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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Tree leaf litter composition drives temporal variation in aquatic beetle colonization and assemblage structure in lentic systems

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Abstract Tree leaf litter inputs to freshwater systems are a major resource and primary drivers of ecosystem processes and structure. Spatial variation in tree species distributions and forest composition control litter inputs across landscapes, but inputs to individual lentic habitat patches are determined by adjacent plant communities. In small, ephemeral, fishless ponds, resource quality and abundance can be the most important factor affecting habitat selection preferences of colonizing animals. We used a landscape of experimental mesocosms to assess how natural populations of aquatic beetles respond over time to variation in tree leaf litter composition (pine or hardwood). Patches with faster-decomposing hardwood leaf litter were initially colonized at higher rates than slower-decomposing pine pools by most species of Hydrophilidae, but this pattern reversed later in the experiment with higher colonization of pine pools by hydrophilids. Colonization did not differ between pine and hardwood for dytiscids and the small hydrophilid *Paracymus*, but there were distinct beetle assemblages between pine and hardwood patches both early and late in the experiment. Our data support the importance of patch quality and habitat selection as determinants of species abundances, richness, and community structure in freshwater aquatic systems, not only when new habitat patches are formed and initial conditions set, but as patches change due to interactions of processes such as decomposition with time.

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Introduction

Ecosystem structure and function are strongly influenced by resource inputs, the assimilation, processing, and transfer of resources, and the interactions among organisms in food webs (Polis et al. 1997; Marcarelli et al. 2011; Stoler and Relyea 2013). Allochthonous inputs of organic matter derived primarily from plant litter drive ecosystem processes and productivity in nutrient-limited freshwater systems (Minshall 1967; Polis et al. 1997; Stoler et al. 2016). These inputs are important resources for invertebrates and other aquatic taxa (Anderson and Sedell 1979) and provide energy and nutrients not only directly to scavengers and decomposers, but also indirectly to herbivores and predators by stimulating primary and secondary productivity (Wilbur 1997; Williams 2005). Total dissolved organic carbon in streams can originate nearly exclusively (99%) from tree litter (Fisher and Likens 1973), supporting higher levels of productivity than autochthonous resources can provide alone (Polis et al. 1997). Although leaf litter inputs are also important carbon sources in lentic systems (Rubbo et al. 2006, 2008; Stoler and Relyea 2011), work has focused primarily on lotic systems (Fisher and Likens 1973; Wallace et al. 1997; Meyer et al. 1998). Spatial subsidies, in both lotic and lentic systems, provide links between habitats, maintain ecosystem function, act as ecosystem services, and support the open nature of many systems (Polis et al. 1997; Loreau and Holt 2004; Earl and Semlitsch 2013).

Interspecific differences among plants in the composition of their primary (involved in growth and development) and secondary compounds (not direct contributors to metabolism), and the chemical composition of living and senesced foliage, results in variation in rates of decomposition, herbivory, and flow of energy from plant matter through food webs (Webster and Benfield 1986; Facelli and Pickett 1991; Scott and Binkley 1997). Variation in litter quality can manifest itself via a variety of characteristics, including nutrient and lignin content, breakdown rate, structural complexity, and leeched secondary compounds, among others (Melillo et al. 1982; Ostrofsky 1997; Swan and Palmer 2006). Among woody plant inputs to aquatic systems, Pinaceae often have slower breakdown rates and Tiliaceae, Magnoliaceae, and Cornaceae faster, whereas other families have intermediate rates, although breakdown rates are often context-dependent (Webster and Benfield 1986). Chemical characteristics of leaf litter can drive microbial activity, both promoting and inhibiting microbial growth, influence physical breakdown of leaf litter and assimilation of litter-derived resources, and inhibit the detection of prey chemical cues (Rubbo and Kiesecker 2004; Maerz et al. 2005; Williams et al. 2008).

Effects of litter composition can be context-dependent, for example, driving differences in species richness in open canopy locations, but not under forest canopy (Deans and Chalcraft 2017). Although associations between litter quality/quantity and species richness of colonizing animals have been observed in lentic (Kok and Vanderveld 1994; Yanoviak 1999; Reiskind et al. 2009; Stoler and Relyea 2011) and lotic systems (Short et al. 1980; Richardson et al. 2004; Egglishaw 2011), other studies in both systems have shown little or no association (Batzer and Wissinger 1996; LeRoy and Marks 2006; Earl and Semlitsch 2013). Furthermore, studies of the effects of litter composition on colonization and structure of aquatic communities have typically focused on snapshots in time in natural communities or endpoints in experiments, with little consideration of temporal variation and the interaction of litter composition with time. Therefore, understanding the full effects of litter composition on aquatic community structure requires assessment of both a greater range of conditions and over time, with more consideration for short-term changes in community responses to the temporal dynamics of litter breakdown.

