

Invasive plant ecosystem engineer facilitates community and trophic level alteration for brackish marsh invertebrates

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Abstract. Wetland habitats are becoming increasingly scarce worldwide while experiencing exceptionally high levels of plant invasion. Invasive plant species affect ecosystems through numerous avenues, including acting as ecosystem engineers, contributing unique plant functional traits, and altering trophic dynamics. We examined the impacts of the invasive weed *Lepidium latifolium* on soil-dwelling and canopy-dwelling invertebrate communities in a brackish marsh of northern California. Invertebrate abundance, species richness, diversity, and community composition were measured in both invaded and non-invaded areas of the marsh in four time periods that correspond with different *L. latifolium* phenologic phases. We observed these different stages of *L. latifolium*, and we recorded alterations in the habitat structure provided by *L. latifolium* as the plant entered senescence. *L. latifolium* had differential impacts on the two invertebrate communities studied. The presence of *L. latifolium* increased abundance of soil-dwelling invertebrates and decreased the species richness of canopy-dwelling invertebrates in the tidal marsh-terrestrial ecotone where *L. latifolium* ameliorates harsh physical conditions. No changes occurred in the tidal marsh plain and fringing tidal marsh where *L. latifolium*'s physical structure is more similar to existing non-*L. latifolium* structure. During full senescence, *L. latifolium* reduced canopy-dwelling invertebrate abundance and altered trophic dynamics, shifting composition to a predator-dominated community. Our results demonstrate that *L. latifolium* can impact brackish marsh ecosystems, and we hypothesize *L. latifolium*'s unique functional traits (large inflorescence and seasonal senescence) enable it to act as an ecosystem engineer that alters community and trophic dynamics. Mechanisms through which plant invaders alter ecosystem processes are dynamic in space and time, thus, future research will require the use of manipulative experiments to inform site-specific management strategies.

Key words: brackish marsh; canopy-dwelling arthropods; ecosystem engineer; infaunal macroinvertebrates; invasive species; *Lepidium latifolium*; plant functional traits; trophic dynamics; wetlands.

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INTRODUCTION

Between 1970 and 1989, 90% of California's naturally occurring tidal wetlands were destroyed by anthropogenic influences (Dahl 1990). Of the remaining 10%, most are highly altered, managed, or impacted by invasive

species. Zedler and Kercher (2004) note that wetlands cover less than 6% of the land surface of the globe, yet 24% of the most invasive weeds (as defined by The Global Invasive Species Database's list of most invasive plants) are invaders of wetland habitat. Wetlands are particularly vulnerable to plant invasions due to the presence of

cross-ecotone water flow, frequent canopy gaps, anoxic soil conditions, and ample nutrient influx (Zedler and Kercher 2004). Despite the potential impacts posed to wetlands by invasion, the study of invasive species in coastal ecosystems has lagged behind terrestrial and other aquatic habitats (Grosholz 2002), and we lack a clear understanding of the characteristics mediating the impacts of specific invaders.

Ehrenfeld (2010) outlines three mechanistic explanations which inform the study of invasive plant-ecosystem relationships: plant species functional traits, strong effects, and trophic interactions. First, invasive plants often possess a suite of unique functional traits not present within the non-invaded plant community (Ehrenfeld 2010). In the context of invasion, Drenovsky et al. (2012) defines plant functional traits as, “the readily measurable morphological, chemical, physiological, and phenological attributes of plants that interact with surrounding biotic and abiotic factors”, and we will use this as our working definition. Second, strong effects of invasive plants are characteristics exerting wide-ranging impacts, such as the ability to act as ecosystem engineers. Jones et al. (1994) defined an ecosystem engineer as an organism exerting indirect or direct control over resource availability through physical state changes in abiotic or biotic materials. For invasive wetland plants, this often manifests through shifts in plant community structure (Chambers et al. 1999, Schooler et al. 2006). In addition to altering floral composition, wetland plant invasions have been demonstrated to change trophic structure either by altering food availability, accessibility, or the exposure of prey to predators (Zedler and Kercher 2004).

While plant functional traits, ecosystem engineering, and trophic alterations are only three of numerous invader attributes controlling ecosystem level impacts, their interacting and compounding effects can be observed in several examples of wetland plant invasions. Specifically, such alterations to vegetation impact ground-dwelling and plant canopy-dwelling invertebrates. On the East Coast and in the northeast of the United States, *Phragmites australis* (common reed) lowered density and abundance of soil macroinvertebrates, decreased canopy-dwelling arthropod species richness, diversity, and abundance, and shifted the trophic structure from

carnivore- to herbivore-dominated community (Angradi et al. 2001, Osgood et al. 2003, Raichel et al. 2003, Gratton and Denno 2005). On the West Coast of the United States, invasive *Spartina alterniflora* crossed with native *S. foliosa*, and invasion by the hybrid plant decreased macrofauna abundance by 75% and lowered biomass of surface-feeding infauna (Levin et al. 2006). Hybrid *Spartina* also altered structural components of marshes (converting mudflats to vegetated areas) causing a bottom-up trophic shift from an algae-based to a detrital-based food web (Levin et al. 2006). Many of these ecosystem engineering and subsequent trophic changes potentially stem from differences between the functional traits of the plant invader as compared to those of the native plant.

These shifts in plant functional trait occurrence, community composition, and trophic structure as a result of ecosystem engineers stand to have long lasting impacts on already imperiled wetland habitats. This study investigates aspects of the species-community relationship for a pervasive wetland invader, *Lepidium latifolium*. Compared to the surrounding native community in most habitats where it invades, *L. latifolium* has the unique functional traits of a large inflorescence and a phenology where the plant structure differs by season. By assessing how *L. latifolium* impacts the structure and function of two components of the invertebrate community within a tidal, brackish marsh in northern California, we can learn how perennial, non-native plants with large inflorescences and other invaders with similar traits can alter the ecosystems they invade.

Project objectives

This study aimed to explore the potential impacts of *L. latifolium* on invertebrate species and trophic group abundance, diversity, and community assemblage. To this end, soil-dwelling and canopy-dwelling invertebrates were sampled within paired stands of *L. latifolium* and non-*L. latifolium* marsh vegetation at four time points, which corresponded with the different phenologic states of *L. latifolium*. Few studies examine both the canopy-dwelling arthropod community in tandem with the soil-dwelling invertebrate community, but these two subsets of the invertebrate community may interact with



Fig. 1. High marsh-terrestrial ecotone (transitional marsh) along margins of grassland, tidal marsh plain (marsh plain), and fringing tidal marsh (fringing marsh) at Rush Ranch Open Space Preserve (modified from Whitcraft et al. 2011).

invasive plants in different ways. With large, inflorescences, *L. latifolium* may provide abundant habitat for canopy-dwelling invertebrates. At the same time, C. R. Whitcraft (*unpublished data*) found that, in some locations with the marsh, soil temperature decreased while humidity increased below the *L. latifolium* canopy, potentially ameliorating abiotic pressure on soil-dwelling invertebrates as compared to the native plant canopy. Thus, we hypothesized that presence of *L. latifolium* would impact invertebrate species and trophic group abundance, species richness, diversity (quantified by the Shannon-Weiner index which includes both evenness and richness), and community composition, increasing abundance of both soil-dwelling and canopy-dwelling invertebrate assemblages while altering the community composition.

