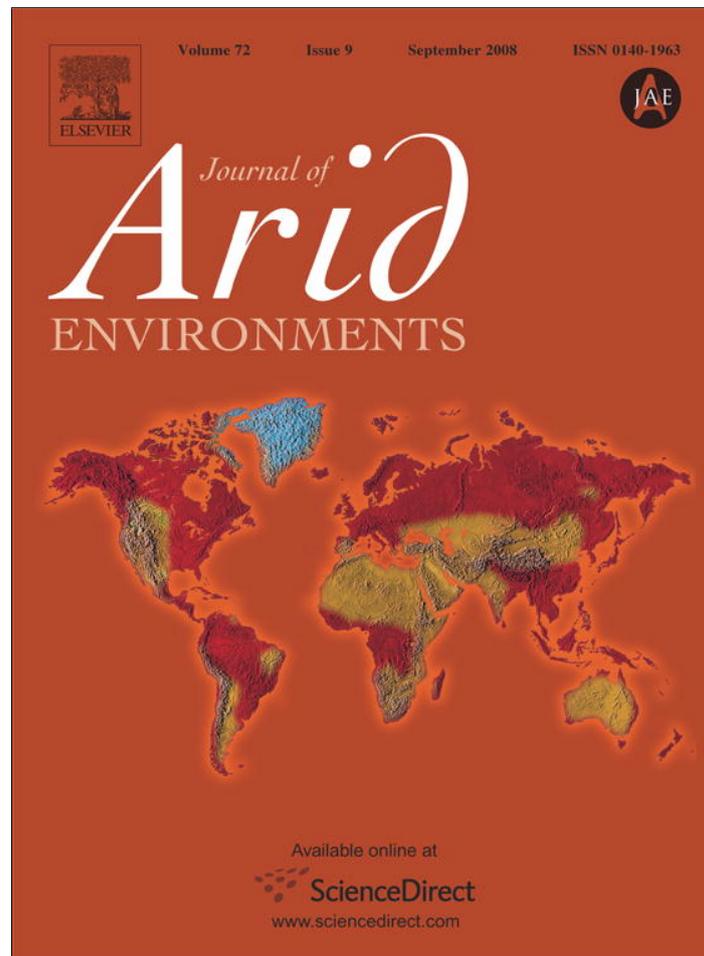


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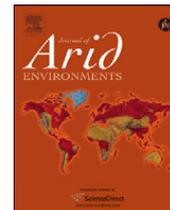
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Temporal variation in the arthropod community of desert riparian habitats with varying amounts of saltcedar (*Tamarix ramosissima*)

S.L. Durst^{a,b,*}, T.C. Theimer^a, E.H. Paxton^b, M.K. Sogge^b^a Department of Biological Sciences, Northern Arizona University, P.O. Box 5640, Flagstaff, AZ 86011, USA^b US Geological Survey, Southwest Biological Science Center, Colorado Plateau Research Station, Northern Arizona University, P.O. Box 5614, Flagstaff, AZ 86011, USA

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ABSTRACT

We used Malaise traps to examine the aerial arthropod community in riparian habitats dominated by native willow, exotic saltcedar, or a mixture of these two tree species in central Arizona, USA. Over the course of three sampling periods per year in 2003 and 2004, native habitats had significantly greater diversity (Shannon–Wiener) and supported different arthropod communities compared to exotic habitats, while mixed habitats were intermediate in terms of diversity and supported an arthropod community statistically indistinguishable from the exotic site. The composition of arthropod communities varied significantly between the two years, and there was an approximately two-fold difference in richness and diversity. Overall, we documented complex interactions indicating that differences among the arthropod communities of riparian habitats may be driven not only by the composition of native and exotic tree species making up these habitats, but also by year and season of arthropod sampling.

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1. Introduction

Invasion by non-native species into ecosystems has been ranked as the second greatest ecological threat worldwide, second only to habitat destruction, and has negatively impacted natural habitats across the globe (Levine et al., 2003; Vitousek et al., 1997). Invasion by exotic plants can reduce native plant species diversity and may also have consequences for organisms at higher trophic levels (Knops et al., 1999). However, relatively little is known about the effects of most alien plants on diversity of native insects (Samways, 2005).

Throughout the southwestern United States, many riparian areas formerly dominated by native cottonwoods (*Populus* spp.) and willows (*Salix* spp.) have transitioned to habitats dominated by exotic saltcedar (*Tamarix* spp.), now covering an estimated 500,000–650,000 ha across the American West (Zavaleta, 2000). Studies of the higher trophic level effects of saltcedar have focused primarily on vertebrates, especially birds (Brode and Bury, 1984; Cross, 1985; Ellis, 1995; Ellis et al., 1997; Hunter et al., 1988; Johnson et al., 1977; Knopf et al., 1988; Sogge et al., 2008; Szaro, 1991). However, because arthropods are an important food source for many amphibians, reptiles, mammals, and birds, the influence of saltcedar on the arthropod community could indirectly influence insectivorous vertebrates utilizing these riparian habitats. Although multiple studies have examined the arthropod communities of exotic saltcedar habitats (Cohan et al., 1978; Ellis et al.,

* Corresponding author at: US Geological Survey, Southwest Biological Science Center, Colorado Plateau Research Station, Northern Arizona University, P.O. Box 5614, Flagstaff, AZ 86011, USA. Tel.: +1 928 523 8142; fax: +1 928 556 7500.

