf enclosures (0.5 m × 0.5 m × 0.16 m) ($n = 20$ for the spring and $n = 28$ for the fall) were filled with 150 g of Fremont or 150 g of narrowleaf litter. Leaves were soaked in stream water for 48 h and then leaf enclosures were randomly placed in reaches, paired with each treatment. Enclosures were placed in the river at locations of equal depth (~15 cm), at least 1 m apart, and weighed down with stream cobble for stability.

Leaf enclosures were considerably larger than leaf packs used in other aquatic leaf litter studies, which have generally used small packs (only a few square centimeters) with between 2 and 5 g of leaves. The large, rectangular frames of these enclosures were constructed with ~1.9-cm (outer diameter) PVC pipe wrapped with Vexar (mesh size 10 × 3 mm) on six sides. These leaf enclosures were large enough for us to measure aquatic insect emergence.

Cage effects

Mean flow (±SE) was lower inside (0.19 ± 0.024 m s^{-1}) (paired *t*-test: $t_{14} = 4.9$; $P = 0.0002$) and 1 m downstream (0.23 ± 0.026 m s^{-1}) (paired *t*-test: $t_{14} = 2.6$; $P = 0.021$) of enclosures compared to 1 m upstream (0.35 ± 0.037 m s^{-1}), where flow was not noticeably affected by cages. Flow, however, was not affected by leaf type ($t_{25.8} = 1.1$, $P = 0.28$). Fremont leaves tended to aggregate in layers like wet sheets of paper, leaving little inter-space area between leaves. Leaves of both species also aggregated toward one end of the enclosures, leaving approximately two-thirds of the bottoms of enclosures free of leaf material after leaves had reached neutral buoyancy.

In a separate trial using the same experimental enclosures, we tested for the effects of enclosures on emergent insect abundance and biomass. The purpose of this trial was to determine how much emergence was influenced by the physical structure of the cages themselves as well as by the presence of predators. We had three treatments ($n = 10$ per treatment): empty leaf enclosures (predators excluded), three-sided enclosures (open to predators), and ambient enclosures (open to predators and free of cage effects, allowing for a good estimate of ambient emergence). While this trial could not account for the cage effect of enhanced resource aggregation (i.e., dense aggregates of leaves in enclosures seen in our other trials), it did allow us to estimate the relative effects of both the physical cages and the presence of predators. The experiment ran for 6 weeks in the spring, with emergent insect samples taken weekly, as described for the leaf litter experiment, below.

Emergent insects

Collections were taken by attaching dark microfiber mesh nets to leaf enclosures at water level; attached to the tops of the nets were clear, Plexiglass containers filled with ~100 mL of 70 % ethanol. Emergent insects traps were set weekly for 48 h, for a total of seven harvests per season. Collections involved removing the clear, alcohol containers and transferring the ethanol and emergent insects into 250-ml cups. Samples were taken to our lab and stored in 70 % ethanol. Insects were sorted at 2× magnification and then identified down to the lowest taxonomic level possible (usually genus) using Lecia MZ75 dissecting microscopes at magnifications between 6.3× and 50×. Insects that

could not be identified using aquatic insect keys (e.g., Merritt and Cummins 1996) were morphotyped. Counts and lengths of each insect taxa were recorded. In total, we censused 73,669 insects from 49 families and ten orders in the spring and 12,164 insects from 27 families and seven orders in the fall. A reference collection was made and archived at the Center for Biodiversity at Northern Arizona University. Biomass was calculated using known length-mass algorithms developed specifically for emergent aquatic insects (see Sample et al. 1993; Sabo et al. 2002).

Decomposition

Remaining leaves and aquatic insects from enclosures were collected after the final emergent insect collection in both the spring and fall. Leaf enclosures were processed within 48 h of harvesting. Sediment and invertebrates were sieved through 250-lm nets for preservation in 70 % ethanol. Remaining leaf material was rinsed with deionized water and dried at 70 °C for 96 h. Dried leaf material was weighed and ground in a Wiley Mill to 425 μm. Ground material was combusted at 550 °C in a muffle furnace (Barnstead International, Dubuque, IA) for 1 h to determine ash-free dry mass (AFDM) according to the methods of Benfield (2006).

Statistical methods

We used a mixed model repeated measures ANOVA (rmANOVA) with the method of moments expected means squares (EMS) estimation (for repeated measures data with an unstructured covariance matrix) in JMP version 9.0 (SAS Institute, 2010) to test whether dependent variables differed between treatment groups. The model included the fixed effects of Treatment (Fremont or narrowleaf), Time (sampling day) and treatment × time interaction. Additionally, the random, nested effect Sample(Treatment) was the effect of the leaf enclosure (i.e., the station in the stream) and the subject for the repeated measures design. The Model term [only reported in electronic supplementary material (ESM)] represented the total effect and fit of each rmANOVA model. We ran separate tests for insect abundance, biomass, species richness and diversity (Shannon's H). Additionally, we used rmANOVA to determine how abundance and biomass of EPT taxa and functional feeding groups differed between treatments. Plecoptera taxa were not analyzed for the spring due to their rarity. Several small floods occurred in the first several weeks of the fall experiment, so statistical analyses were also conducted for only post-flood harvest dates. Excluding the first few weeks only changed the outcomes of shredder biomass and abundance and Plecoptera and Trichoptera abundance.