Given differences in community composition and individual performance in habitats with varying composition of litter inputs, colonizing animals would be expected to exhibit habitat selection preferences that match their performance (expected fitness) (Resetarits 1996; Vonesh et al. 2009; Pintar and Resetarits 2017). In habitat selection theory, patch-specific colonization rates are driven largely by patch quality (Fretwell and Lucas 1970). Variation in composition of litter inputs creates discrete spatial variation in habitat quality in lotic systems because of the closed nature of these systems. Litter composition therefore generates, along with myriad other factors (predator presence, pond area and depth, community composition, etc.), landscapes that are mosaics of habitat patches varying in quality. Habitat selection, a behavioral process, co-determines patterns of local species abundance and diversity along with post-colonization processes (predation, competition), and effects of pre-colonization habitat selection can exceed those of post-colonization sorting (Binckley and Resetarits 2005; Resetarits and Binckley 2009; Vonesh et al. 2009). Understanding the roles of habitat selection and habitat quality in dispersal, and in population and metacommunity dynamics, has increased in importance in ecology and conservation biology in the context of both local and global environmental changes, particularly habitat alteration and climate change (Mortelliti et al. 2010; Doerr et al. 2011).

A useful study system for understanding population and metacommunity dynamics are aquatic beetles, which can form diverse assemblages that dominate in freshwater habitats that are typically small, ephemeral, fishless, and depend on colonization by organisms from other habitats (Jeffries 1994; Schneider and Frost 1996; Fairchild et al. 2000, 2003). These taxa, predominantly those in the families Dytiscidae (predaceous adults, predaceous larvae) and Hydrophilidae (omnivorous adults, predaceous larvae), play important ecological roles in freshwater aquatic communities, and adults select habitats both for themselves and their offspring (Layton and Voshell 1991). To determine how habitat selection of dispersing beetles is influenced by leaf litter composition as ponds age, we examined the effects of leaf litter composition on the dynamics of colonization and the assemblage structure of natural populations of aquatic beetles. We conducted a field experiment using mesocosms with two types of leaf litter (hardwood and pine) and collected colonizing beetles. We hypothesized that colonization by beetles would initially be higher in pools with hardwood leaf litter compared to pools with pine leaf litter due to faster breakdown of hardwood litter than pine litter, but that these differences would disappear over time.

Materials and methods

On 06-June-2014 we set up a 4 × 8 rectangular array of experimental mesocosms (plastic wading pools: 1 m diameter, 0.2 m deep, 110 L, $N = 32$) in a dry pond basin with open canopy at the University of Mississippi Field Station (UMFS) near Oxford, MS, USA (34°25′4″N, 89°23′32″W). The study site was situated at the intersection of bottomland hardwood forest, mixed upland forest, and adjacent wetlands. Pools were filled with water from a nearby spring-fed stream and covered with window screening (1.3 mm^2, 1.13 mm opening) that was depressed below the water surface to separate all but the smallest colonizing beetles (*Paracymus* and *Uvarus*) from leaf litter. Two treatments (16 replicates each, $N = 32$), 0.5 kg dry hardwood leaf litter (primarily *Fagus grandifolia* and *Quercus* spp. with *Acer rubrum*) or 0.5 kg dry pine leaf litter (*Pinus taeda*), were alternated between pools so no pools of the same treatment were adjacent (0.5 m apart at edge). Treatments represent commonly occurring leaf litter assemblages at UMFS. *Pinus taeda* often occurs in monotypic stands whereas *F. grandifolia* and *Quercus* spp. co-dominate hardwood stands in the uplands down to pond edges in the valleys. *Acer rubrum* occurs with *F. grandifolia* and *Quercus* spp. in the transition between bottomland and upland forest.

There are 115 known species of aquatic beetles at UMFS representing eight families, and 94 of these species have been observed colonizing experimental mesocosms (unpublished data). Beginning on 09-June, we collected all adult beetles without replacement weekly with fine mesh nets by removing all colonizing beetles from above the screens (collection dates: 09, 16, 24-June and 01, 08, 15, 22, 29-July), and the experiment was terminated on 29-July. All beetles were preserved in ethanol and identified to species. Due to small size (~2 mm total length) and abundance, not all *Paracymus* were identified to species. Most *Paracymus* identified from UMFS have been *P. subcupreus*, with some *P. confusus* and *P. nanus*.

We analyzed the effect of treatment over time and block (row = distance from north to south) on total beetle abundance, beetle species richness, and abundances of Dytiscidae, Hydrophilidae, and species with total abundances greater than 100 individuals in the experiment, using separate repeated-measures ANOVAs. For PERMANOVA, SIMPER, and NMDS analyses we used groups of sampling dates because we exhaustively sampled all of our pools on a weekly basis without replacement, and there was a lot of temporal variability in dispersal of natural beetle populations. We combined the data from weeks 1 and 2 (samples from 09- and 16-June) into one aggregate "Early" sample and weeks 7 and 8 (22 and 29-July) into one aggregate "Late" sample. To test for differences in assemblage structure, we used PERMANOVA set to 999 permutations to analyze the differences in total beetle, Dytiscidae, and Hydrophilidae assemblages between treatments within each of these two aggregate samples. We also compared the total beetle, Dytiscidae, and Hydrophilidae assemblages between these two aggregate samples using repeated-measures PERMANOVAs with factors of treatment crossed with time, plus pool nested within treatment. PERMANOVA results were visualized with non-metric multidimensional scaling (NMDS). We used SIMPER to determine which species contributed the most to the differences between treatments within Early and Late samples and highlight differences between treatments in SIMPER results using separate univariate ANOVAs on each species in these groups. All analyses used $\alpha = 0.05$ on square root transformed data, and block was excluded from PERMANOVA analyses when $P > 0.25$. PRIMER 7 and the

Table 1 Species and abundances for colonizing beetles ($N = 3362$)