E-mail addresses: scott.durst@nau.edu (S.L. Durst), tad.theimer@nau.edu (T.C. Theimer), eben.paxton@nau.edu (E.H. Paxton), mark_sogge@usgs.gov (M.K. Sogge).

2000; Liesner, 1971; Nelson and Andersen, 1999; Stevens, 1985; Wiesenborn, 2005; Yard et al., 2004), these studies have reached different conclusions suggesting that the effects of saltcedar on arthropod communities may be confounded by wide geographic separation of native and exotic habitats.

We reviewed previous studies of arthropod community responses to saltcedar to identify three hypotheses about how aerial arthropod communities in habitats dominated by saltcedar could differ from those in native willow habitats in areas where these habitats are in close proximity: (1) saltcedar habitats have arthropod communities lower in biomass and diversity compared to willow habitats (DeLoach et al., 2000; Dudley and DeLoach, 2004; Liesner, 1971; Yong and Finch, 1997); (2) saltcedar habitats support high arthropod biomass but the community is dominated by the saltcedar obligate *Opsius stactogalus*, an Old-World leafhopper co-introduced with saltcedar (Carothers and Brown, 1991; Liesner, 1971; Wiesenborn, 2005), and is not as diverse as native habitats (Stevens, 1985; Wiesenborn, 2005; Yard et al., 2004); or (3) saltcedar habitats support a community as diverse and potentially higher in biomass compared to native habitats because saltcedar's profuse and long-lasting flower and nectar resources attract "tourist" species from surrounding riparian and upland habitats (Drost et al., 2003; Nelson and Andersen, 1999).

Understanding the arthropod community associated with saltcedar habitats is made more complex because although saltcedar has formed extensive monocultures in many areas, in others saltcedar co-occurs with native willows and cottonwoods resulting in mixed habitats with both native and exotic components (Shafroth et al., 2005). Although there could be a fundamentally different response of arthropod communities to habitats with a mixture of native willow and exotic saltcedar compared to purely native and exotic habitats, few studies of arthropod abundance and diversity have considered this habitat type. In addition to the hypotheses we presented on how the arthropod communities may differ between purely native and exotic habitats, we propose two alternate hypotheses about arthropod community response in mixed habitats where saltcedar and willow intermingle compared to purely native or exotic habitats: (1) biomass and community composition are intermediate in mixed habitats compared to native and exotic dominated sites because elements of the arthropod community found in of both native and exotic habitats are present (Haddad et al., 2001); or (2) biomass and diversity are higher in mixed habitats because of the increased vegetation diversity compared to native or exotic monocultures (van Riper et al., 2008).

In this study, we examined the biomass, diversity, and community composition of aerial, diurnal arthropods inhabiting riparian habitats in a single drainage with areas dominated by native willow, exotic saltcedar, and mixed areas where these dominant riparian trees co-occurred. We focused on the aerial arthropod community because this group is potentially less tied to the dominant vegetation of a habitat and may be able to exploit different spatially and temporally abundant resources in riparian habitats, like the flowering of saltcedar (McGrath and van Riper, 2005). Although previous studies that compared arthropod communities of native willow and exotic saltcedar habitats often lumped samples across season and year, or examined seasonal or year effects without considering interactions with habitat (Cohan et al., 1978; Ellis et al., 2000; Mund-Meyerson, 1998; Wiesenborn, 2005; Yard et al., 2004), we accounted for temporal variation in the arthropod community by sampling across three seasonal periods during two consecutive years because environmental variation in primary productivity through time could also influence the arthropod community (Boag and Grant, 1984; Cody, 1981; Grant and Grant, 1987; Noy-Meir, 1973).

2. Materials and methods

2.1. Study site

We conducted this study at the Salt River inflow to Roosevelt Lake in central Arizona, USA (33°39'N, 110°58'W) during May–July in 2003 and 2004. The Salt River inflow rests in a broad floodplain ranging from 635 to 650 m in elevation, dominated primarily by approximately 200 ha of patchily distributed mosaic of riparian forest composed of Goodding's willow (*Salix gooddingii*) and saltcedar (*Tamarix ramosissima*). We classified riparian forest patches composed of >90% willow or saltcedar canopy as "native" and "exotic," respectively; and those patches with intermediate levels of willow and saltcedar canopy cover as "mixed". Patch boundaries were delimited by non-riparian vegetation or by different classification of riparian vegetation. Uplands surrounding the riparian floodplain are classified as Sonoran Desert Arizona Upland.