Abundance and biomass data were $\log_{10}$ transformed when needed to meet the assumptions of normality and sphericity for rmANOVA (Sokal and Rohlf 1995; see ESM). As there were no instances where abundance or biomass samples had zero values (i.e., all samples had at least one individual and usually many), we did not need to add constants to any of the $\log_{10}$-transformed data. We tested normality on residuals from our overall rmANOVA models for each response variable. Mauchly's W was used to test for sphericity in rmANOVA. When the assumption of sphericity could not be met for rmANOVA models, we adjusted the df following the Greenhouse-Geisser adjustment (Sokal and Rohlf 1995). We did not use Bonferroni corrections for any of the rmANOVA analyses because this often inflates the probability of committing type II errors (Gotelli and Ellison 2004). Parasitoids (composed of only semi-aquatic Hymenoptera taxa from the family Eulophidae) were rare and data could not be normalized for either season, so Wilcoxon/Kruskal–Wallis rank sums tests were conducted on abundance and biomass data totaled across each respective season.

Species richness and diversity (Shannon's H') were calculated [see McCune and Grace (2002) for equations] using PC-ORD version 5 for Windows (MjM Software Design 2010). Additionally, non-metric multi-dimensional scaling (NMDS) using Bray-Curtis distances was conducted using PC-ORD to examine insect community composition. Multi-response permutation procedure (MRPP) tests were conducted in PC-ORD on both raw data and data relativized for taxa abundances to test if community composition differed among treatment groups. NMDS with MRPP compares the observed intra-group average distances with the average distances from all other possible combinations of the data under the null hypothesis test. Indicator species analysis was also conducted in PC-ORD to determine which species drove ordination patterns.

Decomposition was measured using the following exponential decay model:

$$L_f = L_i e^{-kt} \tag{1}$$

where L_f was the AFDM of remaining leaf material at time t, L_i was the AFDM of initial leaf mass from handling packs [as described by Benfield (2006)], and k was the instantaneous decomposition rate constant. Because we only had two time points for decomposition (the initial AFDM of handling packs and the final AFDM of leaf enclosures), we did not have to calculate ks using the method of Benfield (2006), and, instead, solved for k directly:

$$k = ((\ln L_f) - (\ln L_i))/(-t) \tag{2}$$

Decomposition rate constants k (day^{-1}) were then compared between treatments using Student's t-tests in JMP version 9.0.

Results

Emergence abundance

Contrary to our first prediction, narrowleaf enclosures had 25 % more total emergent insect abundance (insects $m^{-2} day^{-1}$) than Fremont leaf enclosures in the spring (rmANOVA: $F_{1,106} = 4.7$, $P = 0.032$; Fig. 1a). In the fall, however, Fremont enclosures yielded 15 % more total emergent insects, but these differences were not significant (rmANOVA: $F_{1,133} = 1.3$, $P = 0.25$; Fig. 1b). Mean emergent abundance was approximately five times higher in the spring compared to the fall (rmANOVA: Season, $F_{1,251} = 420$, $P < 0.001$; Fig. 1). For both seasons, chironomids were dominant, making up 92.6 % of insect emergence in the spring and 97.8 % of insect emergence in the fall. Emergent chironomids were more abundant from narrowleaf compared to Fremont enclosures for the spring (rmANOVA: $F_{1,106} = 6.6$, $P = 0.012$), but not the fall (rmANOVA: $F_{1,133} = 1.3$, $P = 0.26$).
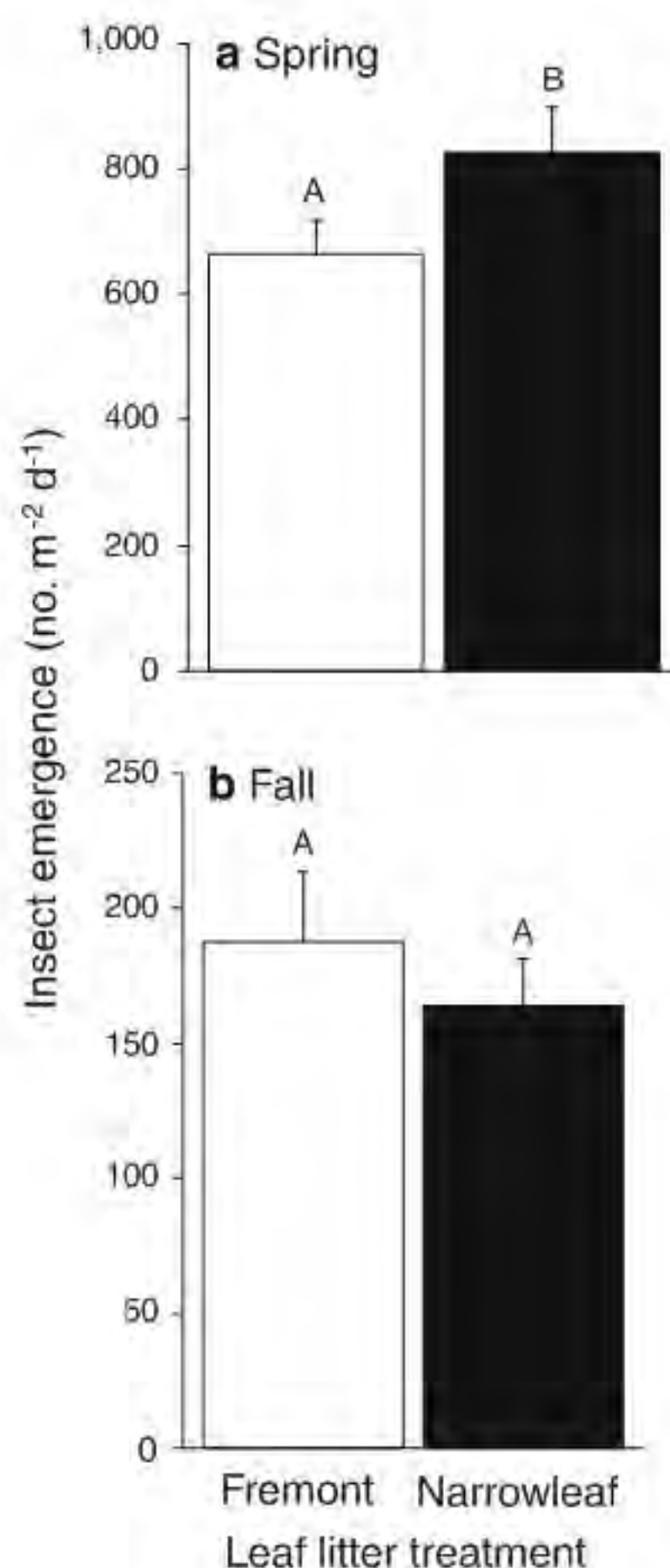

