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ABSTRACT

Throughout the southwestern U.S., riparian gallery forests of cottonwood and willow are being invaded by woody exotics, primarily Russian olive and salt cedar. We wondered what effect this might have on native pollinator populations. Pollinators are indispensable contributors to biodiversity, ecosystem health, and human food production. Recent declines in pollinator abundance and health, such as catastrophic declines in honey bee populations due to Colony Collapse Disorder, has renewed interest in native pollinators and the ecosystem services they provide. Insects were collected from willow, Russian olive and salt cedar throughout April and May of 1997 and 1998 using sweep nets. For each collection day, nets were swept over the target shrubs for a specified number for passes to ensure equal collection effort. Insects were counted and identified to family. Total numbers were adjusted by number of sweep-days. Total insect abundance was greatest for willows (33.5 insects per sweep-day), followed by Russian olive (18.0) and salt cedar (6.8). Willows also had the greatest number of insect orders and families represented. Of the four primary insect pollinator orders, willow had the greatest numbers of dipterans, hymenopterans, and lepidopterans collected per sweep-day. Russian olive had the greatest number of coleopterans. When ants and chalcids were excluded from the hymenopterans, willows still had the greatest numbers and proportions of hymenopterans caught. It appears that the willow habitat is important to pollinating insects, especially bees. In contrast, saltcedar consistently had the lowest numbers and proportions of all four of the pollinator orders.

INTRODUCTION

Along the Middle Rio Grande Valley in central New Mexico, riparian gallery forests of cottonwood (*Populus fremontii*) and willow (*Salix* spp.) are being invaded by woody exotics, primarily Russian olive (*Elaeagnus angustifolia*) and saltcedar (*Tamarix* spp.). The primary cause for this invasion is the lack of pulse-flood regimes due to water diversion and flow regulation (Glenn and Nagler 2004; Katz and Shafroth 2003). These non-native plants often occur in dense thickets with many dead stems, which increase the risk of fire, thereby reducing cover of fire-sensitive native vegetation and creating a high-salinity environment detrimental to native plant re-establishment (Busch and Smith 1995; Di Tomaso 1998; Glen and Nagler 2005; Katz and Shafroth 2003; Kerpez and Smith 1987). This feed-back mechanism favors the expansion of woody exotics, particularly *Tamarix*.

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Much effort and research has gone into exotic species eradication efforts and knowledge syntheses (for example; Di Tomaso 1998; Glenn and Nagler 2004; Horton and Campbell 1974; Katz and Shafroth 2003; Kerpez and Smith 1987; Shafroth and others 2005). One primary area of research has focused on the effects of an altered riparian ecosystem to wildlife. Several studies have focused on the impact of woody plant invasion on wildlife abundance and diversity, including birds (Brown 1990; Ellis 1995; Hunter and others 1988; Knopf and Olson 1984; Stoleson and Finch 2001), small mammals (Ellis and others 1997), amphibians and reptiles (Bateman and others 2008; Jakle and Gatz 1985; Jones 1988), and arthropods (DeLay and others 1999; Ellis and others 2000; Mund-Meyerson 1998; Watts and others 1977).

Despite considerable research on wildlife, including arthropods, few studies have examined the impact of woody exotic invasion on pollinating insects. Pollinators are indispensable contributors to biodiversity, ecosystem health, and human food production. Recent declines in pollinator abundance and health, such as catastrophic declines in honey bee populations due to Colony Collapse Disorder, have renewed interest in native pollinators and the ecosystem services they provide (Greer 1999; NAPPC). In this report, we make use of an existing dataset of insect and other arthropod collections made in the riparian zone of the Middle Rio Grande (data on file at the Forestry Sciences Laboratory, 333 Broadway SE, Albuquerque, NM) to address the following questions: 1) Does the diversity or abundance of arthropods collected from native and non-native woody plant species differ? 2) Are there differences in the insect pollinator groups associated with native and non-native species?

METHODS

Sweep nets were used to collect insects from Russian olive, saltcedar, and coyote willow (*Salix exigua*) at Bosque del Apache National Wildlife Refuge, Socorro County, NM, on multiple days throughout April and May of 1997 and 1998. These species were chosen because they flower concurrently, share similar habitats (Hoddenbach 1989) and are attractive to pollinating insects, providing both nectar and pollen (Anderson 2006; Haddock 2008; Hayes 1976; Katz and Shafroth 2003; Stevens 1989; Wiesenborn and others 2008). A direct comparison is therefore possible.

Collections were made in three habitat types growing in close proximity along the Rio Grande river near the northern boundary of the Wildlife Refuge. Willow collections were made in two homogeneous, dense willow stringers along water conveyance structures (Low Flow, LF; South Willow, SW). Russian olive collections were made in a mixed forest of cottonwood overstory with a middle story of both Russian olive and saltcedar (North Cottonwood, NC). Saltcedar collections were made in the cottonwood forest described above, and in two saltcedar forests containing dense patches of both live and dead saltcedar interspersed with open ground (Saltceda,r SS; South Cottonwood, SC). A total of 80 collections, representing different days and/or collection sites, were made on willow, 15 on Russian olive, and 79 on saltcedar (table 1).