2.2. Arthropod sampling

Since we were interested in characterizing the aerial arthropod community, we used Malaise traps (model 2875AG, BioQuip Corporation, Gardena, CA) in contrast to previous studies that compared the arthropod communities associated with native willow and exotic saltcedar using pitfall trapping (to sample terrestrial arthropods; Ellis et al., 2000) and branch-sampling techniques (to sample arboreal arthropod; Cohan et al., 1978; Mund-Meyerson, 1998; Wiesenborn, 2005). Malaise traps effectively sample flying insects, especially Diptera, Hymenoptera, and Lepidoptera, although they may be biased against groups like Coleoptera and Homoptera that tend to fall to the ground when they encounter a barrier (Owen, 1983). We sampled the arthropod community in the largest native (7.4 ha), mixed (33.6 ha), and exotic (42.8 ha) habitat patches within the Salt River inflow with four Malaise traps during sampling periods in May, June, and July (hereafter

referred to as early, mid, and late sampling periods, respectively) resulting in 12 Malaise trap sampling sessions per habitat per year. We repeatedly sampled the same four randomly selected locations within each habitat across all seasonal periods in both years during approximate 12 h daytime periods (05:00–17:00 h) on a day in the middle of each month with consistently calm wind conditions and clear skies. We visually verified that all sampling locations had $\geq 75\%$ total canopy cover, similar vegetation density and understory cover density. Sampling locations were at least 1.5 km apart and all habitat patches were adjacent to the Salt River but separated from one another by either non-riparian vegetation or smaller riparian habitat patches that we did not sample.

Since only one patch of each habitat type was repeatedly sampled, patch differences could potentially confound any differences observed among habitat types. Therefore, to test for patch differences, we simultaneously sampled two different patches of all the three habitat types on one day after the mid-sampling event in 2003 by placing two Malaise traps at randomly selected locations within each patch. The vegetation characteristics of the sampling locations within the replicate patches were consistent with sampling locations in the repeatedly sampled patches. Each replicate patch was 560–2500 m from all other sampled patches. Patches that were replicates of native habitat were 2.5 and 5.6 ha, mixed replicate patches were 7.3 and 8.3 ha, and exotic replicate patches were 2.6 and 10.7 ha in size.

We stored arthropod samples in 70% ethanol and sorted them in order, family, and morphospecies (Wolda, 1990) according to standard references (Bland and Jaques, 1978; Borror et al., 1976). Morphospecies were numerically coded by order to distinguish among morphologically distinct individuals. We recorded the length to the nearest millimeter on a subset of each morphospecies to estimate biomass using regression equations relating length to biomass for the lowest taxonomic group possible (Hodar, 1996; Rogers et al., 1977).

We characterized the arthropod community with several different metrics, each providing different types of information. Total arthropod biomass can indicate arthropod carrying capacity and may also provide insight into important arthropod structure and functional characteristics in the ecosystem, such as their roles as plant pollinators and as food resources for other organisms (Price, 1984). We used two measures of diversity: richness, the number of morphospecies present for a given habitat and time period; and Shannon–Wiener diversity, measuring the heterogeneity of species within samples (Krebs, 1989). In addition, we used multivariate community analysis of the abundance and distribution of morphospecies to represent the dissimilarity of the arthropod community in Malaise samples among habitats and years.

2.3. Statistical analysis

To test for differences in total arthropod biomass, species richness, and Shannon–Wiener diversity among year, season, habitat, and the interactions among these factors, we used a repeated measures analysis of variance (ANOVA) with year and season as within subject fixed factors and habitat as an among subject fixed factor in SPSS version 14 (SPSS Inc., 2005). We considered each Malaise trap location as a random subject within habitat. We calculated significance of *F*-statistics with denominator degrees of freedom based on the partitioning of the total variance into the variability of subjects within-habitat because subjects were a random effect, while numerator degrees of freedom were calculated based on the levels of each factor or interaction of factors. To meet normality and variance assumptions, we log-transformed biomass values that were standardized by sampling time (Sokal and Rohlf, 1995). We identified samples that may have captured anomalous, highly localized arthropod outbreaks based on an outlier analysis using the program PC-ORD (McCune and Mefford, 1999). Outliers were defined as those samples with a mean Euclidean distance greater than one standard deviation from the grand mean Euclidean distance of all samples. Two Malaise samples in mixed habitat from 2003 (one from early and one from mid sampling periods) were excluded on this basis and were not considered in any summaries or analyses presented herein. Because the repeated measures ANOVA required a balanced sampling design, we used the method of Zar (1999) to estimate biomass, richness, and diversity values for the removed outliers.

To test the hypothesis of no difference among the arthropod communities (incorporating both abundance and composition) by year and habitat within each year, we used a multi-response permutation procedure (MRPP) based on Euclidean distance measure available through PC-ORD (McCune and Mefford, 1999). The number of individuals of each morphospecies was log-transformed to account for the high degree of variability among samples and to compress the impact of those samples with large abundances (McCune and Grace, 2002). We calculated the chance corrected within-group agreement (*A*) for year and habitat comparisons, such that when $A = 1$ all within group samples are identical; when $A = 0$ within-group heterogeneity equals that expected by chance; and when $A < 0$ there is less within group heterogeneity than expected by chance (Zimmerman et al., 1985). Within each year, we conducted post hoc, pair-wise comparisons of differences between the arthropod community between native, mixed, and exotic habitats adjusting the level of statistical significance using a Bonferroni correction ($\alpha = 0.05/3 = 0.017$; Sokal and Rohlf, 1995).