Dytiscidae	1590
Anodocheilus exiguus	2
Bidessonotus inconspicuus	5
Celina angustata	2
Copelatus chevrolati	11
Copelatus glyphicus	346
Coptotomus longulus	1
Desmopachria convexa	9
Hydroporus rufilabris	11
Hydrovatus pustulatus	4
Laccophilus fasciatus	405
Laccophilus maculosus	13
Laccophilus proximus	618
Neobidessus pullus	104
Neoporus undulatus	2
Prodaticus bimarginatus	1
Rhantus calidus	2
Thermonectus basillaris	3
Uvarus granarius	17
Uvarus lacustris	34
Haliplidae	3
Haliplus fasciatus	3
Helophoridae	8
Helophorus linearis	8
Hydrophilidae	1751
Berosus aculeatus	34
Berosus exiguus	80
Berosus infuscatus	685
Berosus pantherinus	2
Berosus peregrinus	137
Berosus pugnax	6
Berosus striatus	181
Cymbiodyta chamberlaini	1
Enochrus consors	1
Enochrus ochraceus	39
Enochrus pygmaeus	6
Helochares maculicollis	5
Paracymus	172
Tropisternus blatchleyi	17
Tropisternus collaris	196
Tropisternus lateralis	189
Noteridae	10
Hydrocanthus oblongus	10

PERMANOVA+ add-on (Anderson et al. 2015; Clarke and Gorley 2015) were used to conduct PERMANOVAs and SIMPER using the Bray–Curtis Index and to construct NMDS plots; all other analyses were conducted in R v. 3.2.2 (R Core Team 2015).

Results

We collected a total of 3362 beetles from 38 species in five families on seven sampling dates (Table 1). Due to an error, on 15-July we have data for only 9 of 32 pools (3 hardwood, 6 pine, 233 beetles), so we did not include this date in our analyses or Table 1, but kept it in Figs. 1, 2 and 3. As expected, we observed significant main effects of time in all but one of the analyses (Hydrophilidae repeated-measures PERMANOVA), representing temporal variation in beetle dispersal from natural populations across the landscape. In the univariate repeated-measures ANOVAs there were significant time × treatment interactions for total beetle abundance, species richness, and the five most abundant hydrophilid species (Table 2; Figs. 1, 2). Hydrophilids preferentially colonized hardwood pools early in the experiment and pine pools late. This interaction was not significant for *Paracymus* (Fig. 2e), *Berosus peregrinus* (Fig. 2f), or any dytiscids (Fig. 3). There were no significant main effects of treatment in the repeated-measures ANOVAs.

In the repeated-measures PERMANOVAs there were significant time × treatment interactions for combined counts of all beetle species (*N* = 1734, 36 species), as well as counts of hydrophilid species (*N* = 1315, 16 species), but not dytiscids (*N* = 409, 17 species) when we compared Early versus Late samples (Table 3; Fig. 4). Individual PERMANOVAs on Early and Late samples had significant effects of treatment for all beetle species (Early *N* = 1029, 31 species; Late *N* = 705, 25 species) and hydrophilids (Early *N* = 655, 14 species; Late *N* = 660, 15 species) (Table 3). The effect of treatment was not significant for Dytiscidae in the Late samples, but was significant for Early samples. The significance of the Early Dytiscidae

