Arthropod-Plant Interactions (2010) 4:237–245
DOI 10.1007/s11829-010-9105-4

ORIGINAL PAPER

Comparisons of arthropod assemblages on an invasive and native trees: abundance, diversity and damage

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Received: 18 March 2009 / Accepted: 3 August 2010 / Published online: 22 August 2010

Abstract The success of exotic plants may be due to lower herbivore loads than those on native plants (Enemies Release Hypothesis). Predictions of this hypothesis include lower herbivore abundances, diversity, and damage on introduced plant species compared to native ones. Greater density or diversity of predators and parasitoids on exotic versus native plants may also reduce regulation of exotic plants by herbivores. To test these predictions, we measured arthropod abundance, arthropod diversity, and foliar damage on invasive Chinese tallow tree (*Triadica sebifera*) and three native tree species: silver maple (*Acer saccharinum*), sycamore (*Platanus occidentalis*), and sweetgum (*Liquidambar styraciflua*). Arthropod samples were collected with canopy sweep nets from six 20 year old monoculture plots of each species at a southeast Texas site. A total of 2,700 individuals and 285 species of arthropods were caught. Overall, the species richness and abundance of arthropods on tallow tree were similar to the natives. But, ordination (NMS) showed community composition differed on tallow tree compared to all three native trees. It supported an arthropod community that had relatively lower herbivore abundance but relatively more predator species compared to the native species examined. Leaves were collected to determine damage. Tallow tree experienced less mining damage than native trees. The results of this study supported the Enemies Release Hypothesis predictions that tallow tree would have low herbivore loads which may contribute to its invasive success. Moreover, a shift in the arthropod community to fewer herbivores without a reduction in predators may further limit regulation of this exotic species by herbivores in its introduced range.

Keywords Arthropod diversity · Community structure · ERH · Herbivory · Invasions · Trophic structure

Introduction

The introduction of invasive species is an increasing problem in many habitats (Mack et al. 2000). Invasive species have been recognized as a major cause of biodiversity loss (Vitousek et al. 1996) and a number of hypotheses have been proposed to explain their success (e.g. Blossey and Nötzold 1995; Keane and Crawley 2002; Shea and Chesson 2002). One hypothesis is the Enemies Release Hypothesis (ERH) that proposes alien species are introduced without their specialist herbivores or diseases from their native range which might give them a competitive advantage over native species (e.g. Colautti et al. 2004; Liu and Stiling 2006).

The Enemies Release Hypothesis has been the subject of numerous studies and there have been a number of reviews (e.g. Maron and Vila 2001; Sakai et al. 2001; Keane and Crawley 2002; Shea and Chesson 2002; Colautti et al. 2004; Liu and Stiling 2006). One insight from these syntheses is that there are a variety of mechanisms gathered

Handling Editor: Walter Carson.

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under this one named hypothesis (Mitchell et al. 2006). First, lower enemy loads (herbivores and diseases) in the introduced range versus native range may cause performance of exotic plants to be superior in the introduced range (Liu and Stiling 2006). Second, such differences in enemies may cause evolutionary reductions in plant defenses such that herbivore resistance is lower for populations in the introduced range versus those in the native range of exotic plants (Blossey and Nötzold 1995; Bossdorf et al. 2005). Finally, the traditional formulation of this hypothesis which dates to Elton (1958) predicts lower herbivore loads on exotic plants versus native plants.

In reviewing this traditional version of the ERH, Colautti et al. (2004) found that a slight majority of studies supported the ERH predictions of lower herbivore abundance or diversity on exotic plants compared to native plants. However, the literature was dominated by single species studies, correlative studies, and short-term community (multiple species) studies in old fields. Since that review, there have been additional tests (e.g. Proches et al. 2008) but none have included multiple-species, been long-term, or been replicated experiments.

The structure of arthropod communities of exotic and native plants may differ in ways other than in herbivore abundance and diversity. For instance, the diversity of higher trophic levels may be lower on exotic plants than on native plants because of the positive dependence of predator and parasitoid species richness on herbivore species richness (Siemann et al. 1998). Moreover, a lower abundance of herbivores may cause a lower abundance of higher trophic levels or a greater abundance of detritivores.

The only test of this to date by Proches et al. (2008), found that exotic plants had lower herbivore abundance and diversity than native plants within congeneric pairs but that the diversity and abundance of other trophic groups (predators, parasitoids, detritivores) were comparable. They suggested that this was due to predators and parasites responding to physical structure which tends to be relatively similar for exotic versus native plants in a genus but a need for a plant to be a suitable food source for herbivores. Moreover, they suggested that detritivores were similar to extremely general herbivores and so would be relatively insensitive to differences in host plants compared to more specialized herbivores.