MATERIALS AND METHODS

Study site

Tidal marshes adjacent to San Francisco Bay cover only 20% of their former area (Greenberg et al. 2006). A component of the San Francisco Bay-Delta Estuary, Suisun Bay is one of these few remaining wetland systems and is composed predominately of brackish marsh habitat (Marshall 1948). Rush Ranch Open Space Preserve (RROSP) is the largest intact area of fully tidal,

brackish marsh persisting in Suisun Bay and has remained largely undiked, escaping this anthropogenic alteration to tidal flow (Whitcraft et al. 2011).

Traditionally, marshes are categorized by elevation zones (low, mid, high). These zones are characterized by plant communities formed through interspecific competition along gradients of soil waterlogging and salinity (Pennings and Bertness 2001 and sources therein). However, within the brackish marsh habitat at RROSP, the diverse flora is structured by a complex mix of geomorphic conditions (Whitcraft et al. 2011). As a result, we will reference to three different locations within the marsh which will be defined based on major estuarine geomorphic units: fringing tidal marsh (hereafter, fringing marsh, areas immediately adjacent to vegetated, subtidal channels), tidal marsh plain (hereafter, marsh plain, drained areas of higher elevation crossed in numerous places by small tidal creeks), and tidal marsh-terrestrial ecotone (hereafter transitional marsh, area of marsh directly adjacent to surrounding upland ecosystems; in our study area an upland grass community) (Fig. 1) (Whitcraft et al. 2011).

Though RROSP has escaped many anthropogenic alterations, numerous invasive plants have become integrated into the complex geomorphology within the site. Whitcraft et al. (2011)

estimate that nearly 27% of the flora at the site is non-native. One particularly aggressive invasive weed, *Lepidium latifolium*, is an issue of concern for land managers and ecologists. *Lepidium latifolium*, also called perennial pepperweed or white-top, occurs naturally in Europe and the central and southwestern regions of Asia (Young et al. 1995). Along the northwest coast of the United States, it is a pervasive invader of wetlands, estuaries, and riparian habitats (Young et al. 1998, Leininger and Foin 2009). Leaf area of perennial pepperweed is highest at the flowerbud stage and has been reported to achieve over 26,528 cm² leaf area/m² in upland habitats (Zouhar 2004). Most leaf area occurs in the top third of the canopy during the flowerbud to fruiting stages with a significant decrease as perennial pepperweed stems flower and fruit (Renz 2000). Perennial pepperweed has a panicle inflorescence that is approximately 25–27.5 cm wide with flowers in dense clusters at the top of the stem. *Lepidium latifolium* outcompetes native grasses, sedges, and rushes, converts formerly diverse ecosystems into large monocultures in some habitats (Blank and Young 2002) and alters soil development and chemistry (Blank 2002, Blank and Young 2002). Co-occurring with natural vegetation in many areas within RROSP, *L. latifolium*'s dense, tall plant cover can decrease habitat quality (Zouhar 2004) and reduce the biomass of other native plant species, altering plant community composition (B. Grewell, *personal communication*; C. R. Whitcraft, *unpublished data*) and threatening endemic species like the Suisun aster (Skinner and Pavlik 1994).

Sampling design

In the fall of 2007, a random numbers table was applied to latitude and longitude within RROSP to select a zone bounded by second-order tidal creeks in the brackish marsh. This zone contained the three geomorphic units discussed above. Within each geomorphic unit, three haphazardly selected paired plots (ones with *L. latifolium* present (*L. latifolium*) and ones with *L. latifolium* absent (non-*L. latifolium*), 9 pairs or 18 total plots across all locations) were sampled for vegetation characteristics and ground-dwelling invertebrate community parameters. Each plot within a habitat was approximately 25% ± 6% (mean ± SE) similar in vegetation composition to

its paired plot; in the transitional marsh, the dominant plant was *Sarcocornia pacifica* (pickleweed) with an average percent cover of 25% ± 5% while in the tidal marsh plain and fringing marsh, *Juncus balticus* (Baltic rush) was the dominant native plant at 24% ± 3% and 24% ± 5%, respectively. For canopy-dwelling invertebrates in each geomorphic unit, two haphazardly selected paired plots (ones with *L. latifolium* present [*L. latifolium*] and ones with *L. latifolium* absent [non-*L. latifolium*], 6 pairs or 12 total across all locations) were sampled. Paired plots were, on average, 10 m apart from one another.

Vegetation characteristics assessment

Vegetation characteristics were measured in 2011 during the three major phases of *L. latifolium* phenology: the rosette stage (April), peak flowering (June), and beginning of senescence (August). Average phenologic state of *L. latifolium* was estimated by eye for the study plot as a whole during each sampling event. Other vegetation measurements were taken within 0.25-m² quadrats. Within the *L. latifolium* plant community, *L. latifolium* stem count and stem angle to the ground were measured. Stem count was measured as absolute stem number as the underground rhizomes of the plant make differentiation of individual plants challenging. Stem angle to the ground was taken by selecting five stems representing the range of stem angles in the quadrat and, using a standard protractor sitting flush on the ground, measuring the stem angle (0°–90°). The phenology of *L. latifolium* changes through the year as discussed above. Stem angle was quantified as a metric of this phenologic change and as a metric of the availability of potential upright habitat. Percent cover of individual species was estimated for quadrats in the *L. latifolium*-invaded and non-*L. latifolium* plant communities.

Invertebrate and arthropod community assessment

Invertebrate samples were taken during *L. latifolium* rosette stage (June 2007), peak flowering (late July 2010), the beginning of senescence (November–December 2007), and full senescence (February 2011). Sampling years are offset due to timing of access permission. Two types of invertebrate samples were taken in order to describe a large portion of the invertebrate

community. Soil cores (2 cm deep, 4.8 cm diameter, 18.1 cm²) were taken to sample soil-dwelling invertebrates below the vegetation ($N = 18$ per time of sampling; $N = 9$ in *L. latifolium* and $N = 9$ in non-*L. latifolium*) in each of the three geomorphic locations (transitional marsh, marsh plain, and fringing marsh). This core size is consistent with published literature on macrobenthos from other tidal marshes in California (Levin et al. 1998, Talley and Levin 1999, Levin and Talley 2002, Levin and Currin 2005). Samples were preserved in 8% formalin for processing in the lab. Soil cores were rinsed on a 300- μ m sieve, and retained invertebrates were identified to the lowest possible taxonomic level using a dissecting microscope.