For each collection unit, heavy-duty sweep nets (Forestry Supplies) were swept back-and-forth over the target shrubs for a total of 10 passes. Each back-and-forth sweep was done in a different location on the plant. Sweeps were conducted on the sides of the plants at chest or head height. If only portions of the plant was flowering, the flowering areas were selected for sweeps. The majority of sweeps were done in the late morning between 9:00 and 11:00 a.m. on days with little or no precipitation and low winds. Collected arthropods were transferred to cyanide kill-jars and transported to the laboratory, where specimens were counted and identified to family.

Arthropod numbers were summed according to plant species, site and year, then adjusted by number of collection units to account for collection effort (table 1). The adjusted abundance data were compared using the univariate option of a Multiple Response Permutation Procedure (MRPP) macro developed by Rudy King, Rocky Mountain Research Station Statistician, and based on methodology of Mielke and Berry (2001). A Bonferroni adjustment of the *P* value was made for the multiple univariate tests presented in table 2 (Miller 1981). Pairwise comparisons used the Peritz closure method (Petrondas and Gabriel 1983), which maintains Type I error at or below the specified value of 0.05. Arthropod richness was compared using the number of orders and families collected from each plant species to construct order- and family-area curves, similar to species-area curves.

Table 1—Insect collection data from Bosque del Apache National Wildlife Refuge. Data shown include collection site, year, number of collections, total number of arthropods caught at each site, and number of arthropod orders and families represented.

Species	Site	Year	No. of Collections	Total Arthropods	Arthropods per Collection	No. of Orders	No. of Families
Salix exigua	LF	1997	32	633	19.8	11	47
	LF	1998	24	1217	50.7	10	43
	SW	1997	24	883	36.8	11	42
Elaeagnus angustifolia	NC	1997	9	185	20.6	7	18
	NC	1998	6	85	14.2	6	20
Tamarix spp.	NC	1997	11	108	9.8	7	21
	NC	1998	12	52	4.3	6	16
	SS	1997	35	77	2.2	7	16
	SS	1998	18	260	14.4	7	23
	SC	1997	3	37	12.3	6	6

Table 2—Numbers of insects of the four major pollinator orders collected from willow, Russian olive and saltcedar at the Bosque del Apache National Wildlife Refuge during the springs of 1997 and 1998. Numbers have been corrected for collection effort. Attained significance values were based on univariate MRPP with a Bonferroni adjustment for multiple comparisons. Adjusted significance values are given in parentheses. Pairwise comparisons were computed using the Peritz closure method with an alpha of 0.05.

Arthropod Orders	*Salix exigua*	*Elaeagnus angustifolia*	*Tamarix* spp.	Attained Significance
Coleopterans per collection	1.55	4.73	1.05	0.0425 (0.255)
Dipterans per collection	11.11	5.87	1.19	0.2433
Lepidopterans per collection	0.16 a	0.00 ab	0.01 b	0.0083 (0.0498)
Hymenopterans per collection	6.81 a	3.53 ab	1.02 b	0.0052 (0.0312)
Hymenopterans minus ants and chalcidoids	0.70 a	0.20 ab	0.05 b	0.0012 (0.0072)
Other orders per collection	14.5	3.87	3.48	0.0571

In addition to the univariate results described above, MRPP was used to examine woody plant differences across the four main potential pollinating orders; *Hymnoptera* (bees, wasps, ants), *Diptera* (flies), *Lepidoptera* (butterflies, moths), and *Coleoptera* (beetles). Response variables were insect numbers of each of the four orders adjusted for collection effort and standardized in the analysis. Principal components were used to provide a visual description of group differences.

A number of sources were used to determine potential pollinator status of the different family groups. These included online sources (North American Pollinator Protection Campaign [NAPPC], Pollinator Conservation Digital Library, Montana State Extension website, U.S. Forest Service Celebrating Wildlife website), standard field guides (Borror and White 1970; White 1983), and individual articles (Franz 2007; Gilbert and Jervis 1998; Kearns 2001; Kevan and Baker 1983; Larson and others 2001; Winterton and others 2005).

RESULTS

Arthropod Abundance and Diversity

Total arthropod abundance was greatest for the willow habitat. A total of 2733 arthropods were collected from willows as compared with 270 from Russian olive and 534 from saltcedar (table 1). When corrected for collection effort, willows averaged 34.2 arthropods per collection, compared to 18.0 for Russian olive and 6.8 for saltcedar. Willow was significantly different than saltcedar based on univariate MRPP results ($p = 0.0278$). The numbers of individuals collected from each plant species are given in appendix 1. Willow collections were dominated by homopterans (cicadas, leafhoppers, aphids; 35 percent), followed by dipterans (33 percent), hymenopterans (20 percent), and coleopterans (5 percent). Russian olive collections were largely composed of dipterans (32 percent), followed by coleopterans (26 percent), hymenopterans (20 percent), and thysanopterans (thrips; 8 percent). Saltcedar collections were largely made up of hemipterans (true bugs; 37 percent), followed by dipterans (18 percent), coleopterans (16 percent), hymenopterans (15 percent), and homopterans (9 percent).