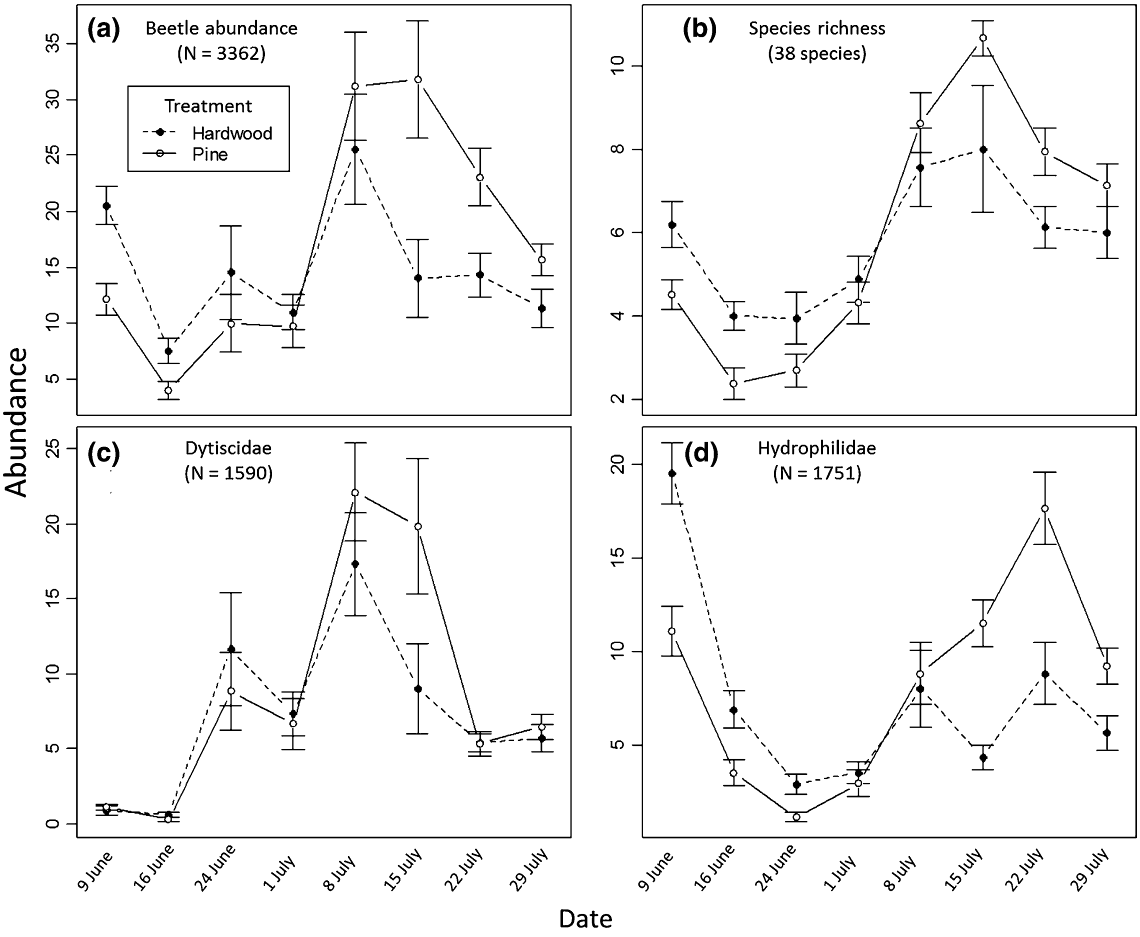

Fig. 1 **a** Average total beetle abundance, **b** beetle species richness, **c** dytiscid abundance, and **d** hydrophilid abundance by date in hardwood (*solid circle*, *dashed line*) and pine pools (*open circle*, *solid line*) (means ± 1 SE)

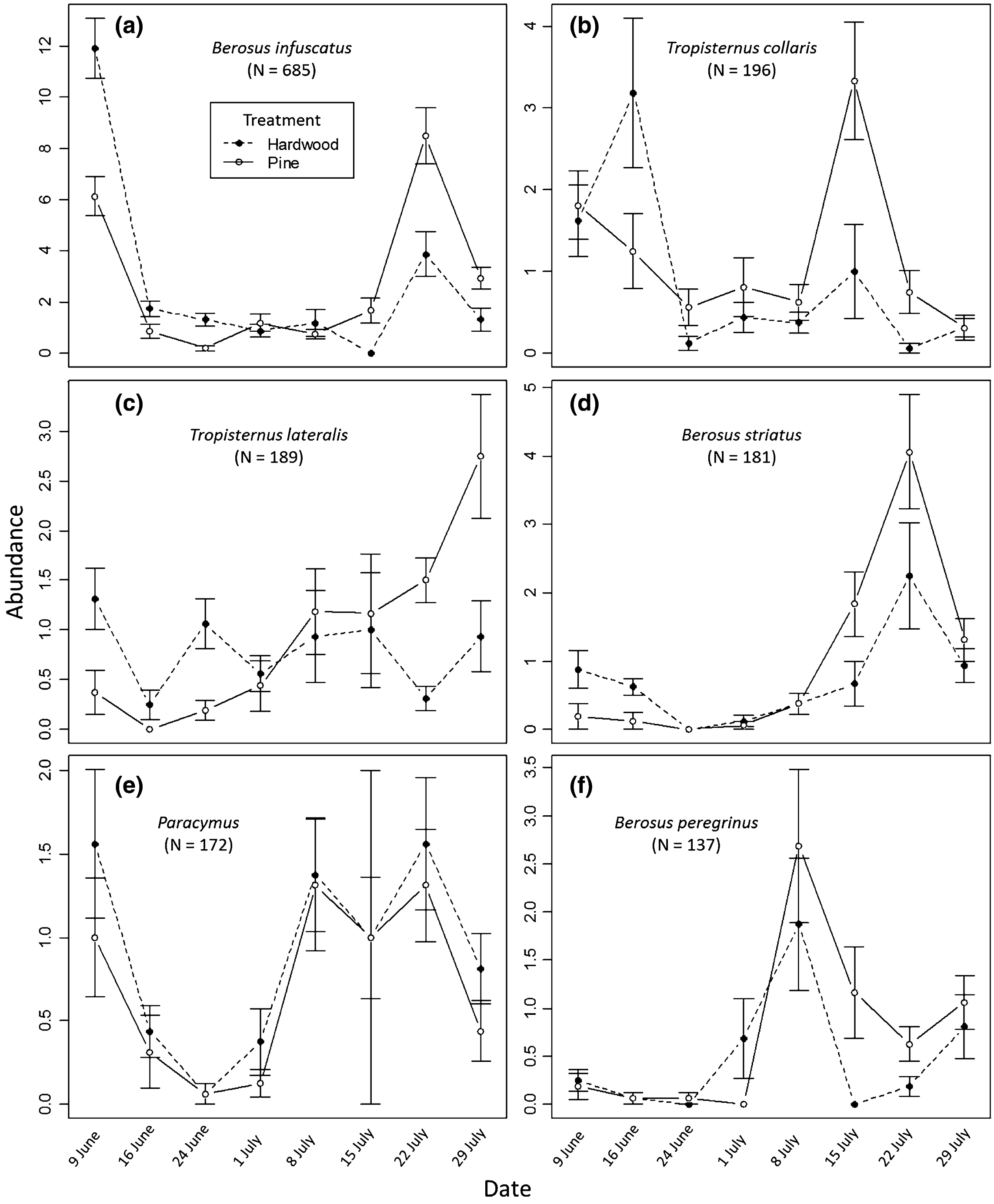

Fig. 2 Average abundances of the six most common ($N > 100$; see Table 1) species of Hydrophilidae by sampling date in hardwood (*solid circle*, *dashed line*) and pine pools (*open circle*, *solid line*) (means ± 1 SE)