We sampled arthropods from replicated, long-term monoculture plantings of the invasive Chinese Tallow Tree and three native tree species in order to test the following predictions: (1) arthropod community composition (trophic structure, abundance and species richness) on tallow tree will be different than the arthropod communities found on the three native tree species; (2) tallow tree will have fewer herbivores, lower diversity of herbivores, and lower levels of damage than the three native trees.

Materials and methods

Focal species

Chinese Tallow Tree [*Triadica sebifera* (L.) Small, Euphorbiaceae, synonyms include *Sapium sebiferum*], is an aggressive invader of coastal prairie, forests, and disturbed areas in the southern United States (Bruce et al. 1997). Originally from Asia, it was introduced to Georgia in the late 18th century and to Texas in the early 20th century. Tallow tree's potential uses such as biomass crop and its status as a popular ornamental have further encouraged its spread (Bruce et al. 1997). It is a dominant invasive species that has the ability to form monospecific stands that may further exclude native flora and fauna. It experiences low levels of herbivory as seedlings in Texas (Siemann and Rogers 2003a, b).

This study was conducted in a mature, established plantation with silver maple (*Acer saccharinum* L. Aceraceae), American sycamore (*Platanus occidentalis* L. Platanaceae), and sweetgum (*Liquidambar styraciflua* L. Hamamelidaceae). These three species are native to the United States. Sweetgum is distributed throughout the east and southeast portions of the United States. American sycamore is widespread in the eastern United States. Silver maple is distributed throughout most of the eastern United States. Although silver maple is not considered native to the state of Texas it commonly co-occurs in the introduced range of tallow tree in Louisiana, Mississippi, Alabama and Florida (Burns and Honkala 1990). For information on specific insects known to attack the native tree species refer to Burns and Honkala (1990).

Study design

The study was conducted at the University of Houston Coastal Center, a 374 ha research area, located 50 km south east of Houston, Texas. Approximately 75% of the research area consists of tallow tree stands in areas that originally would have been tallgrass prairie. This study was conducted in established plantations of monospecific stands. One plantation was established in the 1970s to study the potential of each species as a biomass crop. The plantation is divided into 30 eight by six meter plots. Corridors of 4 m exist between the plots and have sparse undergrowth. Each plot consists of one species either: silver maple (8 plots total), sycamore (8), sweetgum (7), tallow tree (5), or juniper (*Juniperus virginiana* L.–2). Although there were tallow tree and juniper plots in the plantation, they were in poor sampling condition, being patchy and with dense undergrowth. Therefore, tallow tree was sampled from plots in an immediately adjacent plantation planted in the same year (separated by a 3 m mowed alley). This was not an ideal design since it potentially confounds species and location.

In total, six plots of each focal species were chosen. Plots were selected for minimal undergrowth. Within each plot, two-eight meter transect lines were established and treated as one sample. Each plot (transect measuring 16 m) was sampled four times during the season. Plots were sampled in rotation eight at a time (a pair of plots for each species) to allow time for recolonization by arthropods. For instance, maple plots 16 and 27 were sampled on June 21 (2nd sampling), July 12 (5th), July 31 (8th), and September 27 (11th) and maple plots 4 and 15 were sampled on June 29 (3rd), July 17 (6th), August 10 (9th), and October 10 (12th). Using a machete, undergrowth within plots was removed from plots 6 weeks prior to the first sampling and between subsequent sampling events.

Arthropod sampling

Twelve sample sets were collected between June 8th and October 10th during the 2001 growing season. The sampling frequency was established to collect short lived taxa. Each plot was sampled for arthropods using a sweep net (38 cm diameter) reaching 5.8 m into the canopy, at approximately the same time of day (afternoon), and similar weather conditions (sunny, warm and low wind) by MKH. It is estimated that the height of the trees was around 18 m. After 30 sweeps per plot, the contents from the sweep net were emptied into a plastic bag. The bag was then tied and frozen. Although sweep sampling does not capture all arthropods in the community, we found it to be the most efficient method when collecting arthropods from the canopy of these densely planted plantations. Sweep net sampling provides a good measure of relative abundance and relative species richness in grasslands and agricultural systems (Evans et al. 1983). Prior to this study, we tested the use of insecticide fogging, static traps (such as sticky traps), and beating trays, and we found that the sweep net sampling was the most effective at capturing a large diverse arthropod sample.

Arthropod identification

Specimens were sorted and identified to species or morphospecies within family or genus under magnification. Individuals from the order Araneida (spiders) were often not identified beyond order due to their taxonomic complexity and lack of a local reference collection. Morphospecies have been shown to correlate with arthropod taxa identified by entomologists and this technique is often effectively utilized in the characterization of communities (Oliver and Beattie 1996).