Fig. 1 Insect emergence (mean + 1SE no. m^{-2} day^{-1}) for **a** spring and **b** fall leaf litter treatments of Fremont (*white bars*) and narrowleaf (*black bars*) cottonwood. *Different letters* above bars designate statistical differences using repeated measures ANOVA (rmANOVA) at $P \leq 0.05$ (Electronic supplementary material; ESM)

In the spring, emergence of collector-gatherers (insects $m^{-2} day^{-1}$) was higher on narrowleaf compared to Fremont leaves (rmANOVA: $F_{1,106} = 7.9$, $P = 0.0060$; Fig. 2a), but collector-filterer emergence was higher on Fremont leaves (rmANOVA: $F_{1,133} = 15$, $P < 0.001$; Fig. 2a). In the fall, shredder emergence was more abundant from narrowleaf enclosures for the post-flood collection dates (rmANOVA: $F_{1,21} = 5.3$, $P = 0.032$; Fig. 2b). Ephemeroptera, Plecoptera, and Trichoptera (EPT) emergence did not differ among treatment groups in the spring (Fig. 3a; ESM, Appendix 1) or fall (Fig. 3b; ESM, Appendix 1), but post-flood dates in the fall yielded higher Plecoptera emergence from narrowleaf enclosures (rmANOVA: $F_{1,21} = 5.3$, $P = 0.032$; Fig. 3b) and higher Trichoptera emergence from Fremont enclosures (rmANOVA: $F_{1,40} = 7.5$, $P = 0.0094$).