PERMANOVA was likely due to the very low number of dytiscids ($N = 44$, 9 species) during the first 2 weeks compared to the last 2 weeks ($N = 365$, 14 species), and four of the nine species in the Early samples were singletons. These singletons contributed to the occurrence of three outliers in the NMDS plots, which we excluded in Fig. 4. SIMPER results show that the dissimilarities between hardwood and pine pools were dominated by hydrophilids with abundant species predictably contributing more to the assemblage dissimilarity between treatments (Table 4). Abundant dytiscids also contributed to the dissimilarity between treatments, even though means of these species were similar between treatments in Late samples, though this is likely a statistical artefact (Warton et al. 2012).

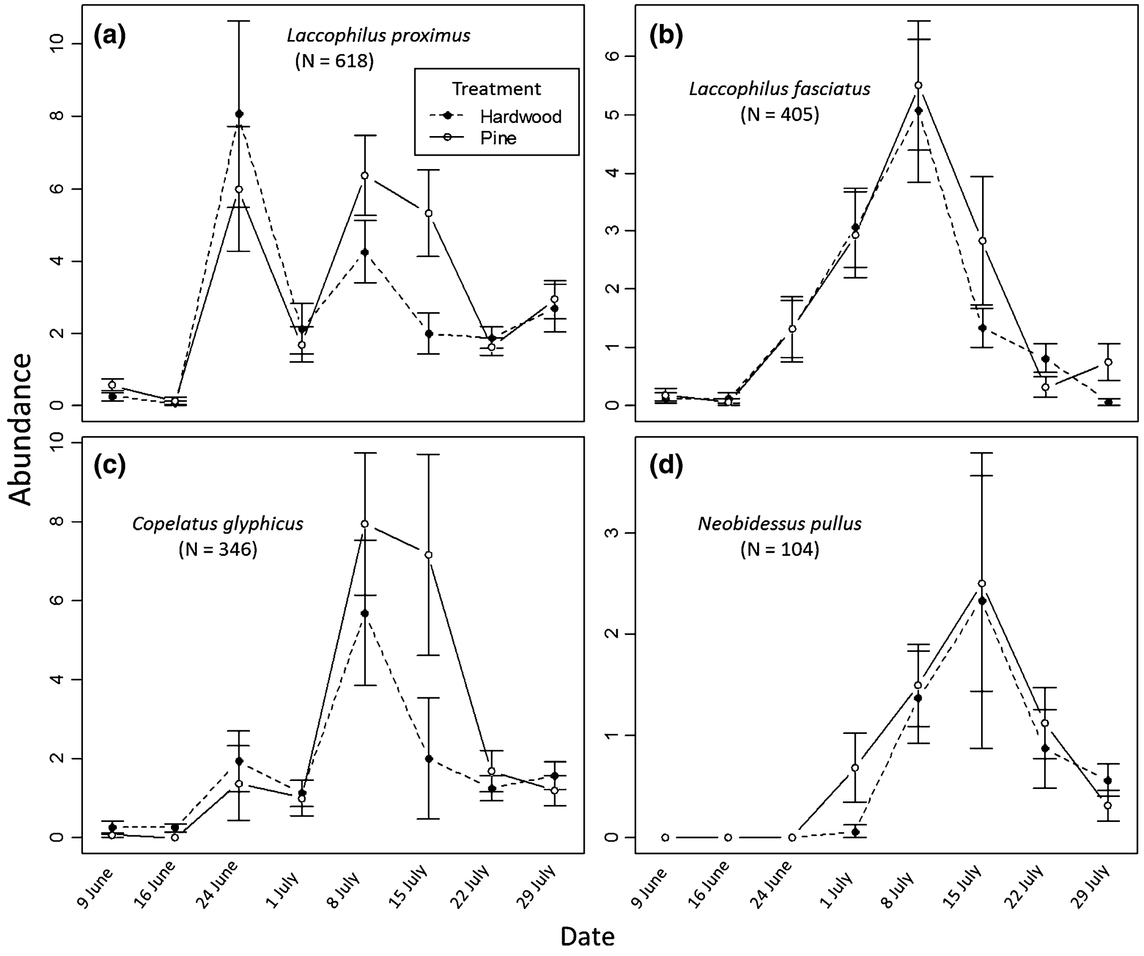

Fig. 3 Average abundances of the four most common ($N > 100$; see Table 1) species of Dytiscidae by sampling date in hardwood (*solid circle*, *dashed line*) and pine pools (*open circle*, *solid line*) (means ± 1 SE)

Discussion

A primary goal of ecology is to understand the mechanisms responsible for generating species distributions and maintaining biodiversity (Chesson 2000). Studies of habitat selection behavior have contributed greatly to this by identifying biotic and abiotic characteristics of habitat patches that drive patterns of colonization (Resetarits and Wilbur 1989; Kraus and Vonesh 2010). Furthermore, linkages between terrestrial and aquatic systems are important determinants of aquatic patch quality and ecosystem structure (Polis et al. 1997; Stoler et al. 2016). Here we observed that leaf litter composition drove differences in aquatic beetle colonization and assemblage structure. Pools containing hardwood litter were initially colonized at higher rates and had higher species richness over the first 3 weeks of the experiment than pine pools, but these differences reversed over the last 3 weeks of the experiment, with higher colonization and richness in pine pools. These differences in colonization were driven by the scavenging hydrophilids, but not the dytiscids, emphasizing that taxa, and often species-specific colonization, are critical determinants of community structure.