To determine morphospecies associated with each habitat and potentially responsible for the patterns observed in the MRPP analysis, we conducted an indicator species analysis by habitat combining both years. An indicator species value (*INDVAL*) is based on specificity (the relative abundance of each morphospecies in each habitat grouping) and fidelity (the relative frequency of each morphospecies in each habitat grouping) (Duf rene and Legendre, 1997). A randomization method was used to determine significant indicator species by randomly assigning sampling units 1000 times, calculating an *INDVAL* and comparing the proportion of randomized *INDVAL*s that were equal to or greater than the *INDVAL* from the

original dataset to arrive at a p -value. We considered significant indicator species associated with a given habitat if they had an $INDVAL > 25$ and were represented by ≥ 100 total individuals across all habitats over both years.

To graphically represent the degree of dissimilarity of the arthropod community among Malaise samples by year and habitat within year, we used non-metric multi-dimensional scaling (NMS; Kruskal, 1964; Mather, 1976). We used PC-ORD to create a Bray-Curtis distance dissimilarity matrix based on the distribution of different morphospecies in each Malaise sample. Multiple iterations of the dissimilarity matrix were run to obtain a configuration of points in space with minimal stress that best represented the actual degree of dissimilarity between the individual samples. We coded samples according to year and habitat to represent the association of the different samples to one another.

To test the hypothesis that our three repeatedly sampled patches were representative of native, mixed, and exotic habitats within the Salt River drainage at Roosevelt Lake, we compared the arthropod communities of the six replicate patches with the three repeatedly sampled patches from the mid sampling event in 2003. We combined Malaise samples within each patch to characterize the mean arthropod community of each patch classified by habitat type (two replicate patches and one repeatedly sampled patch of each habitat type). To test for differences among habitat types and graphically represent the dissimilarity among habitat types, we used the same MRPP and NMS techniques, respectively, as described previously. Statistical significance for all tests was set at $\alpha = 0.05$, except for Bonferroni corrected habitat comparisons ($\alpha = 0.017$). Where appropriate, we presented variance estimates for mean values as standard error of the mean, except as otherwise noted.

3. Results

We captured a total of 24,749 individuals representing 147 morphospecies in 58 families and 14 orders from 70 Malaise traps covering 840 h of sampling.

3.1. Arthropod biomass, richness, and diversity

Total arthropod biomass averaged $38.4 \text{ mg h}^{-1} (\pm 3.2)$ per Malaise trap and ranged from 6.0 to 193.5 mg h^{-1} across the two years of the study. We found a marginally significant interaction between year and season ($F_{2,18} = 3.6, p = 0.05$) but no other significant interactions (year \times season \times habitat: $F_{4,18} = 1.8, p = 0.17$; season \times habitat: $F_{4,18} = 0.4, p = 0.78$; year \times habitat: $F_{2,9} = 1.5, p = 0.27$). Biomass generally decreased in the late sample in 2003 and increased in 2004, and there was a pronounced spike in biomass in the middle period in mixed habitat in 2003 that was not evident in 2004 (Fig. 1a). Considering each factor individually, biomass did not vary significantly between years ($F_{1,9} = 4.3, p = 0.07$), among seasons ($F_{2,18} = 0.2, p = 0.82$), or among habitats ($F_{2,9} = 0.2, p = 0.86$) (Fig. 1a).

Mean morphospecies richness per Malaise trap was $21.0 (\pm 1.1)$; range: 6–48). Again there was a marginally significant interaction, in this case between year and habitat ($F_{2,9} = 4.3, p = 0.05$), but with no other significant interactions (year \times season \times habitat: $F_{4,18} = 2.2, p = 0.11$; season \times habitat: $F_{4,18} = 1.7, p = 0.19$; year \times season: $F_{2,18} = 0.6, p = 0.56$). Mean richness in 2003 (29.0 ± 1.1) was more than double that of 2004 (13.5 ± 0.7) and was higher in all seasons and habitats during 2003 (year: $F_{1,9} = 284.6, p < 0.001$; Fig. 1b), but this annual difference was greatest at the mixed habitat site and smallest for the native habitat site. However, we found no significant differences in richness among habitats ($F_{2,9} = 2.9, p = 0.11$) and only a marginal difference among seasons (early: 22.8 ± 2.1 ; mid: 20.1 ± 2.1 ; late: 18.6 ± 1.7 ; $F_{2,18} = 3.6, p = 0.05$).

We found significant interactions between year and habitat ($F_{2,9} = 10.6, p = 0.004$) and season and habitat ($F_{4,18} = 3.6, p = 0.02$) in Shannon–Wiener diversity, but not between year and season ($F_{2,18} = 1.4, p = 0.28$) or in the three-way interaction ($F_{4,18} = 1.8, p = 0.17$). Mean diversity was consistently higher in 2003 than in 2004 (2.4 ± 0.1 versus 1.5 ± 0.1 , respectively; $F_{1,9} = 180.8, p < 0.001$; Fig. 1c). In 2003, diversity was equal in native and mixed habitats (2.6 ± 0.1) but less in exotic (2.1 ± 0.1); in 2004, diversity was greatest in the native site (1.9 ± 0.2), intermediate in the exotic (1.5 ± 0.1), and least in the mixed site (1.2 ± 0.1 ; Fig. 1c). In 2003, diversity of the native site was consistent through the three sampling periods while diversity in the mixed site increased across the season. In 2004, native and mixed habitats reversed seasonal diversity patterns; native habitat diversity increased through the season and mixed diversity remained constant. The exotic habitat showed similar seasonal diversity patterns each year; diversity was lowest during mid-season sampling periods, but late season diversity reached early-season levels in 2003, while in 2004 it did not.