Emergence production

Emergence production (mg insects $m^{-2} day^{-1}$) followed the same general patterns as the abundance data, but the patterns were weaker. Overall, our estimated mean production ($\pm$SE) was 187 ± 17.3 mg $m^{-2} day^{-1}$ from Fremont packs and 217 ± 21.1 mg $m^{-2} day^{-1}$ from narrowleaf packs in the spring and 64.7 ± 6.44 mg $m^{-2} day^{-1}$ from Fremont packs and 60.0 ± 6.22 mg $m^{-2} day^{-1}$ from narrowleaf packs in the fall. In the spring narrowleaf enclosures yielded 16 % more emergence biomass than Fremont packs, but these differences were not significant (rmANOVA: $F_{1,106} = 2.5$, $P = 0.11$). In the fall, Fremont enclosures yielded 8 % more emergence biomass than narrowleaf packs, but these differences were not statistically significant (rmANOVA: $F_{1,133} = 2.02$, $P = 0.16$). Emergence biomass of functional feeding groups and EPT taxa responded in the same way as abundance, but these patterns were also weaker. In the spring, collector-filterer emergence biomass (mg insects $m^{-2} day^{-1}$) was higher from Fremont enclosures (rmANOVA: $F_{1,106} = 9.1$, $P = 0.0031$; Fig. 2c), but collector-gatherer emergence biomass was higher from narrowleaf enclosures (rmANOVA: $F_{1,106} = 4.2$, $P = 0.040$; Fig. 2c). In the fall, shredder emergence biomass was higher from narrowleaf compared to Fremont enclosures for the post-flood harvests (rmANOVA: $F_{1,21} = 7.2$, $P = 0.014$; Fig. 2d), which was consistent with abundance patterns. Mean emergence production of EPT taxa showed different patterns than those of abundance. In the spring, no differences were found among treatments for Ephemeroptera taxa (rmANOVA: $F_{1,106} = 0.27$, $P = 0.60$), but Fremont enclosures yielded more Trichoptera biomass (rmANOVA: $F_{1,106} = 4.1$, $P = 0.045$). Insufficient Plecoptera emerged in the summer for statistical analyses. In the winter, no differences in emergence production were seen among
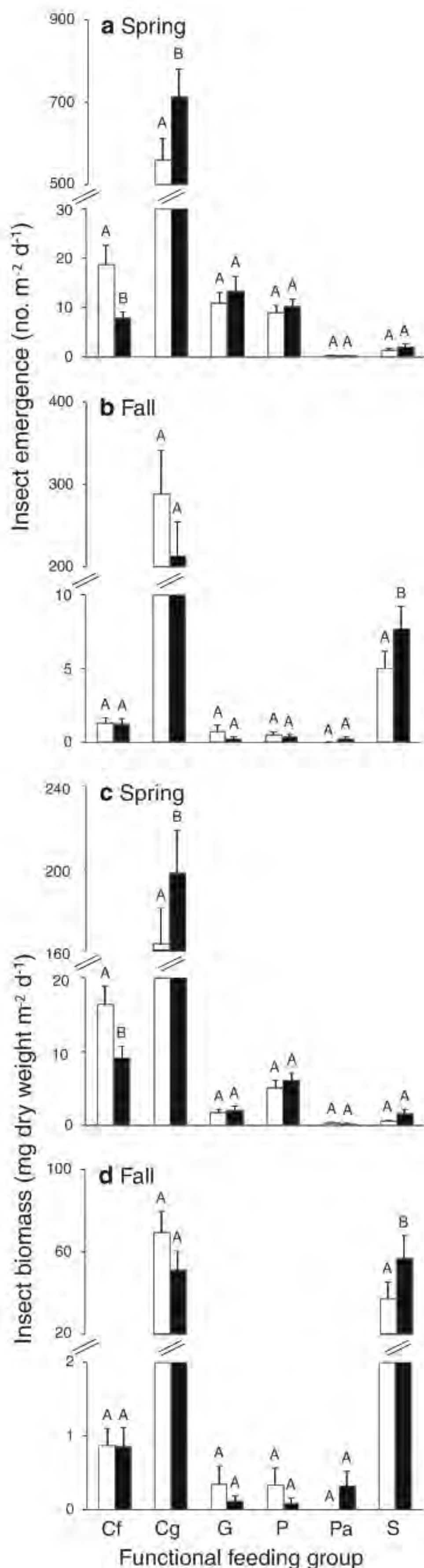
◄ **Fig. 2 a, b** Insect emergence (mean + 1SE no. $m^{-2} day^{-1}$) of aquatic insect functional feeding groups (FFG) and **c, d** biomass (mean + 1 SE mg dry mass $m^{-2} day^{-1}$) for **a, c** spring and **b, d** fall leaf litter treatments of Fremont (*white bars*) and narrowleaf (*black bars*) cottonwood. FFGs included collector-filterers (*Cf*), collector-gatherers (*Cg*), grazers (*G*), predators (*P*), parasitoids (*Pa*), and shredders (*S*). **b, d** Post-flood dates only. *Different letters* above bars designate statistical differences using rmANOVA or Wilcox/Kruskal–Wallis rank sums tests (for parasitoids) at $P \leq 0.05$ (ESM)

treatments for Ephemeroptera, Plecoptera, or Trichoptera (ESM).

Community composition and diversity

In contrast to our third prediction, diversity (Shannon's H') was higher on Fremont compared to narrowleaf enclosures in the spring (rmANOVA: $F_{1,106} = 6.9$, $P = 0.0099$; Fig. 4c), although there were no differences in the fall (ESM). The same patterns were observed for evenness (Simpson's E), which was higher on Fremont compared to narrowleaf packs in the spring (rmANOVA: $F_{1,106} = 8.0$, $P = 0.0056$; Fig. 4b), but not the fall (ESM). Species richness did not differ in the spring (rmANOVA: $F_{1,106} = 0.011$, $P = 0.92$) or fall (rmANOVA: $F_{1,133} = 0.84$, $P = 0.36$; Fig. 4a). Overall, community patterns did not differ between enclosures in the spring (MRPP: $A = -0.016$, $P = 0.65$), fall (MRPP: $A = -0.023$, $P = 0.60$) or post-flood dates in the fall (MRPP: $A = -0.020$, $P = 0.74$). Relativizing the data by taxa abundances did not changes these patterns. Only one indicator taxa was found, a single morphospecies of Hydropsychidae, in the spring (indicator value = 51, $P = 0.036$).