While hydrophilids as a family were largely responsible for generating differences in overall colonization between hardwood and pine pools both early and late in the experiment, colonization patterns were not uniform across all species in the family. The four most abundant species in that family, two *Berosus* species (*B. infuscatus* and *B. striatus*) and two *Tropisternus* species (*T. collaris* and *T. lateralis*), were largely responsible for the overall colonization pattern with greater colonization of hardwood early in the experiment and pine late. Of the six most abundant hydrophilids, only *Paracymus* did not exhibit any suggestion of significant time × treatment interaction. *Paracymus* also preferentially colonized hardwood pools across the entirety of the experiment, although the variance on most sampling dates is relatively high (Fig. 2e). The subfamily Hydrobiinae, includes *Paracymus*, along with *Cymbiodyta*, *Enochrus*, and *Helochares*, but abundances of the five species in these other genera were too low to analyze individually or cumulatively (Table 1; $N = 52$) to determine whether lack of response in *Paracymus* is genus-specific or present elsewhere in the subfamily. However, in other habitat selection studies, *Paracymus* often exhibits colonization behaviors different from other hydrophilids, often aligning more with the responses of dytiscids, and reasons for these differences requires further study (Resetarits and Pintar 2016).

Although we observed inter-generic differences in colonization among the hydrophilids, colonization was consistent across the four most abundant dytiscid species (in three genera). In contrast to most hydrophilids, for which leaf litter drove colonization over time, there were no significant differences between treatments at any point in the experiment for total dytiscid abundance or the four most common species (Fig. 3). Adult dytiscids (predaceous diving beetles) are predators, whereas adult hydrophilids (water scavenger beetles) are omnivores. Differential decomposition between pine and hardwood leaf litter can drive resources that are responsive over shorter timescales (periphyton, algae, fungi, biofilms), which would be used by hydrophilids. Conversely, dytiscids feed on organisms dependent on dispersal from surrounding habitats or resting stages (zooplankton and larval insects), which react in a delayed manner to increases in primary productivity (Batzer and Wissinger 1996).

By driving differential colonization of hydrophilids, leaf litter composition resulted in distinct beetle assemblages in pine and hardwood pools both Early and Late in the experiment. Assemblages were most distinct temporally, but significant differences existed between litter treatments among the total beetle and hydrophilid assemblages in both Early and Late samples, as visualized by the spatial differences among clusters in the NMDS plots (Fig. 4). Although there were significant assemblage differences between treatments, there was still considerable overlap of treatment clusters. This stands in contrast to the more distinct assemblages generated by fish presence and fish species identity (Resetarits and Pintar 2016), which pose a much stronger and immediate threat to the fitness of colonizing beetles than does differential resource quality or abundance. Nevertheless, in small, ephemeral, fishless habitats it is not surprising that resource quality can drive assemblage structure. Early arrival at recently formed habitat patches allows colonizing animals to maximize fitness by obtaining more resources and avoiding predators and competitors. These priority effects can shape future community structure (Alford and Wilbur 1985), but this may further interact with variation in litter characteristics and the quality of the resource base over time.

Over the 8-week duration of our experiment, colonization of hardwood pools exhibited less inter-week variation in total beetle abundance, hydrophilid abundance, and species richness than pine pools. This suggests that the multi-species leaf litter assemblage in hardwood pools provided a more stable resource base than the single species in pine pools over these 8 weeks. Multi-species litter assemblages would be expected to provide a more temporally stable resource base than a single litter species (Swan and Palmer 2006), but diversity of litter species is unlikely to be the only determinant of this lower variability. Species with faster litter decomposition rates are quickly available to consumers, but remain available for a limited time, whereas those with slower decomposition rates have delayed availability but remain available longer. The lower inter-week variability in hardwood pools could be partially attributed

Table 2 *F* statistics and *P* values from repeated-measures ANOVAs on total beetle abundance, beetle species richness, Dytiscidae, Hydrophilidae, and species with $N > 100$ in rank order of abundance (see Table 1)

	Between pools		Within pool	
	Treatment *df* (1,23)	Block (7,23)	Time (6,180)	Treatment × time (6,180)
Total abundance	0.039	5.118	19.359	4.037
	0.8450	**0.0013**	**<0.0001**	**0.0008**
Species richness	0.529	1.948	26.621	4.184
	0.474	0.108	**<0.0001**	**0.0006**
Dytiscidae	0.117	3.994	38.647	0.947
	0.7354	**0.0054**	**<0.0001**	0.463
Laccophilus proximus	0.529	2.387	24.058	0.678
	0.4743	0.0544	**<0.0001**	0.668
Laccophilus fasciatus	0.187	6.221	28.605	1.413
	0.6693	**0.0004**	**<0.0001**	0.212
Copelatus glyphicus	0.089	1.086	36.594	1.312
	0.768	0.404	**<0.0001**	0.254
Neobidessus pullus	0.354	0.353	15.762	1.141
	0.558	0.920	**<0.0001**	0.34
Hydrophilidae	0.289	2.304	38.468	8.541
	0.5960	0.0618	**<0.0001**	**<0.0001**
Berosus infuscatus	0.086	6.004	59.85	11.43
	0.7720	**0.0005**	**<0.0001**	**<0.0001**
Tropisternus collaris	0.642	2.081	8.475	2.440
	0.4314	0.0874	**<0.0001**	**0.0272**
Tropisternus lateralis	0.132	2.489	7.212	8.242
	0.7194	**0.0466**	**<0.0001**	**<0.0001**
Berosus striatus	0.133	0.634	24.661	5.202
	0.719	0.723	**<0.0001**	**<0.0001**
Paracymus	3.418	1.056	10.759	0.401
	0.0774	0.4216	**<0.0001**	0.878
Berosus peregrinus	0.632	1.106	13.380	1.388
	0.435	0.393	**<0.0001**	0.222