Mobile canopy-dwelling invertebrates were sampled from plant canopies in three geomorphic locations (transitional marsh, marsh plain, and fringing marsh) using a leaf blower modified to take in air ($N = 12$ per time of sampling across all locations; $N = 6$ in *L. latifolium* and $N = 6$ in non-*L. latifolium*, two paired plots in each location). Specimens were vacuumed from the marsh plant canopy for 1 minute (beginning of senescence and rosette stage) or 30 seconds (full senescence and peak flowering) per sample and gathered in cloth netting. Sample time was decreased from one minute to 30 seconds due to the high invertebrate abundance per sample gathered in 2007 and concerns about disturbance of bird breeding. Samples were frozen until processing when invertebrates were identified to lowest possible taxonomic level using a dissecting microscope (Oliver and Beattie 1996). Because not all identification was to species level, our analyses were conducted at the morphospecies level. Although the use of morphospecies may introduce some uncertainty when quantifying species diversity, this approach has been shown to accurately estimate species number in other studies (Oliver and Beattie 1996). If anything, taxonomically difficult groups (e.g., families of wasps, flies) are likely to be underestimated by morphospecies, making this a conservative approach (Derraik et al. 2010).

Data analysis

Square root-transformed percent cover data were tested using ANOVAs to examine differences in *L. latifolium* characteristics across times

of sampling. Stem angle data could not be transformed to meet the assumptions of normality or equal variance. Thus, for stem angle, the Welch's ANOVA (1951) was used to examine differences in *L. latifolium* between times of sampling.

To quantify the effects of *L. latifolium* on invertebrate abundance, species richness, and diversity (H'), we calculated the log response ratio (LRR; Goldberg et al. 1999) as $\ln[L. latifolium/\text{non-}L. latifolium]$ between paired plots. The LRR is symmetric about zero and does not impose an upper bound on the maximum possible effect size (Berlow 1999, Goldberg et al. 1999, Lajeunesse and Forbes 2003); the logarithm linearizes the metric and normalizes the sampling distribution (Hedges et al. 1999). A LRR value of 0 indicates no effect of *L. latifolium*, a negative value indicates a decrease in variable of interest in *L. latifolium* areas as compared to non-*L. latifolium* areas, and a positive value indicates an increase in the variable of interest in response to *L. latifolium* (invertebrate abundance, species richness, and diversity [H']).

Differences among locations and phenologic states in LRRs for abundance, species richness, and diversity of soil-dwelling and canopy-dwelling invertebrates were determined via two-way analyses of variance (ANOVAs) in Minitab v. 16.2.4. When necessary, data were first transformed to meet the assumptions of equal variance and normality. Where appropriate, ANOVAs were followed by Student-Newman-Keuls (SNK) tests to identify significant differences among means (Underwood 1997). To determine if the LRRs were significantly different from zero (i.e., indicating a significant effect of *L. latifolium*), one-sample t-tests within season or location (depending on two-way ANOVA results) were performed on abundance, species richness, and diversity of soil-dwelling and canopy-dwelling invertebrates in Minitab v. 16.2.4. When necessary, data were first transformed to meet the assumptions of normality. Given the strength of patterns in our data, a Bonferroni or similar correction would be unwarranted and overly conservative (Hurlbert and Lombardi 2012). Complete reporting of test statistics and p-values will enable readers to understand the tests and data as analyzed. Abundance data from the beginning of senes-

cence and rosette phenologic stages were divided by two to account for longer sampling duration in these sampling times. Rank abundance curves demonstrated that richness and diversity were not impacted by increased sampling time.

Once data analysis had been performed on the morphospecies level, species were grouped based on order and trophic mode. Order and trophic mode were assigned to each morphospecies using the following resources: Smith (1928), McBrayer and Reichle (1971), Fauchald (1977), Steneck and Watling (1982), Rushton and Hassall (1983), Jervis and Kidd (1986), Stribling and Seymour (1988), Penry and Jumars (1990), Hunt (1991), Hiol et al. (1994), Ruppert and Barnes (1994), Lewis et al. (1998), Lee et al. (2002), Serrano-Pinto and Caraveo-Patiño (2002), Triplehorn and Johnson (2005), Carlton (2007), Merritt et al. (2008), Krantz and Walter (2009), Goyal et al. (2010), Robinson et al. (2011). Samples containing unidentifiable specimens were not used in this analysis. Once morphospecies were grouped by order and trophic mode, analyses were performed as described previously. For groups where species identity was unknown, trophic mode was assigned by examination of feeding structures or placed in an “unknown” category if the previously mentioned technique was inconclusive. Trophic modes were classified as predator, detritivore, herbivore, kleptoparasites, mycophagivores, coprophagivores, multiple feeding types, and unknown (Appendix A). Analysis of LRRs for trophic abundance, trophic species richness, and trophic diversity of soil-dwelling and canopy-dwelling invertebrates were also performed via two-way analyses of variance (ANOVAs) and t-tests in Minitab v. 16.2.4. However, no significant differences existed so no results are provided.

Differences in community composition as a function of invader presence and location in the marsh were tested with two-way analyses of similarity on invertebrate abundance and on invertebrate trophic abundance (ANOSIM) within time of sampling using Primer v. 6.1.6. Raw data were used to calculate matrices of Bray-Curtis similarity coefficients before analysis. The Bray-Curtis similarity/dissimilarity coefficient is suitable for presence-absence, abundance or biomass data. A triangular matrix of inter-sample similarities is produced and used in an agglomerative clustering procedure where samples that

are most similar to each other are grouped together (Clarke and Ainsworth 1993). All data were fourth root transformed to adjust for extremely abundant taxa. Contribution to the level of Bray-Curtis similarity or dissimilarity was explored via similarity percentage (SIMPER) analysis.

All graphs display untransformed data with error bars showing one standard error about the mean. Different letters indicate statistically significant differences between means at the 0.05 alpha level.

RESULTS

Vegetation traits

Compared to other times of sampling, percent cover of *L. latifolium* was significantly higher when plants within the study site were transitioning between rosette and full bloom stage than at other stages ($F_{2,20} = 18.94$, $P < 0.0001$; average % cover *L. latifolium*: beginning senescence $18.26\% \pm 2.94\%$, full senescence $6.67\% \pm 1.05\%$, rosette stage $59.71\% \pm 3.70\%$, peak bloom $23.67\% \pm 3.29\%$). *Lepidium latifolium* stem angle to the ground changed throughout the course of the plant's phenology. Stems were most upright in April, then decreased their angle to ground throughout the course of the flowering season (Welch's ANOVA, $F_2 = 120.36$, $P < 0.001$).