Determination of trophic level

For each species or morphospecies, a trophic group was determined for the developmental stage at which the individual was caught by referring to relevant literature (Arnett 1960, 1993; Borror and White 1970; McAlpine et al. 1981, 1987). The functional groups were the following: herbivore, detritivore, predator, parasitoid, omnivore, non-feeding, xylophage and unknown. Herbivores included any arthropod feeding primarily on living plant material. Detritivores were defined as arthropods feeding on dead material. Predators were defined as arthropods that fed by killing and consuming prey. Paraistoids were defined as arthropods that spend part of their life cycle as a parasite but emerge killing their host. Xylophages were defined as arthropods that consume wood. Omnivores were defined as individuals feeding commonly on plants and animals. There are some arthropods that only feed in their larval stage; therefore, a non-feeding group was included. The group ‘unknown’ was assigned for those whose trophic grouping could not be determined through lack of available knowledge or insufficient taxonomic determination. Little is known about feeding habits for some taxa, especially those without agricultural or medical importance.

Damage

To measure foliar insect damage, two trees were randomly selected within each plot (a total of 12 trees selected per species) and marked. Twenty leaves were then removed from each marked tree using a branch cutter that reached 5.8 m into the canopy on September 1st of 2004. The leaves were placed into plastic bags that were put into a cooler. Leaves were scanned using a flat bed scanner, and area analyses were undertaken using imaging software Scion Image (Meyer Instruments, Inc.) to determine the total area and area removed or damaged for each leaf. When damage was on the edge of a leaf, the leaf edge was drawn based upon the symmetry of the leaf shape. The percent of damage was calculated for each leaf and the average damage per tree was used in analyses.

Data analyses

Repeated measures analysis of variance (ANOVA) was used to test whether arthropod communities differed across tree species during the growing season. For the analyses of arthropods, the twelve sampling events were grouped into 4 periods since the plots were sampled in rotation (1, 2, 3; 4, 5, 6; 7, 8, 9; 10, 11 12). Repeated measures ANOVAs were performed for the response variables: total arthropod species richness and abundance, and the abundance and species richness of trophic groups. ANOVAs were performed to determine whether estimated damage types differed significantly between the four tree species examined. Estimated damage data was square root transformed prior to analysis. Partial difference adjusted means post-hoc tests were performed for tree species for repeated measures ANOVAs and Fishers PLSD post hoc tests were performed for damage ANOVAs (Proc Mixed, SAS 9.1, SAS Institute Inc., Cary, NC, USA.).

To assess differences in the tallow tree arthropod community from those of the native trees, non-metric multidimensional scaling (NMS) ordinations were conducted for herbivores, predators, parasites, and detritivores (4 ordinations). NMS is a non-parametric, iterative technique based on ranked distances among sites (McCune and Grace 2002; dos Santos et al. 2007). The number of dimensions was determined by a minimal stress (departure from monotonicity). The distance matrix of species used for ordination was 1-Ds, in which Ds is Sørensen's similarity index. A MANOVA was performed with the relative abundances of trophic groups (responses) to test whether the community structure depended on tree species (treatment).

Results

A total of 2,700 individuals and 285 species of arthropods within 15 orders and 72 families were caught (Appendix). The dominant orders caught were the Araneida (spiders), Homoptera (leaf hoppers), Diptera (flies) and Acari (mites) consisting of 22, 20, 16 and 15%, respectively, of the local arthropod community. Species richness was highest in the Diptera, Coleoptera (beetles), Hymenoptera (wasps and ants), and Homoptera (28, 14, 13 and 12%, respectively). Overall, 18% of taxa were identified to species and 56% were identified to morphospecies within a genus. Both the abundance and species richness of arthropods varied significantly with tree species but tallow was not distinguishable from all native species for either (Table 1; Fig. 1). The abundance and species richness of arthropods varied during the growing season but there were no interactions with tree species (Table 1).