3.2. Arthropod community composition

The arthropod communities were significantly different between the two years ($A = 0.107, p < 0.0001$) and clearly separated in ordination space (Fig. 2a). Within each year, the arthropod communities of the native, mixed, and exotic habitat sites were significantly different (2003: $A = 0.085, p < 0.0001$; 2004: $A = 0.041, p < 0.0001$), and more distinct by habitat in 2003 compared to 2004 (Fig. 2b).

Based on pair-wise comparisons of each habitat within 2003 and 2004 (Bonferroni corrected $\alpha = 0.017$), the arthropod community of the native habitat was significantly different from the mixed (2003: $A = 0.060, p = 0.003$; 2004: $A = 0.047, p = 0.001$) and exotic habitat (2003: $A = 0.106, p < 0.001$; 2004: $A = 0.053, p < 0.001$) in both years. However, there was no

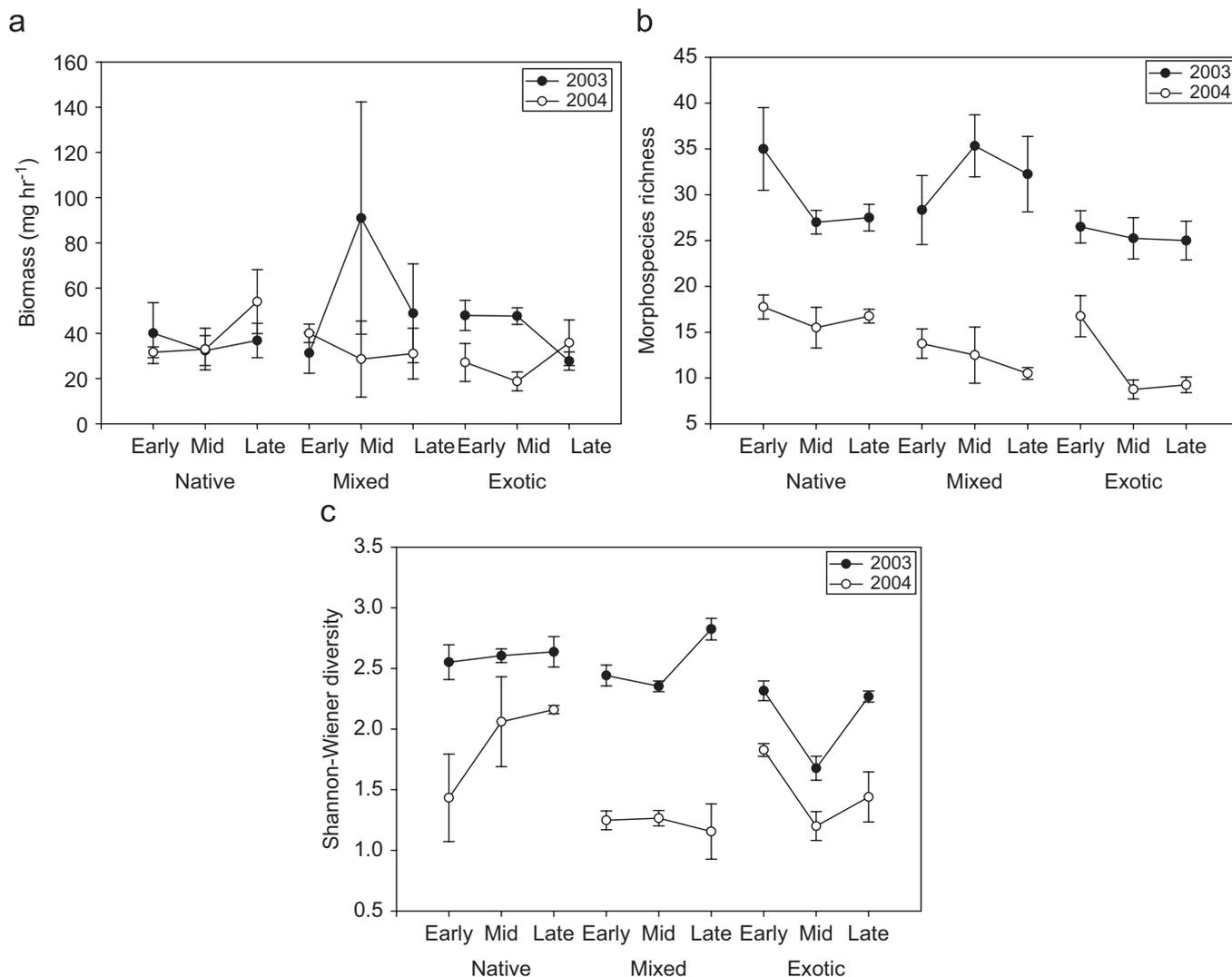


Fig. 1. Mean (\pm S.E.) total arthropod biomass (mg h^{-1}) (a), morphospecies richness (b), and Shannon–Wiener diversity (c) in three seasons of 2003 (solid circles) and 2004 (open circles) in sites dominated by native, mixed or exotic vegetation.

statistical difference between the arthropod communities of mixed and exotic habitats in either year (2003: $A = 0.028$, $p = 0.026$; 2004: $A = -0.004$, $p = 0.654$).