Soil-dwelling invertebrate community and diversity

Location was an important controlling factor on soil-dwelling invertebrate abundance with LRR in the transitional marsh differing significantly from the marsh plain and the fringing marsh ($F_{3,23} = 4.66$, $P = 0.020$; Fig. 2; Appendix A). Log response ratios of species richness and species diversity did not differ by time of sampling or location (Table 1). As indicated by a LRR different than zero, the presence of *L. latifolium* increased soil-dwelling invertebrate abundance in the transitional marsh ($t_{12} = 2.18$, $P = 0.052$; Table 2, Fig. 2; Appendix A). The presence of *L. latifolium* did not affect species richness or species diversity.

Community structure differed among *L. latifolium* phenologic stages (ANOSIM, global $R = 0.36$, $P = 0.001$; pairwise ANOSIM results in Table 3). During *L. latifolium* senescence, community

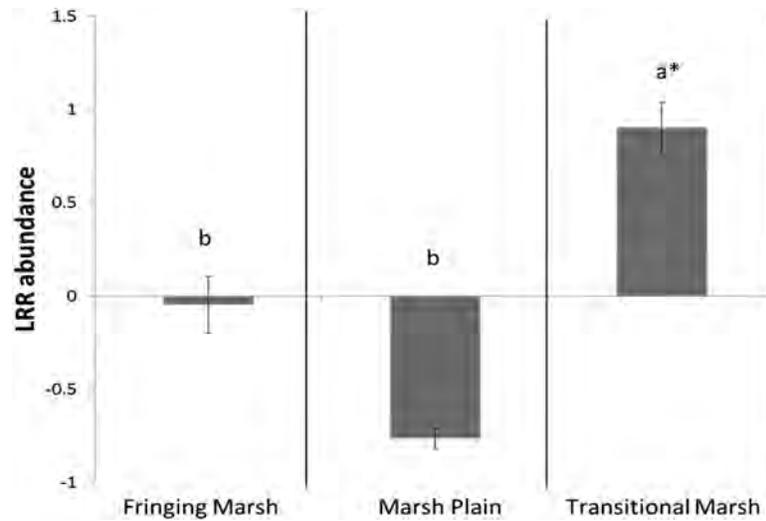


Fig. 2. Log response ratio (LRR) of soil-dwelling invertebrate abundance by phonologic state of sampling (averaged across location). Lower case letters indicate significant differences in LRR among time of sampling by SNK post-hoc comparison. An asterisk indicates LRRs that are significantly different from zero, indicating effect of *L. latifolium*.

structure did not differ based on the presence of the invader, but did differ significantly among locations within the marsh (ANOSIM, global $R = 0.19$, $P = 0.041$; pairwise ANOSIM results in Table 3). The marsh plain and the transitional marsh are 87.9% dissimilar, with this pattern being driven primarily by the presence of *Traskorchestia traskiana* (amphipod) in the marsh plain (11.03% dissimilarity) and Sminthuridae (Collembola) in the transitional marsh (11.82% dissimilarity) (SIMPER marsh plain and transitional marsh, average dissimilarity 87.90%). Similarly, during full *L. latifolium* senescence community structure

was not impacted by the presence of the invader but did differ significantly between locations (ANOSIM, global $R = 0.19$; $P = 0.034$; pairwise ANOSIM results in Table 3). The transitional marsh was distinct from other zones, driven by the consistent presence of Chironomidae (Diptera) larva (25.79% of similarity) and Isotomidae (Collembola) (10.46% of similarity) in this location (SIMPER transitional marsh, average similarity 45.00%). Community structure during *L. latifolium* rosette stage did not differ by invader presence or location. However, during *L. latifolium* peak flowering community was significantly

Table 1. Results of the two-way ANOVAs for soil-dwelling invertebrates.

Response variable	Source	Result	df	Adj MS	<i>F</i>	<i>P</i>
LRR abundance	season	ns	3	0.531	0.43	0.731
	location	(Trans) ≠ (Fring = Plain)	2	5.711	4.66	0.020
	season × location	ns	6	2.931	2.39	0.061
	error		23	1.225		
LRR sp. richness	season	ns	3	0.2705	0.58	0.637
	location	ns	2	0.1959	0.42	0.664
	season × location	ns	6	0.4495	0.96	0.475
	error		23	0.4689		
LRR <i>H'</i>	season	ns	3	0.1487	0.15	0.928
	location	ns	2	0.6765	0.68	0.515
	season × location	ns	6	0.605	0.61	0.718
	error		23	0.9883		

Notes: Significant *P*-values ($P < 0.05$) indicated by boldface. Abbreviations are: LRR, log response ratio; Trans, transitional marsh; Fring, fringing marsh; Plain, marsh plain; ns, nonsignificant.

Table 2. Results of one-sample t-tests on LRR of soil-dwelling invertebrate abundance.

Location	Result	df	<i>t</i>	<i>P</i>
Fringing	ns	12	-0.15	0.885
Plain	ns	12	1.61	0.139
Transitional	≠0	12	2.18	0.052

Note: Abundances pooled across phenologic states based on two-way ANOVA results.

structured by location (ANOSIM, global $R = 0.14$; $P = 0.018$; pairwise ANOSIM results in Table 3), but the presence of the invader still had no impact on soil-dwelling invertebrate community structure. These differences were significant between the marsh plain and the transitional marsh, and this finding appears to be driven by the abundance of oribatid mites (13.57% dissimilarity) in the transitional marsh (SIMPER 53.00% dissimilarity).

Canopy-dwelling invertebrate community and diversity

The LRR for abundance of canopy-dwelling invertebrates differed among phenologic stages of *L. latifolium* ($F_{3,23} = 8.95$, $P = 0.002$; Table 4, Fig. 3). Abundances during peak flowering and the beginning of senescence were nearly twice those observed during full senescence or rosette stage (Appendix A). As indicated by a LRR different than zero, the presence of *L. latifolium* decreased canopy-dwelling invertebrate abundance during full senescence ($t_6 = -3.79$, $P = 0.013$; Table 5, Fig. 3). Interestingly, during *L. latifolium*'s peak flowering stage presence of the invader augmented canopy-dwelling arthropod abundances relative to other phenologic stages (Table 4), though the LRR was not significantly different from zero (Table 5, Fig. 3). SIMPER analysis shows the decreased abundance observed during

full senescence was driven by the presence of two species of macrochelid mites, a group of very small terrestrial mites, and Archaeognatha in non-*L. latifolium* invaded plots (mites: macrochelid: 4.45% dissimilarity, small terrestrial mites: 3.65% dissimilarity; Archaeognatha: 3.46% dissimilarity). The abundance of macrochelid mites was over four times higher in the non-*L. latifolium* area of the marsh plain than any other area of the marsh (Appendix A). SIMPER analysis showed the major organism driving increases in abundance in *L. latifolium* plots during peak flowering was the thrip, which had very high abundance in the *L. latifolium* plots.