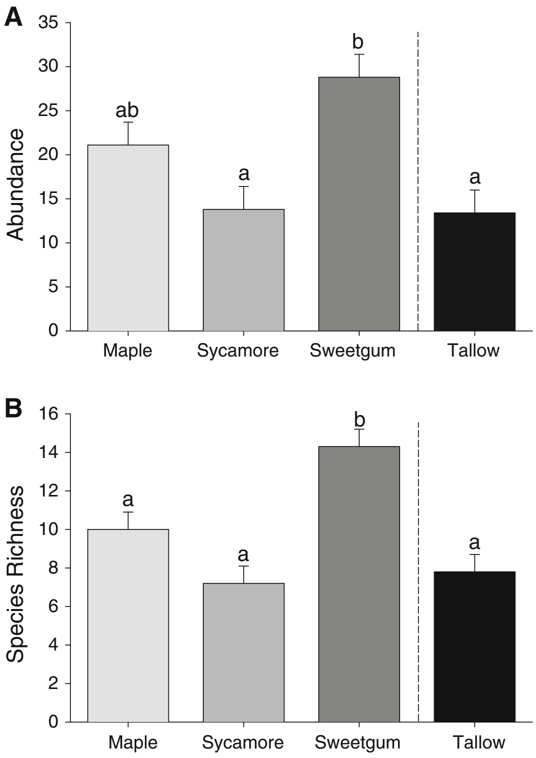

Fig. 1 Arthropod abundance (**a**) and species richness (**b**) from the four focal tree species sampled. Abundance and species richness are the average numbers of arthropods and arthropod species that were collected per plot per sampling event (four samples per plot over the growing season). *Different letters* denote means that are statistically different ($P < 0.05$). Adjusted means from repeated measures ANOVA + SE

Table 1 The dependence of overall arthropod abundance, overall arthropod species richness, and the relative abundance of different trophic groups of arthropods on the tree species sampled, sampling period, and their interaction in repeated measures ANOVAs

	Species ($F_{3,30}$)	Time ($F_{3,60}$)	Species*Time ($F_{9,60}$)
Total abundance	7.34***	5.53**	1.35 (0.23)
Total species richness	11.06***	5.06**	1.16 (0.34)
Herbivore abundance	5.28**	3.45*	0.74 (0.67)
Herbivore species richness	13.82****	3.50*	0.61 (0.78)
Detritivore abundance	2.83 (0.06)	3.14*	1.77 (0.09)
Detritivore species richness	6.16**	4.89**	1.66 (0.12)
Predator abundance	2.63 (0.08)	4.32*	1.17 (0.33)
Predator species richness	10.43***	0.09 (0.97)	0.74 (0.68)
Parasitoid abundance	6.84**	1.45 (0.24)	1.33 (0.24)
Parasitoid species richness	5.06**	1.82 (0.15)	1.27 (0.27)

**** $P < 0.0001$, *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. For non-significant results, the P-value is shown in parentheses

Trophic group responses

Herbivores and parasitoids but not other trophic groups, varied in their abundances with tree species (Table 1). Tallow trees had fewer herbivores than any of the native trees (Fig. 2a). Parasitoids were more abundant on maple and sweetgum than on sycamore and tallow (Fig. 2c). The MANOVA indicated that the trophic composition of arthropod communities on tree species varied significantly (Wilk's lambda [21,213.04 df] = 1.96, $P < 0.01$; Roy' Greatest Root [7,76 df] = 4.59, $P < 0.01$). The species richness of each trophic group depended on tree species (Table 1) with the highest number of herbivore, predator, and parasitoid species found on sweetgum, tallow, and maple or sweetgum, respectively (Fig. 2b, d, f).

Ordination

The arthropod herbivore community on tallow tree was distinctly different from the communities found on native species with no overlap of tallow with any native species in the NMS ordination (Fig. 3). Similar ordinations for predators, parasitoids, and detritivores all yielded overlapping sets of points for tallow and native species (not shown).