Cage effects

We found a significant treatment effect on log10-transformed abundance (insects $m^{-2} day^{-1}$) (rmANOVA: $F_{2,173} = 25$, $P < 0.0001$), with Tukey honest significant difference (HSD) post hoc comparisons ($\alpha = 0.05$) revealing ambient treatments had two to three times significantly fewer emergent insects (means ± SEs) (165.8 ± 24.9) than the no-leaf (485.4 ± 62.5) and three-sided (340.8 ± 31.2) treatments, respectively. No-leaf and three-sided treatments were not statistically different for emergence abundance. Emergence production (mg insects $m^{-2} day^{-1}$) followed the same basic pattern (rmANOVA: $F_{2,173} = 3.3$, $P < 0.039$), with Tukey HSD post hoc comparisons ($\alpha = 0.05$) revealing ambient treatments had ∼3.5 times lower biomass (means ± SEs) (15.7 ± 3.5) compared to no-leaf treatments (57.9 ± 20.1). Three-sided treatments (17.8 ± 3.4) were not significantly different from no-leaf or ambient treatments for emergence production.
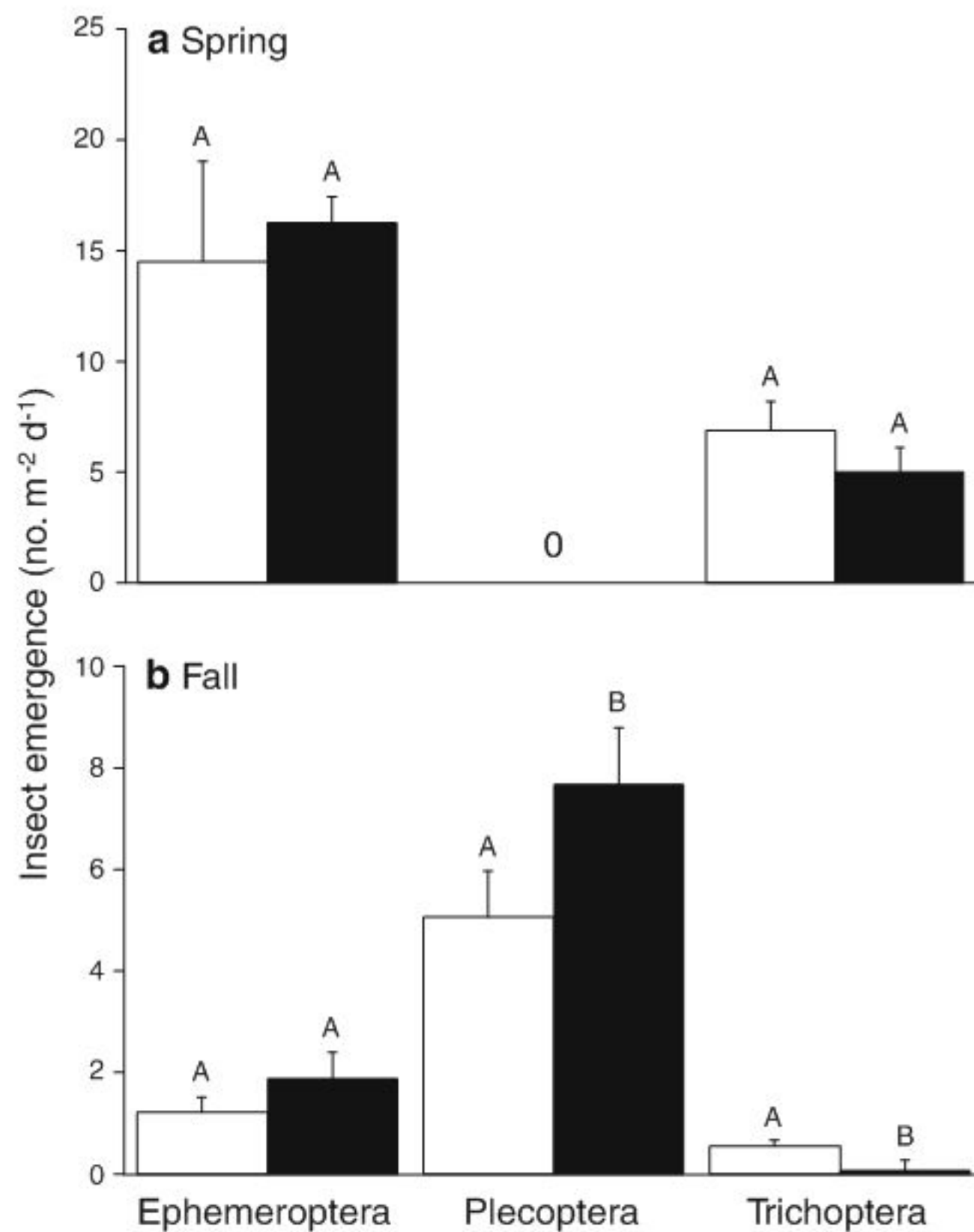
Fig. 3 Insect emergence (mean + 1SE no. m^{-2} day^{-1}) of Ephemeroptera, Plecoptera and Trichoptera taxa for **a** spring and **b** fall leaf litter treatments of Fremont (*white bars*) and narrowleaf (*black bars*) cottonwood. No Plecoptera taxa were sampled in the spring (**a**), so no data are shown. **b** Post-flood dates only. *Different letters* above bars designate statistical differences using rmANOVA at $P \leq 0.05$ (ESM)

Fig. 4 **a** Species richness, **b** evenness (Simpson's *E*), and **c** diversity (Shannon's *H'*) for spring leaf litter treatments of Fremont (*white bars*) and narrowleaf (*black bars*) cottonwood (mean + 1SE). *Different letters* above bars designate statistical differences using rmANOVA at $P \leq 0.05$ (ESM)