Bold indicates significance ($P < 0.05$)

Table 3 PERMANOVA results

Source	*df*	SS	MS	Pseudo-*F*	*P*	Unique perms
Early versus Late (repeated measures)						
All beetle species						
Treatment	1	1609.1	1609.1	1.5051	0.150	999
Pool (treat)	30	32,073	1069.1	1.2304	0.091	999
Time	1	26,363	26,363	30.34	**0.001**	999
Time × treat	1	5781.1	5781.1	6.6534	**0.001**	999
Residuals	30	91,893	868.9			
Dytiscidae						
Treatment	1	3540.9	3540.9	1.6629	0.168	998
Pool (treat)	22	46,846	2129.4	1.1789	0.184	999
Time	1	23,185	23,185	12.836	**0.001**	998
Time × treat	1	3320	3320	1.8381	0.111	999
Residuals	22	39,736	1806.2			
Hydrophilidae						
Treatment	1	2098.6	2098.6	2.2766	0**.038**	998
Pool (treat)	30	27,654	921.79	1.2749	0.065	999
Time	1	16,078	16,078	22.238	**0.001**	999
Time × treat	1	6028.8	6028.8	8.3384	**0.001**	999
Residuals	30	21,690	723.02			
Early						
All beetle species						
Treatment	1	4478.1	4478.1	4.2422	**0.001**	998
Residuals	30	31,668	1055.6			
Dytiscidae						
Treatment	1	6848.3	6848.3	12.899	**0.001**	999
Block	7	10,666	1523.8	2.87	**0.001**	998
Residuals	15	7964	590.93			
Hydrophilidae						
Treatment	1	3939	3939	4.6183	**0.001**	999
Residuals	30	25,587	852.92			
Late						
All beetle species						
Treatment	1	2912.1	2912.1	3.3003	**0.001**	999
Residuals	30	26,472	882.39			
Dytiscidae						
Treatment	1	209.27	209.27	0.18031	0.949	998
Residuals	30	34,819	1160.6			
Hydrophilidae						
Treatment	1	4188.3	4188.3	5.2891	**0.001**	999
Residuals	30	23,757	791.89			

The reduced number of residual degrees of freedom in the Dytiscidae analyses is due to pools with 0 beetles, which cannot be included in these analyses

Bold indicates significance ($P < 0.05$)

to overall higher nutrient concentrations in hardwood leaf litter. However, due to interactions of chemical compounds in different species of leaves, mixtures of litter species can decrease primary productivity relative to a single species, such as decreased productivity in a maple-oak mixture relative to oak alone (Rubbo and Kiesecker 2004; Stoler and Relyea 2011). A mixture of pine and hardwood litter might be expected to generate more temporally consistent colonization at rates intermediate between pools of a single litter type, but potential interactions between different litter types