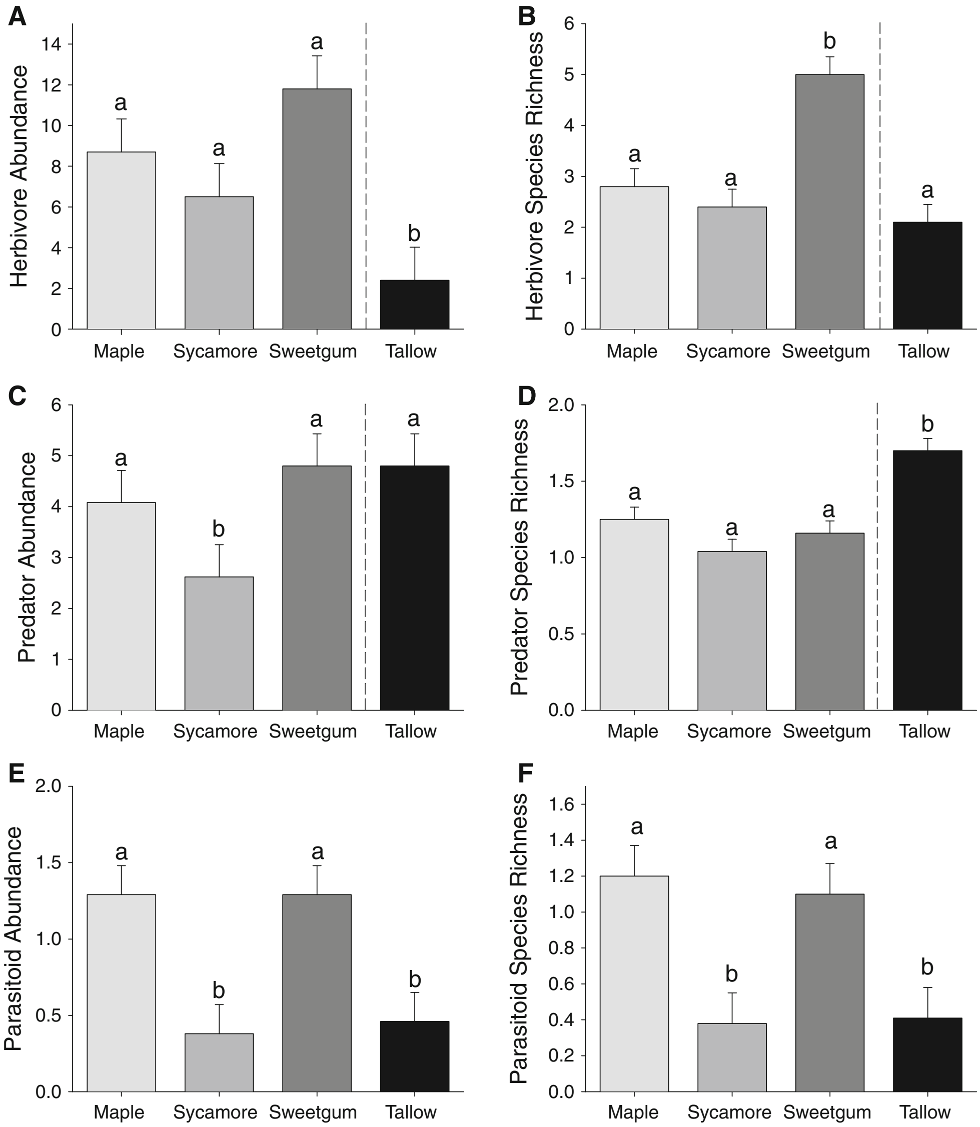

Fig. 2 Abundance and species richness of arthropod trophic groups from the four focal tree species. Abundance and species richness are the average numbers of arthropods and arthropod species that were collected per plot per sampling event (four samples per plot over the growing season). *Different letters* denote means that are statistically different ($P < 0.05$). Adjusted means from repeated measures ANOVA + SE

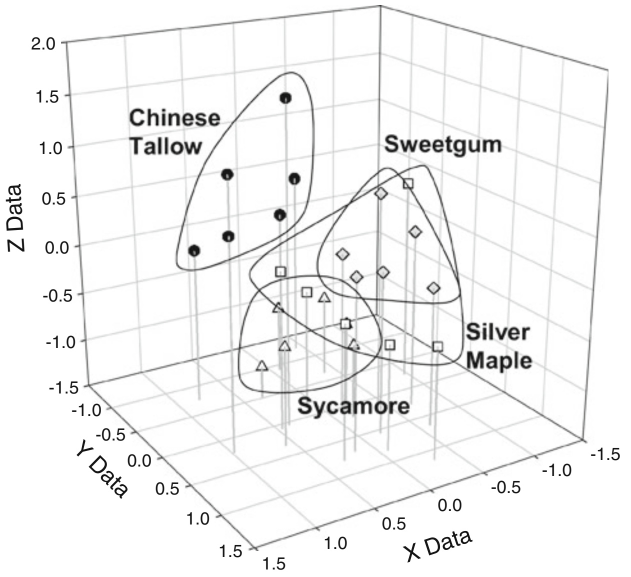

Fig. 3 Non-metric multidimensional scaling of the arthropod herbivore communities found on the four different tree species. This figure represents the three dimensional solution found by PCORD. Each point represents the sum of the arthropod herbivore community sampled on a single tree species transect for the sampling season. The graph is overlaid with shapes visually grouping each tree species' community. For other trophic groups (detritivores, parasitoids, predators) the groupings for tallow and native species overlapped and are not shown