Unlike patterns observed in abundance, *L. latifolium* altered species richness based on location within the marsh, not phenologic state of the invader ($F_{3,23} = 5.45$, $P = 0.021$; Table 4, Fig. 4). With nearly twice the number of species (Appendix A), the *L. latifolium* invaded plots in fringing marsh had higher species richness than the transitional marsh (Table 4), where *L. latifolium* presence significantly decreased the number of species recorded ($t_8 = -3.05$, $P = 0.018$; Table 6, Fig. 4). We observed no impact of *L. latifolium* on diversity (H') among the different phenologic states of *L. latifolium* or locations within the marsh (Table 4).

Among all times of sampling (corresponding to different *L. latifolium* phenologic states) the community structure of canopy-dwelling invertebrates differed significantly (ANOSIM, global $R = 0.60$, $P = 0.001$). Location within the marsh seemed to be the major structuring factor for canopy-dwelling arthropod communities. During the beginning of *L. latifolium* senescence, community composition was structured by location within the marsh, rather than presence of the invader (ANOSIM, global $R = 0.61$, $P = 0.001$;

Table 3. Results of pair-wise ANOSIMs by location within the marsh.

Location	Beginning senescence		Full senescence		Rosette		Peak bloom	
	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>
Soil-dwelling macrofauna								
Fringing marsh × marsh plain	0.91	0.190	0.05	0.268	0.01	0.437	0.05	0.232
Fringing marsh × transitional marsh	0.20	0.078	0.25	0.039	0.08	0.160	0.13	0.130
Marsh plain × transitional marsh	0.29	0.035	0.27	0.037	0.141	0.903	0.32	0.004
Canopy-dwelling arthropods								
Fringing marsh × marsh plain	0.30	0.057	0.08	0.314	0.25	0.143	0.31	0.057
Fringing marsh × transitional marsh	0.98	0.029	0.28	0.114	0.92	0.029	0.87	0.029
Marsh plain × transitional marsh	0.79	0.029	0.27	0.143	0.75	0.029	0.72	0.029

Note: Significant *P* values ($P < 0.05$) indicated in boldface.

Table 4. Results of the Two-way ANOVA for canopy-dwelling invertebrates.

Response variable	Source	Result	df	Adj MS	F	P
LRR abundance	season	(beg. sens. = rosette) \neq full sens. \neq peak	3	5.4844	8.95	0.002
	location	ns	2	1.3394	2.18	0.155
	season \times location	ns	6	1.309	2.14	0.124
	error		12	0.613		
LRR sp. richness	season	ns	3	0.1157	1.37	0.298
	location	(Fring. = Plain) \neq (Trans. = Plain)	2	0.44221	5.45	0.021
	season \times location	ns	6	0.10996	1.35	0.308
	error		12	0.08119		
LRR H'	season	ns	3	0.08675	1.54	0.256
	location	ns	2	0.04799	0.85	0.452
	season \times location	ns	6	0.08364	1.48	0.264
	error		12	0.05647		

Notes: Significant *P*-values ($P < 0.05$) indicated in boldface. Abbreviations are: LRR, log response ratio; Fring., fringing marsh; Plain, marsh plain; Trans., transitional marsh; beg. sens., beginning senescence; full sens., full senescence; peak, peak bloom.

pairwise ANOSIM results in Table 3). The distinctiveness of the canopy-dwelling invertebrates in the transitional marsh appears to be driven by presence of oribatid mites in this marsh location (SIMPER, percent similarity of transitional marsh samples due to oribatid mites, 12.09%). SIMPER results for canopy dwelling-invertebrates produce much lower values of similarity than SIMPER results for ground-dwelling invertebrates due to the specious nature of these samples. While *L. latifolium* was fully senescent, community composition was structured by both location within the marsh (ANOSIM, global $R = 0.23$, $P = 0.044$; pairwise

ANOSIM results in Table 3) and the presence of the invader (ANOSIM, global $R = 0.22$, $P = 0.045$). SIMPER analysis revealed that macrochelid mites drove 4.45% of the dissimilarity between *L. latifolium* and non-*L. latifolium* during this phenologic phase. Yet, during rosette stage, community structure was once again structured by location within the marsh rather than presence of *L. latifolium*. During this phase, the canopy-dwelling arthropod community in the transitional marsh differed from both the marsh plain and the fringing marsh (ANOSIM, global $R = 0.674$, $P = 0.002$; pairwise ANOSIM results in Table 3). Oribatid mites drove dissimilarity

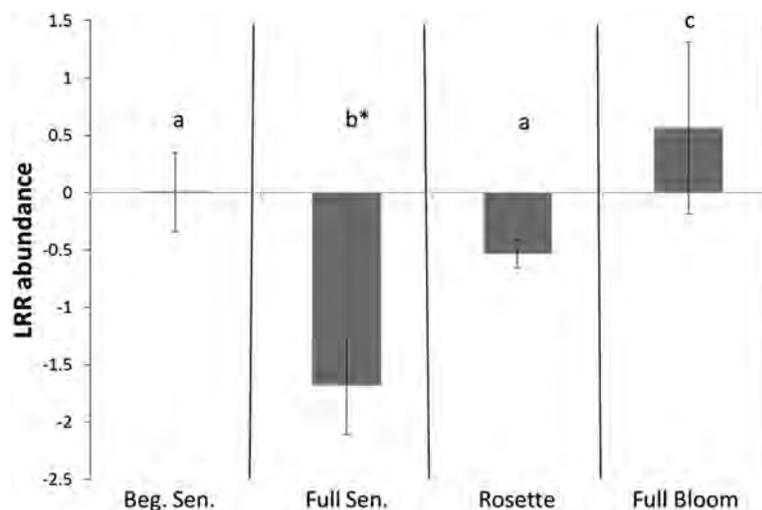


Fig. 3. LRR of canopy-dwelling invertebrate abundance by phenologic state sampling (averaged across location). Lower case letters indicate significant differences in LRR among time of sampling by SNK post-hoc comparison. An asterisk indicates LRRs that are significantly different from zero, indicating effect of *L. latifolium*. Abbreviations are: Beg. Sen., beginning senescence; Full Sen., full senescence; Rosette, rosette stage.