Twelve morphospecies were significantly associated with a habitat when results were combined across years. Seven morphospecies associated with native habitats included representatives from Diptera, Homoptera, and Hymenoptera. Three morphospecies were significantly associated with mixed habitats, including two Diptera and one Hymenoptera. Finally, exotic habitat had two morphospecies associated with it, one Diptera and one Homoptera (*O. stactogalus*) (Table 1). Although *O. stactogalus* was a significant indicator species of exotic habitat, two Diptera morphospecies (in the families Dolichopodidae and Muscoidea) were more abundant (Table 1). We also found two morphospecies (a different member of the family Dolichopodidae and the same member of Muscoidea abundant in exotic habitat) that were numerous in all three habitats and equally or more abundant in mixed and exotic habitats than native habitats (Table 1).

3.3. Replicate patch sampling

The arthropod communities of both the replicate and repeatedly sampled patches differed significantly among native, mixed, and exotic habitat types ($A = 0.148$, $p = 0.023$; Fig. 3), indicating that patches were more similar within than among habitat types. The pattern we observed in the repeatedly sampled patches, that the arthropod community of the native habitat was more distinct compared to mixed and exotic patches, was similar to that documented in the replicate samples (Fig. 3). Additionally, the overlap evident between the replicate mixed and exotic habitat patches (Fig. 3) was also observed in our repeated sampling effort. Together, these results suggest that the patterns we noted in the repeatedly sampled patches were representative of native, mixed, and exotic habitat patches within the Roosevelt Lake drainage.

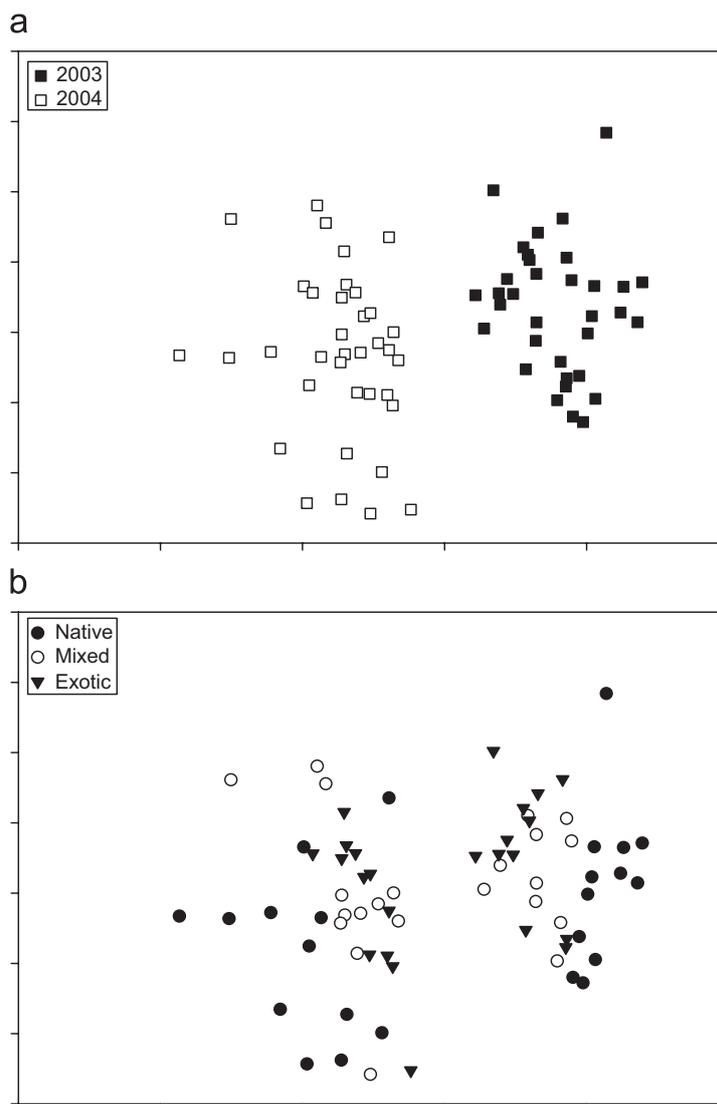


Fig. 2. Two-dimensional NMS ordination of the arthropod communities by year (a) and habitat (b). Each point represents the arthropod community of one Malaise sample (classified by year and habitat) in ordination space. We presented the two-dimensional ordination (final stress = 21.9) for the sake of graphic simplicity although the three-dimensional ordination best represented the data (final stress = 13.6). The variation expressed in the third axis did not alter the interpretation of our results.