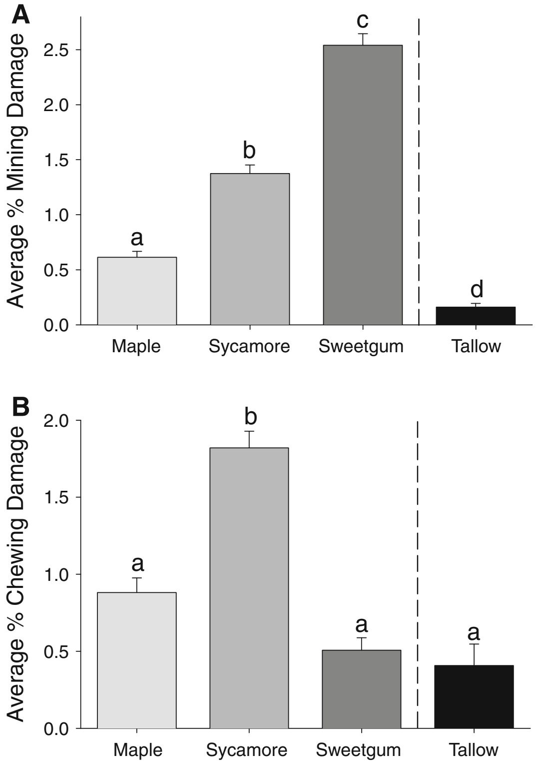

Fig. 4 The dependence of estimated damage types (chewing and mining) on tree species. Damage was calculated as the average percent of leaf area removed by chewing or affected by mining. *Different letters* denote means that are statistically different ($P < 0.05$). Mean + SE

Estimated damage

Foliar damage was evident on all the tree species sampled. Both estimated damage types depended significantly on host tree species (Fig. 4, mining: $F_{3,44} = 203.1$; $P < 0.0001$, chewing: $F_{3,44} = 35.3$; $P < 0.0001$). Sweetgum had the highest amount of mining damage and tallow tree had the least (Fig. 4a). Chewing damage was highest on sycamore (Fig. 4b).

Discussion

Our study indicated that the arthropod assemblage on tallow tree differed from those on all three native tree species, both in terms of the abundances and species richness of trophic groups. In particular, tallow tree had very low abundances of herbivores (Fig. 2a). Consistent with this was the low amount of herbivore damage on tallow tree compared to the three native tree species (Fig. 4). Such a paucity of herbivores and herbivore damage on tallow tree is consistent with predictions from the Enemies Release Hypothesis (Keane and Crawley 2002). However, there was not a corresponding low diversity or abundance for higher trophic levels as predator and parasitoid abundances were comparable to the numbers found on native trees. Furthermore, the species richness of predators was higher on tallow than on any of the native trees (Fig. 2d). This is very similar to the results of Proches et al. (2008) who found that only herbivores were less abundant on exotics compared to natives.

A number of explanations have been proposed that might explain the fewer herbivores and less damage on tallow tree: species area relationships, time since introduction, and taxonomic isolation (Strong et al. 1984). The range of tallow tree covers a large extent of the southern United States and the tree is locally abundant so there is no strong reason to consider the contemporary range of tallow tree to be a contributing factor to low herbivore abundances (Southwood 1961; Lawton 1978; Strong 1979). However, tallow tree has only been present in Texas for about 100 years which would be a period in which herbivores are likely still rapidly accumulating (Thomas et al. 1987; Auerbach and Simberloff 1988; Andow and Imura 1994). So, the recent introduction of tallow tree could be a contributing factor in its low herbivore loads and the low diversity of herbivores we found associated with it. Indeed, tallow tree has higher herbivore loads in Georgia compared to native tree seedlings where it has been present longer (~230 years) than in Texas (~100 years; Siemann et al. 2006). Finally, tallow tree is taxonomically isolated in that there are confamilial species in its North American range but no congeners and there are no other trees in the Euphorbiaceae in tallow tree's North American range. The combination of functional group or growth form together with taxonomy may interact to influence tallow tree's herbivore assemblage since greater novelty is associated with greater invasiveness (Strauss et al. 2006).

The typical abundance of predators, but low number of herbivores on tallow tree led to very different ratios of predators to herbivores on tallow tree (2.8:1) compared to all three native trees (from 0.6:1 up to 1.4:1). This suggests that tallow tree does not represent enemy free space for herbivores (Gratton and Welter 1999; Denno et al. 1990; Berdegue et al. 1996) but rather that predation levels might be quite high. If these predators feed on herbivores present in tallow tree stands, this may further reduce the strength of top down regulation by herbivores.

There was substantial variation in arthropod diversity and abundance among the native species with sweetgum supporting the highest species richness and abundance of arthropods and sycamore supporting the lowest (Fig. 4). The large range of variation among the native trees indicates that comparisons of exotic plants to a single native plant could give widely different results depending on the choice of native species. In this study, tallow tree was at the low end of the range for arthropod diversity and abundance such that pairwise comparisons could have indicated that tallow tree had low or typical numbers of arthropods or arthropod species present.