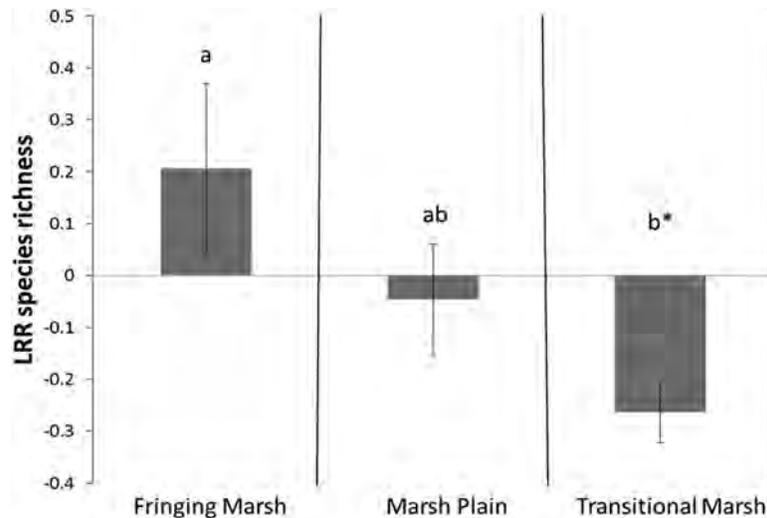


Fig. 4. LRR of canopy-dwelling invertebrate species richness by location (averaged across phenologic state of sampling). Lower case letters indicate significant differences in LRR among locations by SNK post-hoc comparison. An asterisk indicates LRRs that are significantly different from zero, indicating effect of *L. latifolium*.

between the transitional marsh and the other two locations (SIMPER, transitional marsh vs. marsh plain 2.83% of dissimilarity, transitional marsh vs. fringing marsh oribatid mites 2.99% of dissimilarity). While *L. latifolium* was in peak flower, community structure, again, differed based on location not the presence of the invader (ANOSIM, global $R = 0.60$, $P = 0.001$; pairwise ANOSIM results in Table 3). SIMPER results show these differences are predominately driven by several morphospecies of planthoppers which are not as prevalent in the transitional marsh (SIMPER, highest contribution to percent similarity in transitional marsh by planthoppers 1.12%).

Trophic community structure differed based on invader presence during *L. latifolium* rosette stage (ANOSIM, global $R = 0.252$, $P = 0.032$).

Table 5. Results of one-sample t-tests on LRR of canopy-dwelling invertebrate abundance.

Location	Result	df	<i>t</i>	<i>P</i>
Beginning senescence	ns	6	0.01	0.994
Full senescence	≠0	6	-3.79	0.013
Rosette	ns	6	-1.95	0.108
Full bloom	ns	6	1.19	0.289

Notes: Abundances pooled across marsh locations based on two-way ANOVA results. Significant *P*-value ($P < 0.05$) indicated in boldface.

SIMPER results indicate this pattern was driven by the detritivore and herbivore trophic groups (53.45% dissimilarity between plant types). Non-*L. latifolium* plots had significantly higher percent composition of detritivores than *L. latifolium*-invaded plots (ANOVA, $F_1 = 4.62$, $P = 0.057$). For full categorization of trophic groups, see Appendix B.

DISCUSSION

Returning to the hypothesized mechanisms previously discussed (based on Ehrenfeld 2010), our results support multiple possible mechanistic explanations for the observed impacts of *L. latifolium* on invertebrate communities in this brackish marsh. Although we cannot demonstrate causal links without manipulative studies, it is clear that *L. latifolium* impacts in the brackish

Table 6. Results of one-sample t-tests on LRR of canopy-dwelling invertebrate species richness.

Location	Result	df	<i>t</i>	<i>P</i>
Fringing marsh	ns	8	1.63	0.148
Marsh plain	ns	8	-0.43	0.682
Transitional marsh	≠ 0	8	-3.05	0.018

Note: Abundances pooled across phenologic states based on two-way ANOVA results. Significant *P*-value ($P < 0.05$) indicated in boldface.

marsh ecosystem are significant. Our findings suggest that the unique functional traits of *L. latifolium* (tall stems, large inflorescences, and seasonal senescence) allow the plant to act as an ecosystem engineer altering both trophic and community structural metrics.

Impacts of structural traits of *L. latifolium*: taller stems

Lepidium latifolium is distinctive within marsh habitats due, in large part, to the unique physical structure it creates. The transitional marsh zone within RROSP is characterized by upland grasses co-occurring with tidal marsh plants such as *Sarcocornia pacifica* (pickleweed), *Distichlis spicata* (salt grass), *Cressa truxillensis* (spreading alkaliweed), and *Frankenia salina* (alkali heath) (Whitcraft et al. 2011). *Lepidium latifolium*'s plant canopy is significantly taller (2 to 3 times) than that of native marsh plants in the transition zone (C. R. Whitcraft, unpublished data), which leads to altered conditions under *L. latifolium* as compared to under the non-*L. latifolium* canopy. Specifically, in some studies, *L. latifolium* allowed more light to penetrate to the marsh surface and decreased soil moisture (Reynolds and Boyer 2010); however, in other studies conducted in the same plots used for this study, C. R. Whitcraft (unpublished data) found *L. latifolium* reduced light penetration, increased humidity and decreased temperature in the transitional marsh within RROSP. Thus, in our study site *L. latifolium* ameliorates harsh abiotic conditions in the transitional marsh, coinciding with the increased abundance of soil-dwelling invertebrates and decrease in species richness of canopy-dwelling invertebrates we observed in invaded plots. Within marsh plain and the fringing marsh, where *L. latifolium* impacts were non-significant, the non-*L. latifolium* plant community is composed of taller vegetation including emergent macrophytes such as *Schoenoplectus* spp., and *Typha* spp., and the ameliorating advantage of *L. latifolium* observed in the transitional marsh may not be present. Our results demonstrate that the difference between *L. latifolium*'s canopy structure and that of non-*L. latifolium* canopy structure may impact the abiotic conditions and thus the soil-dwelling invertebrate communities in *L. latifolium*-invaded areas. These findings were consistent across different stages of *L. latifolium*

phenology, indicating the importance of both living and senescent vegetation on the outcomes of invasion.

Impacts of structural traits of *L. latifolium*: large seasonal inflorescence

Our data demonstrate that *L. latifolium* provides a variable physical habitat throughout the growing season by altering both percent cover and canopy structure (via stem angle to the ground) throughout the year. *L. latifolium* also produces an inflorescence that dwarfs other such phenologic events within RROSP (R. D. Wigginton and C. R. Whitcraft, personal observations) and provides a seasonal pulse of productivity. The abundance response of the canopy-dwelling arthropod community seems to be more influenced by the time sensitive, functional traits of *L. latifolium* (large inflorescence, stem angle to ground), while the response of the soil-dwelling invertebrates is influenced by the consistently present functional traits (tall stems).