Decomposition

Fremont litter decomposed ~67 % faster than narrowleaf litter in the spring ($t_{3.0} = -4.2$, $P = 0.025$), when mean decomposition (k, day^{-1}) ($\pm$SE) was 0.0731 ± 0.00405 for Fremont litter and 0.0439 ± 0.00565 for narrowleaf litter. Mean leaf litter half-life ($\pm$SE) for the spring was 9.48 ± 0.525 days and 15.8 ± 2.03 days for Fremont and narrowleaf, respectively. At the end of the spring experiment, only 1.7 % of initial Fremont litter remained, compared to 9.5 % of initial narrowleaf litter. In the fall, decomposition was not different between Fremont and narrowleaf litter ($t_{18.4} = 0.91$, $P = 0.37$). Mean decomposition (k, day^{-1}) ($\pm$SE) in the fall was 0.0248 ± 0.00212 for Fremont litter and 0.0284 ± 0.00332 for narrowleaf litter. Mean leaf litter half-life ($\pm$SE) for the fall was 27.9 ± 2.39 and 24.4 ± 2.85 days for Fremont and narrowleaf, respectively. At the end of the fall experiment, 26 % of initial Fremont litter and 24 % of initial narrowleaf litter remained.
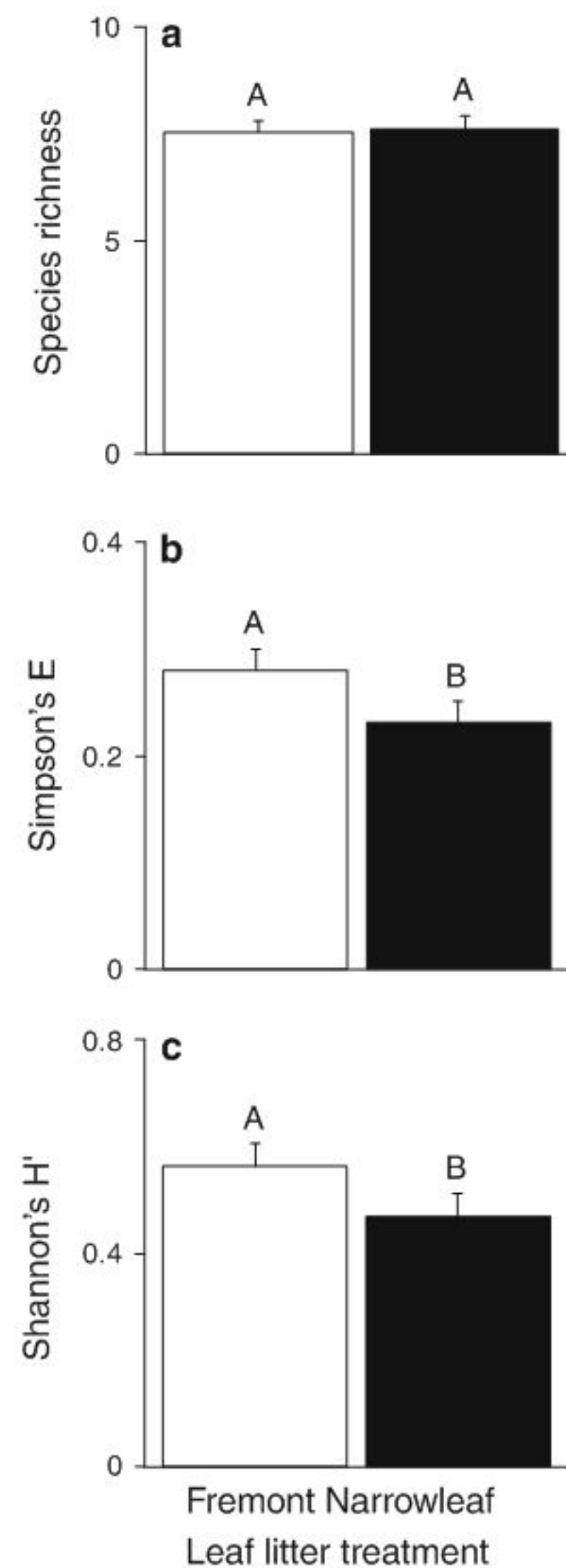
Seasonal and temporal dynamics of emergence

While there were strong seasonal (see above) and temporal (ESM) effects on emergence, effects of leaf quality on emergence did not change through time, as noted by the lack of treatment × time interactions in either of our studies (ESM). Instead, the flood regime dictated overall temporal emergence patterns (i.e., the large amount of significant Time effects in the rmANOVA models), with emergence generally lower after spates and floods. In spite of these flood events, leaf quality differences generally persisted throughout the experiment, with similar relative differences before and after floods (as noted by the lack of treatment × time interactions in our two studies). This was also seen visually when plotting our data, especially in the

spring (data not shown); narrowleaf treatments were always relatively higher than Fremont treatments, though week-to-week overall abundance changed with the flood regime (i.e., there were pronounced dips after spates and floods). While decomposition was higher in Fremont enclosures in the spring, total emergence abundance differences persisted even when the final two dates (weeks 7 and 8, when relatively little leaf material of either species remained) were removed from the analysis (rmANOVA: $F_{1,88} = 4.7$, $P = 0.034$), with narrowleaf significantly higher than Fremont.

Discussion

Slow-decomposing litter increased aquatic insect emergence

The prediction that faster decomposing Fremont (*P. fremontii*) litter, which has lower contents of defensive compounds (e.g., tannins and lignin) compared to narrowleaf (*P. angustifolia*) litter (see Table 1), would yield higher insect abundance was not supported; *P. angustifolia* litter produced more emergent insects in the spring. We pose three hypotheses to help explain this result—the first, our main hypothesis, and two other alternative hypotheses:

(a) Physical leaf structure, which provided habitat and protection from predators, was more important than other leaf attributes (i.e., leaf phytochemistry and nutrient content).

(b) Compounds in fast-decomposing litter were leached out in the form of dissolved organic carbon (DOC) before they were available to aquatic insects.

(c) Leaf quality mediated differences in microbial colonization such that microbial assemblages on narrowleaf leaves were more nutritious.