It appeared that of the tree species tested, each native tree was susceptible to at least one type of damage while tallow tree experienced only low levels of both. Interestingly, leaf miners (immature Coleoptera, Diptera, Lepidoptera and Hymenoptera) are considered particularly specialized (Gaston et al. 1992), and the least mining damage was encountered on tallow tree (Fig. 4b). This is in contrast to the results of Auerbach and Simberloff (1988) in which two introduced tree species in the Fagaceae accumulated a diverse leaf miner fauna within 20 years of introduction. This difference may reflect the presence of native congeners in their study. In addition a study by Lankau et al. (2004), examining generalist chewing herbivores (Acrididae: Orthoptera) feeding on tallow tree and *Celtis laevigata* (Hackberry) found low levels of feeding on tallow tree in field settings but high rates of consumption in laboratory feeding trials which suggests that the low levels of herbivory we encountered on tallow tree may be due to behavioural avoidance rather than chemical defences.

In an earlier study we found that tallow tree monocultures supported arthropod assemblages that had a lower relative diversity of herbivores compared to arthropod assemblages on diverse, native plant dominated habitats in Texas (Hartley et al. 2004). Our results here indicate that this result may be at least partly due to a low number of herbivore species on tallow tree on a per species basis compared to some native species. Such an effect might work in combination with the positive relationship between plant diversity and herbivore diversity (Siemann et al. 1998) to cause large losses of arthropod diversity when exotic monocultures replace native communities.

Conclusions

Community composition and trophic structure differed on tallow tree in comparison to the native tree species examined. Tallow tree had low herbivore abundance and experienced less damage, but supported typical numbers of detritivores and predators in contrast to the native species. Surprisingly, arthropod species richness and abundance were not lower on tallow tree than on the native tree species sampled. The Enemies Release Hypothesis was supported by our study in that tallow tree has experienced low herbivore abundances that may contribute to its invasive success. Further studies of the animal communities that characterize communities of native and exotic plants may increase our understanding of both the mechanisms underlying plant invasions and the impacts they have on the communities they invade.

Acknowledgments We thank Glenn Aumann, Ann Awantang, Brad Butterfield, Tim Becker, Candy Donahue, Joe Elias, Jacob Ferris, Will Gordon, James Hammer, Stephanie Hsia, June Keay, Viki Keener, Rick Lankau, Erin Loggins, Mary Mackay, Daniel Mee, Summer Nijjer, and Liz Urban for assistance; US EPA (EPA R82-8903), US NSF (DEB-9981654, NSF DEB-0315796) and a Wray-Todd Fellowship (for MKH) for financial support and UHCC for access. Voucher specimens are maintained at Rice University.

Appendix

See Table 2.

Table 2 The abundance and species richness of all arthropod orders encountered

Order	Family		Abundance	Species richness
Acari			412	28
		Oripodidae	181	6
Araneae			593	–
Coleoptera	*(15)*		201	39
		Chrysomelidae	125	8
Collembola	*(2)*		11	5
Dictyoptera	*(2)*		2	2

Table 2 continued

Order	Family		Abundance	Species richness
Diptera	*(13)*		441	81
		Chironomidae	171	19
		Dolichopodidae	67	14
		Lauxaniidae	109	11
		Sciaridae	37	11
Ephemeroptera			2	1
Hemiptera	*(7)*		11	8
Homoptera	*(10)*		550	35
		Cicadellidae	146	11
		Coccidae	356	9
Hymenoptera	*(11)*		151	37
		Braconidae	75	13
		Formicidae	42	7
Lepidoptera			26	5
Neuroptera	*(5)*		82	12
		Coniopterygidae	39	3
		Chrysopidae	36	5
Orthoptera	*(2)*		30	7
		Gryllidae	25	4
Psocoptera	*(3)*		148	18
		Pseudocaeciliidae	65	7
		Psocidae	75	10
Thysanoptera	*(2)*		27	7
Unknown			13	–
Total 15	*(72)*		2,700	285

The fifteen most abundant families are listed, including their abundance and species richness. The total number of families identified within each order is in brackets in italics. Total shows the total number of orders, families, abundance and species richness. Data shown is from the entire sampling season and the four tree species sampled

References

Andow DA, Imura O (1994) Specialization of phytophagous arthropod communities on introduced plants. Ecology 75:296–300

Arnett RH (1960) The beetles of the United States (A manual for Identification). Catholic University of America Press, Washington

Arnett RH (1993) American insects: a handbook of the insects of America north of Mexico. Sandhill Crane Press, Florida

Auerbach M, Simberloff D (1988) rapid leaf-miner colonization of introduced trees and shifts in sources of herbivore mortality. Oikos 52:41–50

Berdegue M, Trumble JT, Hare JD, Redak RA (1996) Is it enemy-free space? The evidence for terrestrial insects and freshwater arthropods. Ecological 21:203–217

Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants—a hypothesis. J Ecol 83:887–889

Borror DJ, White RE (1970) Peterson field guides—insects. Houghton Mifflin Company, Boston