When *L. latifolium* is largely senescent, abundance of canopy-dwelling invertebrates decreased; we hypothesize that these changes in available habitat (i.e., plant canopy) drive the abundance changes as observed in other systems. In terrestrial communities, canopy complexity has been shown to reduce abiotic stress, increase hunting or prey capture efficiency, or offer more predation protection for spiders (Gruner 2004 and the sources therein). Moreover, additional refugia offered by an increasingly complex plant canopy augmented arthropod predator abundance in soybean fields (Halaj et al. 2000). The importance of refuge habitat created by *L. latifolium* may be especially important in tidal wetlands where frequent tidal events result in the need to retreat higher into the plant canopy.

Trophic impacts of *L. latifolium*

In *L. latifolium* areas in the beginning senescent period, we observed a shift from an herbivore- and detritivore-based community to one dominated by predaceous species (detailed in Appendix B, dominant examples include carabid beetles and small predaceous mites). This compliments the results of Reynolds and Boyer (2010) who found *L. latifolium* stands had significantly higher densities of spiders. At RROSP, we found *L. latifolium* stem angle to the ground decreased

throughout its phenology, resulting in a large volume of layered standing stock, potentially creating more canopy complexity than what is found in dormant non-*L. latifolium* stands.

This implies that active, flowering *L. latifolium* might be beneficial to canopy-dwelling invertebrates, but senescent *L. latifolium* has the opposite effect. From this observation, we hypothesize that flowering *L. latifolium* is useful to canopy-dwelling invertebrates as a food source, but, as it progresses through its phenology and becomes more a structural than a trophic resource, its usefulness to invertebrates is turned into a detriment. Additional studies of invasion throughout the year will shed light on how living and senescent vegetation can impact communities in profound ways.

CONCLUSIONS

By examining multiple communities at the same time, this study revealed the *L. latifolium* invasion is impacting canopy-dwelling invertebrates to a greater degree than soil dwelling invertebrates. The changes observed in invertebrate assemblages may be due, predominantly, to the physical structure provided by the plant and the way this structure changes through the course of *L. latifolium*'s phenology. Additionally, both these groups of invertebrates are rarely studied in brackish marshes. These changes in invertebrate communities, brought on by a change in the plant community, could have cascading trophic effects, impacting higher order consumers such as marsh birds and fishes.

RROSP is a unique habitat, whose particular combination of human impacts result in a distinctive hydrology, plant community, and animal assemblage. Due to RROSP's condition as an altered fragment of tidal, brackish marsh, researchers must make predictions about how it will respond to climate change, salinity intrusion, and further plant invasion based on a smaller pool of data than when predicting outcomes for more naturally structured marshes in the estuary. By examining multiple invertebrate communities at once, we were able to determine that *L. latifolium* has differential impacts between communities, most strongly affecting canopy-dwelling invertebrates in the tidal marsh-terrestrial ecotone. Future studies should use such multi-

faceted approaches in order to inform short and long term land management.

Returning to the Ehrenfeld mechanisms (2010), our results highlight the interaction between multiple mechanistic explanations concerning invasive plant species-ecosystem relationships. Our results demonstrate that *L. latifolium*'s impacts on brackish marsh ecosystems are significant and potentially due to *L. latifolium*'s unique functional traits (tall stems, large inflorescence, and seasonal senescence) that enable it to act as an ecosystem engineer that alters community and trophic dynamics.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. Abundance, species richness and diversity (H') (mean \pm SE) for soil-dwelling invertebrates.

Diversity index	Location	Plant type	Beginning senescence	Full senescence	Rosette	Peak bloom
Abundance (N)	Transitional	LELA	34.33 \pm 3.48	66.67 \pm 13.45	21.67 \pm 12.25	53.67 \pm 17.97
		non-LELA	7.00 \pm 5.51	71.00 \pm 33.23	6.33 \pm 0.88	66.00 \pm 37.07
	Plain	LELA	11.00 \pm 5.20	17.33 \pm 6.36	5.67 \pm 1.45	51.33 \pm 28.17
		non-LELA	29.33 \pm 7.69	27.67 \pm 3.38	6.00 \pm 3.00	40.33 \pm 9.74
	Fringing	LELA	6.00 \pm 1.73	20.33 \pm 7.54	4.33 \pm 1.45	75.00 \pm 49.50
		non-LELA	9.33 \pm 3.84	20.33 \pm 5.78	11.00 \pm 1.53	17.33 \pm 4.63
Species richness	Transitional	LELA	5.67 \pm 0.33	6.67 \pm 2.03	2.67 \pm 0.88	6.00 \pm 1.53
		non-LELA	4.33 \pm 1.20	8.33 \pm 2.40	1.67 \pm 0.33	4.67 \pm 1.20
	Plain	LELA	3.33 \pm 0.88	3.33 \pm 0.33	3.33 \pm 0.88	3.67 \pm 0.33
		non-LELA	3.00 \pm 1.53	5.67 \pm 1.33	3.00 \pm 1.00	3.00 \pm 0.58
	Fringing	LELA	3.00 \pm 1.00	5.33 \pm 1.20	3.33 \pm 1.45	5.67 \pm 2.19
		non-LELA	5.67 \pm 1.20	5.00 \pm 1.73	2.67 \pm 1.20	5.00 \pm 1.53
Shannon-Weiner (H')	Transitional	LELA	1.67 \pm 0.06	1.07 \pm 0.31	0.35 \pm 0.22	1.12 \pm 0.49
		non-LELA	1.00 \pm 0.35	1.29 \pm 0.50	0.43 \pm 0.22	0.72 \pm 0.14
	Plain	LELA	0.89 \pm 0.21	0.77 \pm 0.24	0.88 \pm 0.14	0.45 \pm 0.11
		non-LELA	0.77 \pm 0.49	1.13 \pm 0.25	0.66 \pm 0.55	0.37 \pm 0.03
	Fringing	LELA	0.94 \pm 0.31	1.28 \pm 0.34	0.62 \pm 0.42	0.88 \pm 0.54
		non-LELA	1.55 \pm 0.23	1.12 \pm 0.38	0.69 \pm 0.41	1.05 \pm 0.36

Note: Abbreviations are: LELA, *L. latifolium* present; non-LELA, *L. latifolium* absent.

Table A2. Abundance, species richness and diversity (H') (mean \pm SE) for canopy-dwelling arthropods.