The most likely hypothesis as to why narrowleaf produced more insects than Fremont leaves is that emergence was driven more by structural leaf attributes than phytochemical and nutritional differences. We believe structural leaf attributes drove emergence patterns in our study for two reasons. First, leaf litter decomposition rates were very high, especially in the spring, where only ~2 % of Fremont litter versus ~10 % of narrowleaf litter remained at the end of the 8-week study. Consequently, there was very little resource left in Fremont compared to narrowleaf enclosures at the end of the experiment. Additionally, there were probably large differences in the available habitat remaining in the enclosures. When wet, Fremont leaves stick together in large, paper-like sheets with few interspaces between, whereas narrowleaf leaves have more heterogeneous aggregates, likely providing more habitat

for small larval insects. Second, emergence was dominated by collector-gatherer taxa that probably did not consume leaf litter in the enclosures but, rather, used it as habitat. Taken together, then, we believe our results were driven largely by physical factors of the leaves and their enclosures, but that our treatment differences were robust.

An alternative, but not mutually exclusive, hypothesis as to why narrowleaf litter produced more emergent insects than Fremont litter is that emergence was also driven, in part, by differences in leaf chemistry. Because Fremont leaves have higher leaching rates relative to narrowleaf leaves (Compson et al., unpublished data), it is possible compounds were leached out of Fremont litter before they could be utilized by aquatic insects. For example, our finding that abundance and biomass of collector-filterer taxa were higher on Fremont leaves while collector-gatherer and shredder biomass and abundance were higher on narrowleaf leaves could have been due to high leaching rates and fast breakdown of Fremont leaves. Fremont leaves leach significantly more DOC and contain higher bacterial abundance compared to narrowleaf leaves, which have relatively higher fungal abundance (Wymore et al., unpublished data), and Simuliidae blackfly larvae (which made up >95 % of our collector-filterer emergence) utilize dissolved organic matter (Ciborowski et al. 1997) and bacterial extracellular polysaccharides (Couch et al. 1996). While the travel distance of microbes is long in streams, our enclosures significantly reduced flow compared to stream flow (see "Materials and methods"), which meant there were likely greater concentrations of fine particulate organic matter (FPOM) in fast-decomposing Fremont litter enclosures. Collector-filterer taxa, then, might have been able to take advantage of FPOM and associated bacteria coming from Fremont leaves, whereas collector-gatherers and shredders likely needed both the structure and long-term carbon availability afforded by more recalcitrant narrowleaf leaves.

Differences in microbial colonization between leaf types might also have explained some of the observed differences in emergence. Fungi, which are more abundant on decomposing narrowleaf compared to Fremont litter, modify leaf litter physico-chemistry, rendering leaves more palatable and increasing leaf quality to shredders; consequently, they are expected to have a greater role than bacteria in leaf breakdown of slow-decomposing leaves (van der Heijden et al. 2008). Hyphae allow fungi to bypass the more recalcitrant outer leaf layers and form hyphal bridges, allowing them to alleviate nutrient limitations of leaf decomposition through reallocation of nutrients (Hendrix et al. 1986; Holland and Coleman 1987). Fungi can readily break down lignin, cellulose and hemicellulose (reviewed by de Boer et al. 2005). Additionally, fungi themselves can provide more nutrition to aquatic shredders

compared to bacteria (see Findlay et al. 1986). Shredders (and perhaps detrital scrapers and some collector-gatherers) then, can take advantage of fungi by direct consumption or accessing these reallocated nutrients from slowly decomposing leaves. Consequently, slow-decomposing leaves likely provide a more stable resource through time.

High emergence production likely caused by cage effects

Our emergence production estimates were two to six times higher than those estimated in Sycamore Creek, Arizona, a low-elevation desert stream very close to our study site (34.2 ± 10.3 mg m^{-2} day^{-1}) (Grimm 1987). Another estimate of emergence production from Sycamore Creek was 58.4 mg m^{-2} day^{-1} (Jackson and Fisher 1986). Emergence production estimates from cooler streams are even lower. For example, emergence production from a tallgrass prairie stream was 20.3 mg m^{-2} day^{-1} (Gray 1989). Additionally, Iwata (2007) reported even lower total emergence production for pools (11.7 ± 6.3 mg m^{-2} day^{-1}) and riffles (2.6 ± 2.4 mg m^{-2} day^{-1}) for a stream in northern Japan.

The exceptionally high emergence production from leaf enclosures was likely due to cage effects caused by the high concentration of leaf litter and low predation pressure inside enclosures. These conditions probably constituted a favorable habitat and artificially increased immigration of insects into enclosures. While this would not, by itself, explain the differences between Fremont and narrowleaf treatments, these cage effects could have interacted with the differential decomposition rates to overestimate differences between the treatments, especially toward the end of the experiment when very little Fremont litter remained. Although small-scale enclosure experiments on benthic invertebrates tend to be driven by emigration dynamics (Cooper et al. 1990), the direction of effects can be extrapolated to larger scales and may even underestimate treatment effects (Kohler and Wiley 1997). Secondary production of functional feeding groups can be influenced by the physical characteristics of mesoscale stream habitats (e.g., bedrock outcrops, riffles and pools), which determine resource availability and mode of delivery to consumers (Huryn and Wallace 1987; Iwata 2007), ultimately influencing aquatic insect emergence and web-building spider abundance (Iwata 2007). Additionally, structures providing both predation refuge and food for aquatic insects (e.g., floating algal mats) can enhance local emergence (Power and Rainey 2000; Power et al. 2004).