4. Discussion

We detected relatively small differences in measures of biomass, richness, and diversity among native, mixed, and exotic riparian habitats in part due to the influence of temporal variation on the arthropod community. Our results offered some support for all three competing hypotheses that we identified about how aerial arthropod communities could differ among purely native and exotic habitats, but no one hypothesis was entirely supported. While our data did not support the hypothesis that exotic saltcedar habitats have arthropod communities lower in biomass and richness compared to native willow habitats, native habitat did have consistently higher diversity than exotic habitats despite significant seasonal and yearly interactions. The lack of a significant difference in biomass between native and exotic habitats suggests that these two habitats have the potential to support similar amounts of arthropods, even if the diversity comprising that biomass is lower in exotic habitats. The equivalent arthropod biomass and lower diversity of exotic habitats compared to native habitats offered support for the second hypothesis, but exotic habitats were not entirely dominated by *O. stactogalus*. Although *O. stactogalus* was a significant indicator species of exotic habitat in our study, it was not the most numerous species detected in this habitat, unlike saltcedar-dominated habitats in other studies (Carothers and Brown, 1991; Stevens, 1985; Wiesenborn, 2005; Yard et al., 2004). Two Diptera morphospecies were approximately twice as abundant as *O. stactogalus* and the combined abundance of these three groups accounted for more than 60% of the total abundance in exotic habitat and likely together contributed to lower the overall diversity of exotic habitat compared to native habitat. The numerical dominance of *O. stactogalus* in exotic habitats documented at other study sites (Carothers and Brown, 1991; Liesner, 1971; Stevens, 1985; Wiesenborn, 2005) may in part be driven by differences in sampling methodology.

Table 1

The four most abundant arthropod morphospecies by habitat and all morphospecies significantly associated with a particular habitat over both years

Habitat	Morphospecies	Family	<i>n</i>	<i>INDVAL</i>	<i>p</i>
Native	Diptera-28 ^a	Dolichopodidae	1230	–	–
Native	Diptera-9	Chironomidae	611	–	–
Native	Diptera-60 ^a	Muscidae	442	–	–
Native	Diptera-62	Culicidae	299	34.6	0.028
Native	Diptera-30	Pipunculidae	290	27.8	0.01
Native	Hymenoptera-12	Ichneumonidae	163	33.8	0.013
Native	Homoptera-4	Cixiidae	137	59.9	0.001
Native	Hymenoptera-17	Ichneumonidae	112	41.7	0.002
Native	Hymenoptera-44	Formicidae	106	43.2	0.001
Native	Hymenoptera-5	Pompilidae	98	28.9	0.045
Mixed	Diptera-28 ^a	Dolichopodidae	3220	43.3	0.004
Mixed	Diptera-60 ^a	Muscidae	1128	–	–
Mixed	Homoptera-3	Cicadellidae (<i>Opsius stactogalus</i>)	874	–	–
Mixed	Hemiptera-1	Miridae	485	–	–
Mixed	Diptera-25	Tephritidae	371	33	0.034
Mixed	Hymenoptera-46	Formicidae	57	27.6	0.023
Exotic	Diptera-59	Dolichopodidae	2479	–	–
Exotic	Diptera-60 ^a	Muscidae	2053	39.6	0.006
Exotic	Homoptera-3	Cicadellidae (<i>Opsius stactogalus</i>)	1154	43.8	0.006
Exotic	Diptera-28 ^a	Dolichopodidae	1018	–	–

The number of individuals captured by habitat is represented by “*n*” along with the *INDVAL* and *p*-value. Morphospecies without an *INDVAL* were among the four most abundant arthropods in a given habitat but were not significantly associated with that habitat.

^a Morphospecies common to all three habitats.

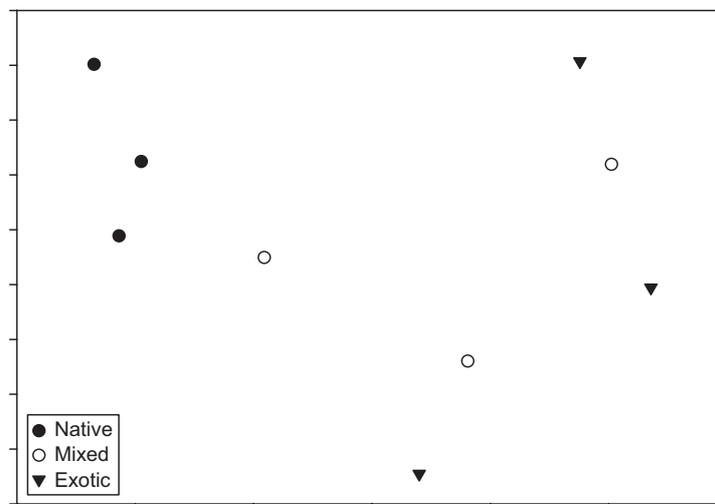


Fig. 3. Two-dimensional NMS ordination of the arthropod communities by habitat for repeatedly sampled patches from the mid-sampling period in 2003 and two replicate patches for each habitat sampled the following day. Each point represents the mean arthropod community of one patch. The two-dimensional solution was most suitable for this data (final stress = 4.8).