Diversity index	Location	Plant type	Beginning senescence	Full senescence	Rosette	Peak bloom
Abundance (N)	Transitional	LELA	588.25 \pm 399.75	72.50 \pm 42.50	91.25 \pm 24.75	142.00 \pm 40.00
		non-LELA	320.00 \pm 219.50	493.00 \pm 13.00	230.25 \pm 128.25	203.00 \pm 40.00
	Plain	LELA	460.75 \pm 204.25	73.50 \pm 28.50	240.75 \pm 108.75	650.50 \pm 29.50
		non-LELA	459.50 \pm 173.00	560.00 \pm 104.00	355.75 \pm 135.75	643.00 \pm 127.00
	Fringing	LELA	368.75 \pm 196.25	36.50 \pm 6.50	199.00 \pm 51.50	984.00 \pm 3.00
		non-LELA	623.75 \pm 280.25	109.50 \pm 73.50	293.25 \pm 56.75	128.50 \pm 4.50
Species richness	Transitional	LELA	28.00 \pm 0.00	14.00 \pm 3.00	36.00 \pm 6.00	25.50 \pm 6.50
		non-LELA	33.00 \pm 3.00	21.00 \pm 5.00	42.50 \pm 4.50	34.00 \pm 1.00
	Plain	LELA	38.00 \pm 4.00	17.00 \pm 2.00	39.50 \pm 1.50	44.50 \pm 0.50
		non-LELA	38.00 \pm 6.00	26.00 \pm 11.00	33.00 \pm 3.00	46.50 \pm 3.50
	Fringing	LELA	35.50 \pm 0.50	18.50 \pm 0.50	50.00 \pm 2.00	53.50 \pm 0.50
		non-LELA	37.50 \pm 3.50	17.50 \pm 5.50	46.00 \pm 2.00	27.00 \pm 0.00
Shannon-Weiner (H')	Transitional	LELA	1.54 \pm 0.46	2.24 \pm 0.14	2.86 \pm 0.06	2.37 \pm 0.53
		non-LELA	1.97 \pm 0.65	2.32 \pm 0.27	2.21 \pm 0.44	2.89 \pm 0.03
	Plain	LELA	1.99 \pm 0.23	2.12 \pm 0.51	1.99 \pm 0.47	2.53 \pm 0.07
		non-LELA	1.83 \pm 0.27	1.46 \pm 0.54	2.14 \pm 0.15	2.57 \pm 0.09
	Fringing	LELA	2.05 \pm 0.24	2.66 \pm 0.04	2.59 \pm 0.38	2.55 \pm 0.00
		non-LELA	1.88 \pm 0.04	2.16 \pm 0.08	2.14 \pm 0.15	2.54 \pm 0.07

Notes: Abundance for beginning of senescence and rosette stage are divided in half to account for longer sampling duration. Abbreviations are: LELA, *L. latifolium* present; non-LELA, *L. latifolium* absent.

APPENDIX B

Table B1. Trophic modes for canopy-dwelling invertebrates.

Taxonomic group	Predators	Detritivores	Herbivores	Klepto-parasites	Mycophagivores	Copro-phagivores	Multiple feeding types	Unknown
Subclass: Acari	Bdellidae sp. 1-6 Macrochelidae sp. <i>Neomolgus</i> sp.	Oribatida sp. 1 Oribatida sp. 2 <i>Traskorchestia</i> sp.						Acari sp. 1-3
Order: Amphipoda								
Order: Araneae	Araneidae sp. Gnaphosidae sp. Lycosidae sp. Oxyopidae sp. Salticidae sp. Thomisidae sp. Araneae sp. 1-2							
Order: Basommatophora			<i>Pseudosuccinea</i> sp. 1					
Order: Coleoptera	Carabidae sp. 1-5 Coccinellidae sp. 1-4 Melyridae sp. 1-3 Staphylinoidae sp.		Anobiidae sp. Byrrhidae sp. Chrysomelidae sp. 1-3 Elateridae sp. Leiodidae sp. Tenebrionidae sp. 1-2 Curculionidae sp. 1-3 Sminthuridae sp. 1				Ptilodactylidae sp.	Coleoptera sp. 1-2
Class: Collembola		Collembola sp. 1 Collembola sp. 2			Poduridae sp.			
Order: Diptera	Asilidae sp. Ceratopogonidae sp. 1-3 Dolichopodidae sp. 1-3 Muscidae sp. 1-5 Mythicomyiidae sp. Rhagionidae sp. Simuliidae sp. 1-3	Sphaeroceridae sp. 1 Tipulidae sp. 1 Ulidiidae sp. 1	Cecidomyiidae sp. 1-2 <i>Sciara</i> sp.			Sphaeroceridae sp. 1	Calliphoridae sp. Culicidae sp. Empididae sp. Phoridae sp.	Diptera sp. 1-39
Order: Hemiptera	Nabidae sp. 1-7 Geocoridae sp. 1-3 Hebridae sp. 1-5 Asopinae sp. 1-2 Reduviidae sp. 1-6		Cicadellidae sp. 1-23 Berytidae sp. Largidae sp. Pentomidae sp. 1-3 Murgantia histrionica Heteroptera sp. 1-9					Nymph sp. 1 Hemiptera sp. 1-3

Table B1. Continued.

Taxonomic group	Predators	Detritivores	Herbivores	Klepto-parasites	Mycophagivores	Copro-phagivores	Multiple feeding types	Unknown
Order: Hymenoptera	Bethylidae sp. <i>Trypoxylon</i> sp.		Tingidae sp. Halictidae sp.	Halictidae sp. 1 Bethylidae sp. 1			<i>Linepithema humile</i> <i>Tapinoma sessile</i> Braconidae sp. 1-5 Chalcidoidea sp. 1-2 Figitidae sp. 1-2 Ichneumonid sp. Mischocyttarus sp. Mymaridae sp.	Hymenoptera sp. 1-6
Order: Isopoda		<i>Porcellio scaber</i>						
Order: Lepidoptera			Lepidoptera sp. 1-4					
Order: Mantodea	<i>Mantis</i> sp.							
Order: Microcoryphia		Archeognatha sp. 1 Thysanura sp. 1						
Order: Neuroptera	Neuroptera sp.							
Order: Odonata	Odonata sp.							
Order: Orthoptera			Orthoptera sp. 1-5					
Order: Psocoptera							Psocoptera sp. 1-15	
Order: Pseudoscorpiones	Pseudoscorpiones sp.							
Order: Thysanoptera	Aeolothripidae sp. 1-2		Thysanopter sp.					

Notes: Organisms are listed within trophic classifications by the lowest taxonomic level possible. For the unknowns, this is primarily order. However, for other trophic categories this can be order, family, subfamily, genus or genus and species.