Leaf enclosures used in this experiment created a buffet for insects, with dense resource aggregates (i.e., leaf litter in enclosures) compared to the rest of the stream, sheltering insects from the effects of most predators. Our cage effects trial suggests cage effects were driven largely by reduced flow and resource aggregation in cages, and not by the exclusion of predators. That said, leaf enclosures might have simply induced deposition of passively drifting insects (e.g., midges) that spent a relatively small amount of time as larvae in the cages before emerging; this could be why there was so much variation among the different taxonomic groups. We believe, then, that while our treatment-level results (i.e., *P. fremontii* vs. *P. angustifolia* litter) are robust, our emergence production estimates largely over-estimate actual fluxes to the riparian zone and are not truly comparable to whole-stream emergence rates.

Fast-decomposing leaves yield higher emergent insect diversity

Our third prediction, that diversity would be higher on narrowleaf litter treatments, was not supported. In spite of the findings that narrowleaf litter had higher bacterial and fungal diversity compared to Fremont litter (Marks et al. 2009), we found that emergent insect diversity was higher on Fremont litter treatments. One explanation for these contrasting patterns is that narrowleaf litter, which could provide more nutrition and habitat for aquatic insects, as discussed above, attracted a competitive dominant (in our case, collector-gatherer chironomids) that lowered diversity in these treatments by depressing other taxa.

Our finding that chironomids were dominant, making up 92.6 and 97.8 % of emergent insect abundance in the spring and fall, respectively, is consistent with other studies that have found chironomid midges made up 96 % of the abundance and 98 % of the biomass in shallow wetlands in the southeastern US (Stagliano et al. 1998), 59.7 % of the abundance and 48.2 % of the biomass in Sycamore Creek (Jackson and Fisher 1986), and 51.0 % of the abundance and 34.9 % of the biomass in lowland streams of northern Australia (Lynch et al. 2002).

Seasonal and temporal dynamics mediate differences in leaf quality

Higher insect emergence in the spring relative to the fall experiment was likely due to temperature differences and timing of life cycles of aquatic insects. The difference between leaf litter treatments was more prominent in the spring when decomposition rates were higher. In the fall, leaves decomposed more slowly and likely provided more time for insects to colonize and utilize faster-decomposing Fremont leaves. Additionally, the fall sampling period experienced much higher precipitation and stream flows compared to the spring, which was typical for the study area during this time of year. In particular, several large spates occurred during the late fall and early winter which visibly moved leaf enclosures and seemed to reset the

emergence insect communities in enclosures (Z. G. Compson, personal observation). These high flow events likely washed out treatment differences for emergent insects and decomposition in the fall.

Though our experiments ran for a relatively long time (8 weeks), temporal patterns were largely driven by stochastic flooding events occurring in both the spring and the fall, and not by changes in the leaves themselves (i.e., mass loss, conditioning) over time. Two lines of evidence lead us to this conclusion. First, while our statistical analyses showed many significant Time effects, there were no treatment × time interactions in either the spring or fall studies (ESM). Second, while relatively little leaf litter of either species remained in the enclosures at the end of the spring sampling period, when we eliminated the last two dates (weeks 7 and 8) from our analysis, our total emergence abundance results did not change. Thus, while leaf quality is surely changing through time (in terms of conditioning and availability), these changes are not affecting overall emergence patterns, which, as a whole, are governed by the flood regime, even though relative leaf-type differences persist during and after flooding.

A restoration context

Our results demonstrate that leaf quality is not a simple function of decomposition and that emerging insects respond differently to leaf attributes. Although overall abundance was higher on narrowleaf leaves, diversity of emergent insects was higher on Fremont leaves. Additionally, there were differing patterns for functional feeding groups and taxonomic groups, with some preferring Fremont but most preferring narrowleaf leaves. In this system, aquatic insects benefit from fast-decomposing leaves, which promote diversity; terrestrial predators, however, while not measured in this study, may have access to a larger subsidy from slow-decomposing leaves, which yield more emergent insects. These results mirror those found in streams of British Columbia, where a coniferous-dominated watershed yielded higher abundance but a deciduous-dominated watershed yielded higher diversity of emergent insects (Kominoski et al. 2012). Because aquatic insects feed back to affect the adjacent forest, small leaf quality consequences could reverberate to affect the riparian forest, where emergent insects can provide 25–100 % of the requisite energy or carbon to coupled riparian predators (e.g., birds, bats, lizards, and spiders) seasonally (Baxter et al. 2005). Although the scope of this study precluded direct measurement of predation rates, the ~25 % higher emergence subsidy from slowly decomposing leaves could have major impacts on riparian predators at reach and watershed scales, especially over long periods of time.

Understanding how leaf quality influences emergent insect communities is important in the context of expensive restoration projects that often overlook the species and genetic diversity of riparian plantings. Yet genetic identity (Crutsinger et al. 2008; Keith et al. 2010) and genetic diversity (Crutsinger et al. 2008; Wimp et al. 2004) of host plants have been shown to influence associated insect communities, diversity or trophic levels. With $10 billion spent on river restoration in North America in the past decade (Bernhardt et al. 2005), it is imperative that we understand how riparian restoration plantings will influence aquatic and terrestrial ecosystem processes. Knowledge about how riparian tree identity (at species, hybrid, and genotype scales) influences aquatic and terrestrial ecosystem processes will enable land managers to optimize restoration plantings. Furthermore, by planting a diverse assemblage of trees, managers will provide aquatic ecosystems with a diverse suite of resources that can maximize aquatic species diversity and subsidies to adjacent forests, preserving important ecosystem functions in both systems.

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