Bossdorf O et al (2005) Phenotypic and genetic differentiation between native and introduced plant populations. Oecologia 144:1–11

Bruce KA, Cameron GN, Harcombe PA, Jubinsky G (1997) Introduction, impact on native habitats, and management of a woody invader, the Chinese tallow tree, *Sapium sebiferum* (L) Roxb. Nat Area J 17:255–260

Burns RM, Honkala BH (1990) Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654. U.S.D.A. Forest Service, Washington

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecol Lett 7:721–733

Denno RF, Larsson S, Olmstead KL (1990) Role of enemy-free space and plant-quality in host-plant selection by willow beetles. Ecology 71:124–137

dos Santos K, Kinoshita LS, dos Santos FAM (2007) Tree species composition and similarity in semideciduous forest fragments of southeastern Brazil. Biol Cons 135:268–277

Elton CS (1958) The ecology of invasion by plants and animals. Chapman and Hall, London

Evans EW, Rogers RA, Opfermann DJ (1983) Sampling grasshoppers (Orthoptera, Acrididae) on burned and unburned tallgrass prairie - night trapping vs sweeping. Environ Entomol 12:1449–1454

Gaston KJ, Reavey D, Valladares GR (1992) Intimacy and fidelity - internal and external feeding by the British microlepidoptera. Ecol Entomol 17:86–88

Gratton C, Welter SC (1999) Does "enemy-free space" exist? Experimental host shifts of an herbivorous fly. Ecology 80:773–785

Hartley MK, DeWalt S, Rogers WE, Siemann E (2004) Characterization of arthropod assemblage supported by the Chinese Tallow tree (*Sapium sebiferum*) in southeast Texas. Tex J Sci 56:369–382

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Tree 17:164–170

Lankau RA, Rogers WE, Siemann E (2004) Constraints on the utilisation of the invasive Chinese tallow tree *Sapium sebiferum* by generalist native herbivores in coastal prairies. Ecol Entomol 29:66–75

Lawton JH (1978) Host-plant influences on insect diversity: the effects of space and time. In: Mound LA, Waloff N (eds) Diversity of insect faunas. Blackwell, Oxford, pp 105–125

Liu H, Stiling P (2006) Testing the enemy release hypothesis: a review and meta-analysis. Biol Inv 8:1535–1545

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

Maron JL, Vila M (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. Oikos 95:361–373

McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (1981) Manual of Neartic Diptera: vol. 1. Research Branch, Agriculture Canada (Monograph No. 27)

McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (1987) Manual of Neartic Diptera: vol. 2. Research Branch, Agriculture Canada (Monograph No. 28)

McCune B, Grace JB (2002) Analysis of ecological communities. Mjm Software Design, Gleneden Beach, Oregon

Mitchell CE et al (2006) Biotic interactions and plant invasions. Ecol Lett 9:726–740

Oliver I, Beattie AJ (1996) Invertebrate morphospecies as surrogates for species: a case study. Cons Biol 10:99–109

Proches S, Wilson JRU, Richardson DM, Chown SL (2008) Herbivores, but not other insects, are scarce on alien plants. Austral Ecol 33:691–700

Sakai AK et al (2001) The population biology of invasive species. Ann Rev Ecol Syst 32:305–332

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Tree 17:170–176

Siemann E, Rogers WE (2003a) Herbivory, disease, recruitment limitation, and success of alien and native tree species. Ecology 84:1489–1505

Siemann E, Rogers WE (2003b) Increased competitive ability of an invasive tree may be limited by an invasive beetle. Ecol Appl 13:1503–1507

Siemann E, Tilman D, Haarstad J, Ritchie M (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. Am Nat 152:738–750

Siemann E, Rogers WE, Dewalt SJ (2006) Rapid adaptation of insect herbivores to an invasive plant. Proc Roy Soc B 273:2763–2769

Southwood TRE (1961) The number of species of insect associated with various trees. J Anim Ecol 30:1–8

Strauss SY, Webb CO, Salamin N (2006) Exotic taxa less related to native species are more invasive. PNAS 103:5841–5845

Strong DR (1979) Biogeographic dynamics of insect-host plant communities. Ann Rev Entomol 24:89–119

Strong DR, Lawton JH, Southwood TRE (1984) Insects on plants: community patterns and mechanisms. Blackwell, Oxford

Thomas CD, Ng D, Singer MC, Mallet JLB, Parmesan C, Billington HL (1987) Incorporation of a European weed into the diet of a North American herbivore. Evolution 41:892–901

Vitousek PM, Dantonio CM, Loope LL, Westbrooks R (1996) Biological invasions as global environmental change. Am Sci 84:468–478