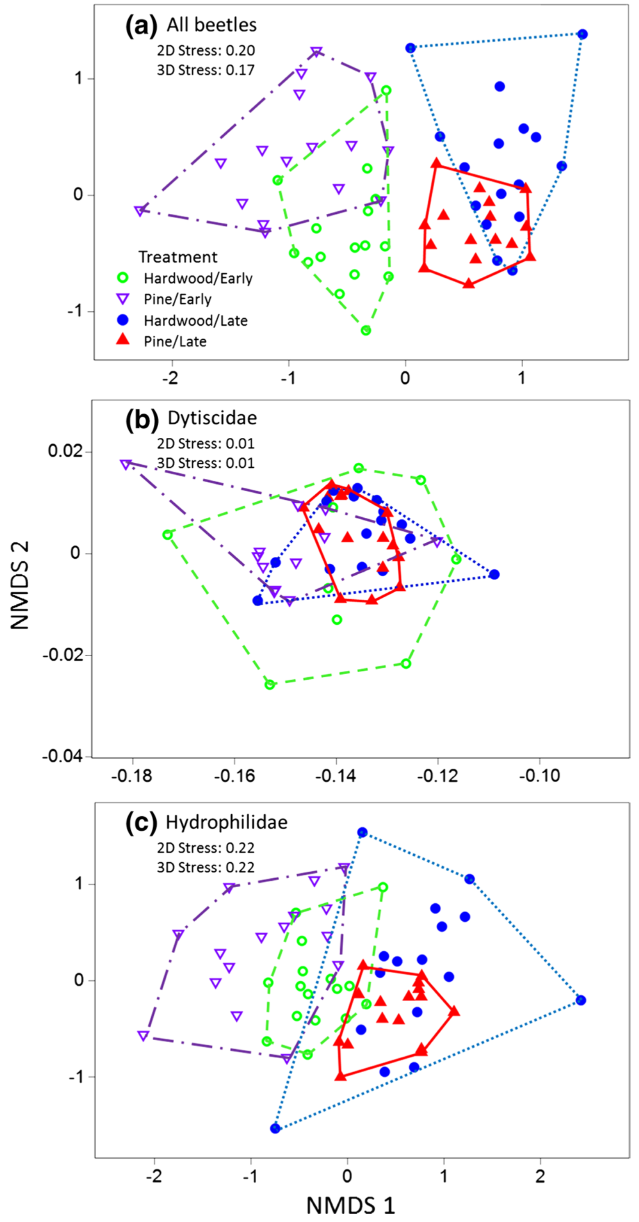

Fig. 4 NMDS plots with minimum convex polygons for Early versus Late samples on **a** all beetle species, **b** Dytiscidae, and **c** Hydrophilidae. **b** Excludes three outliers

Table 4 The ten species contributing the most to the dissimilarity between beetle assemblages in pine and hardwood pools in Early and Late samples determined with SIMPER

Species	Average abundance		Contributing
	Hardwood	Pine	percent
Early			
Berosus infuscatus	**13.69**	7.00	11.54
Tropisternus collaris	4.81	3.06	10.64
Paracymus	2.00	1.31	9.53
Tropisternus lateralis	**1.56**	0.38	9.18
Berosus striatus	**1.50**	0.31	9.15
Berosus exiguus	1.19	1.38	7.54
*Laccophilus proximus**	0.31	**0.69**	5.85
Tropisternus blatchleyi	0.31	0.06	4.37
Enochrus ochraceus	**0.44**	0.00	3.76
Berosus peregrinus	0.31	0.25	3.75
Cumulative percent			75.31
Late			
Berosus infuscatus	5.19	**11.44**	10.88
Tropisternus lateralis	1.25	**4.25**	9.99
Berosus striatus	3.19	5.38	8.89
*Laccophilus fasciatus**	2.81	2.88	7.62
Paracymus	2.38	1.75	6.40
*Neobidessus pullus**	1.44	1.44	6.20
Copelatus glyphicus	0.88	1.06	5.74
Berosus peregrinus	1.00	**1.69**	5.31
*Laccophilus proximus**	4.56	4.56	5.23
Tropisternus collaris	0.38	1.06	5.18
Cumulative percent			71.44

Average abundances are means of raw beetle abundances in Early and Late groups, and contributing percent was calculated from square root transformed data

Bold indicates significantly higher colonization ($P < 0.05$)

* Dytiscidae; all others are Hydrophilidae

may generate patterns different from those expected. Longer term data would be necessary to determine if, and at what point, both treatments would be perceived as equivalent quality to colonizing animals. Habitat selection behaviors are nonetheless critical to determining colonization patterns over the short timescales used in our experiment.

The ability to assess habitat quality during colonization enables organisms to select habitats with the highest expected fitness. For aquatic beetles in particular, this behavioral response to patch quality is a critical decision given the energetic costs of dispersal and potential fitness consequences of selecting poor quality patches, since adults select habitats both for themselves and their offspring (Zera and Denno 1997; Binckley and Resetarits 2008). The variation in habitat selection preferences among the Hydrophilidae across the relatively short duration of our experiment suggest they are selecting habitats based on the immediate perceived quality of the patches rather than potential long-term differences between patches, if such long-term differences exist. Changes in the relative quality of habitat patches over time may offset fitness reductions associated with colonizing a habitat that is initially of low quality or reduce the benefit of colonizing a habitat that is initially of high quality. However, maximizing growth earlier in development, thus achieving larger sizes sooner and gaining a competitive advantage over later colonizers, should be more important than maximizing later growth (Werner and Gilliam 1984). In addition, the initial preferential colonization of hardwood pools by hydrophilids could reduce available resources in these patches, resulting in a loss in preference for this habitat type, as we observed. Nevertheless, colonization patterns generated by variation in litter composition are important for individual fitness, population dynamics, and community structure, placing further emphasis on the importance of aquatic–terrestrial linkages.

Our study highlights the importance of tree species composition in driving community structure in freshwater systems. Changes in tree species composition can alter nutrient cycling, overall species composition, and food web structure, resulting in functionally different systems. These effects on colonization can be driven both by the local composition of pond litter resulting from patchy variation in tree species composition, and the larger habitat matrix in which the local site is embedded (Deans and Chalcraft 2017). Since the early twentieth century, forests in North America have undergone drastic human-driven changes in their composition, such as the loss of *Castanea dentata*, once one of the most important trees in eastern North America (Smock and MacGregor 1988). *Ulmus americana*, *Fraxinus* spp., *Tsuga canadensis*, and *Quercus* spp. are all important, widespread taxa that have been, or are currently being, decimated by disease, insect infestation, or overbrowsing (Abrams 2003). Further changes to forest structure from logging and fire suppression provide opportunities for invasive or opportunistic species and alter successional dynamics of habitat patches. Understanding the effects of tree species composition on habitat use by aquatic animals is critical for projecting distributions and abundances of species as forests continue to change due to anthropogenically driven processes, including climate change. Knowing how tree species composition drives community structure and ecosystem processes in embedded freshwater systems provides a basic framework for localized efforts to restore and protect the habitat quality of freshwater systems and the ecosystem services they provide.

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