O. stactogalus is a Cicadellid leafhopper that feeds on vegetative substrates and may be more likely to be captured in higher proportions using branch sampling techniques compared to Malaise traps (Durst, 2004). It was difficult to assess the level of support for the aspect of our third hypothesis that saltcedar dominated habitats may attract “tourist” species (Drost et al., 2003; Nelson and Andersen, 1999). While our results did not support the hypothesis that saltcedar-dominated habitats have higher arthropod biomass and are as diverse as native habitats, we did document morphospecies that were as abundant or more abundant in exotic habitats than native habitats. For example, of the three most abundant morphospecies documented in native habitat (all Diptera), one was found in greater than five times the abundance and one was found in approximately equal abundance in exotic habitat; however, to what degree this represents movement to saltcedar-dominated habitats from native habitats to exploit flowering resources would require an assessment of the morphospecies’s ecology (e.g., whether they are pollinators) and evaluation of saltcedar flowering phenology. Nevertheless, we did identify morphospecies that were able to use a variety of habitats, including those dominated by both native willow and exotic saltcedar.

The entirety of evidence accumulated from biomass, richness, diversity, and community composition measures indicated considerable overlap between the arthropod communities in exotic and mixed habitats across both years, possibly driven by the saltcedar component common between these habitats. These results provide more support for the hypothesis that mixed habitats are intermediate between purely native and purely exotic habitats (Haddad et al., 2001) than the hypothesis that mixed habitats have greater biomass and diversity because of increased vegetation diversity (van Riper et al., 2008). Support for the former hypothesis is consistent with results that aerial arthropod were found in intermediate abundance in areas where exotic giant reed (*Arundo donax*) grew interspersed with native willows compared to abundance in purely exotic and native stands of these vegetation types (Herrere and Dudley, 2003). However, the proportional mixture of native to exotic vegetation in these mixed habitats will likely influence the degree of overlap in the arthropod communities.

How general our findings are beyond the patches we studied remains an important question. At our study site, native, mixed, and exotic habitats occurred in relatively close proximity to each other and to upland Sonoran Desert habitat, so the potential existed for aerial arthropods to move among the adjacent riparian and surrounding upland habitat types. Although there was overlap in some morphospecies across all riparian habitats, we were able to document significantly different arthropod communities in native and exotic habitats. Still, overlap in species composition among riparian habitats at our study site could indicate that species which we detected in any one habitat occurred there only because of the close proximity of the other habitats. When entire drainages are dominated by an exotic species like saltcedar or when riparian habitats are set within an agricultural or urban matrix that supports a depauperate or different arthropod fauna compared to the relatively species-rich Sonoran Desert Uplands of our study region, aerial arthropod communities may show different patterns than we documented. For example, butterflies associated with agriculture (such as Orange Sulphur, *Colias eurytheme*) were found both in sites dominated by saltcedar and by native riparian vegetation that were in close proximity to agricultural fields (Nelson and Andersen, 1999). Clearly, studies of arthropod communities in riparian habitats will reach different conclusions in part due to landscape-level differences in the distance, size, composition, and arrangement of riparian patches but also due to effects of the vegetation surrounding these habitats.

Our findings suggest that temporal factors of year and season may have a larger effect on arthropod abundance and diversity than vegetation composition. These temporal differences may be an additional reason why studies reach divergent conclusions on how arthropod communities vary among riparian habitats. The substantial temporal variation we found in richness and diversity was likely due to the influence of environmental variation on the primary productivity that ultimately supports the aerial arthropod community (Boag and Grant, 1984; Cody, 1981; Grant and Grant, 1987; Noy-Meir, 1973). There were strong annual differences in richness and diversity, with 215% more species present and 160% greater diversity in 2003 than in 2004. This large difference in the arthropod communities between years was driven by both changes in relative abundances of some morphospecies and the appearance or loss of some morphospecies that were detected in only one of the two years. Only half as much late winter and early spring rain fell at Roosevelt Lake in 2004 compared to 2003 and that may have in part driven the annual differences in richness, diversity, and community composition. Because the arthropod community serves important ecological roles such as pollinators and as prey for insectivores (Price, 1984), these temporal differences could influence trophic levels above and below the arthropod community in these riparian habitats. For example, in the same drainage studied here, Durst et al. (in review) found substantial yearly variation in the diet of Southwestern Willow Flycatchers (*Empidonax traillii extimus*), a diurnal, insectivorous passerine, likely in response to the temporal variation in arthropod availability that we documented in this study.

Overall, our study indicates that, at the spatial scales we considered, exotic saltcedar-dominated habitats supported similar arthropod biomass but a less diverse and distinct arthropod community than nearby native habitats. The effect of these differences between exotic and native habitats on higher trophic level interactions will depend on how dependent individual insectivores are on specific components of the arthropod community. This could be of important management concern in the southwestern United States for several candidate and endangered insectivorous bird species, including Least Bell's Vireos (*Vireo bellii pusillus*), Southwestern Willow Flycatchers, and Western Yellow-Billed Cuckoos (*Coccyzus americanus occidentalis*) (US Fish and Wildlife Service, 1986, 1995, 2007). If these birds are able to exploit the abundant arthropod community present in saltcedar dominated habitats, then the amount of food resources available in exotic and native habitat should be similar. Alternatively, for those species unable to utilize the major components of the arthropod community (including *O. stactogalus*) in habitats dominated by saltcedar then these habitats may be less suitable than native habitats. However, differences in the arthropod communities among the riparian habitats we studied were far less striking than differences due to temporal variation, underscoring that comparisons of aerial arthropod communities across desert riparian habitat types should consider the potential for patterns to vary across years and seasons.

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