The homopterans collected were primarily leafhoppers (*Cicadellidae*), which have piercing and sucking mouthparts and feed almost exclusively on plant sap. Dipterans collected from both willow and saltcedar were largely non-biting midges (*Chironomidae*) and frit-flies (*Chloropidae*), whereas those collected from Russian olive were dance flies (*Empididae*). Frit-fly adults occur in grasses and flowers, and may serve as pollinators of small-flowered plants (for example; Neel and others 2001). Adult non-biting midges are short-lived and most do not eat. Dance flies are mostly predaceous, but are also found on flowers and may serve as pollinators of some species (Pollinator Conservation Digital Library). Hemipterans collected from saltcedar were largely seed-feeding bugs (*Lygaeidae*). Thysanopterans, or thrips (*Thripidae*), are common plant and flower feeders that may also pollinate a few flower species such as phlox (Strakosh and Ferguson 2005). Coleopterans collected from all three woody plant species were primarily soft-winged flower beetles (*Melyridae*), with a lesser number of leaf beetles (*Chrysomelidae*) and false flower beetles (*Scraptiidae*). Soft-winged flower beetles, in particular, constitute an important pollinator group (Mawdsley 2003). Hymenopteran collections were dominated by ants (*Formicidae*), followed by chalcidoids (*Chalcidoidea*). Chalcidoids are a large group of tiny wasps whose larvae are parasitic on other insects (Borror and White 1970). Adults feed on high-carbohydrate energy sources such as nectar and honeydew, as do other parasitoid wasps (Fielder and Landis 2007).

Willows had the greatest number of arthropod orders and families represented. Fourteen orders and 72 families were collected from willow; seven orders and 30 families were collected from Russian olive; and 10 orders and 46 families were collected from saltcedar. Order- and species-area curves show higher accumulation rates for willow as compared with saltcedar (figure 1). Russian olive had too few collection units for a meaningful comparison.

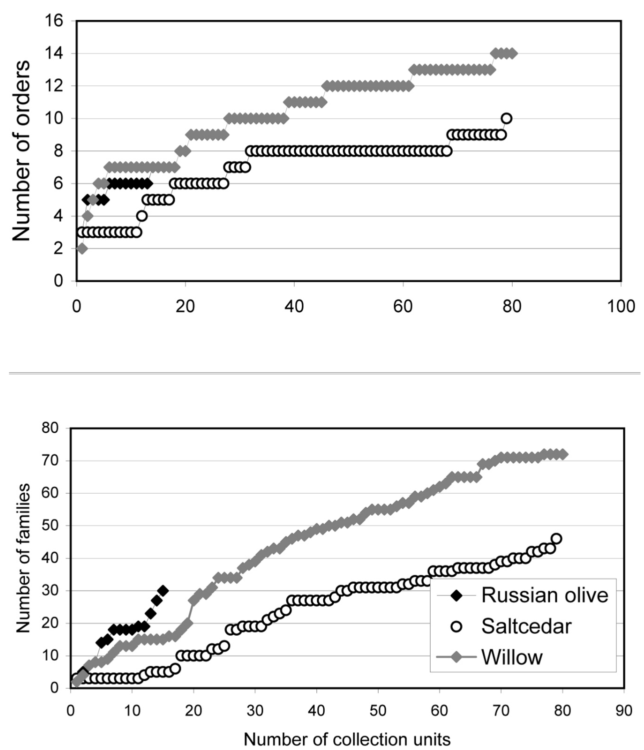

Figure 1—Order- and family-area curves for arthropods collected from willow, Russian olive, and saltcedar.

Potential Pollinators

Results of the multivariate MRPP on the four primary insect pollinator orders showed a significant difference in the potential pollinator assemblage of willow versus saltcedar (p = 0.0008). Willow had significantly greater numbers of both lepidopterans and hymenopterans per collection, even when ants and chalcidoids (the largest groups) were excluded from the hymenopterans (table 2). Russian olive had the greatest number of coleopterans collected, although this was only marginally significant.

The difference between the insect assemblage of willow as opposed to the two exotic species is depicted through principal components in figure 2. The first component, representing 53 percent of the variation, is a comparison of coleopterans against all other insect orders collected (table 3). The second component, comprising 26 percent of the variation, contrasts coleopterans and, to a lesser extent hymenopterans, with other non-pollinator orders. Relatively speaking, willow had fewer coleopterans whereas Russian olive had high numbers. The 1997 saltcedar collection from the NC site was similar to Russian olive in having relatively high numbers of coleopterans. These two species co-occurred at this site, which consisted of a cottonwood overstory with a mixed exotic middle story.

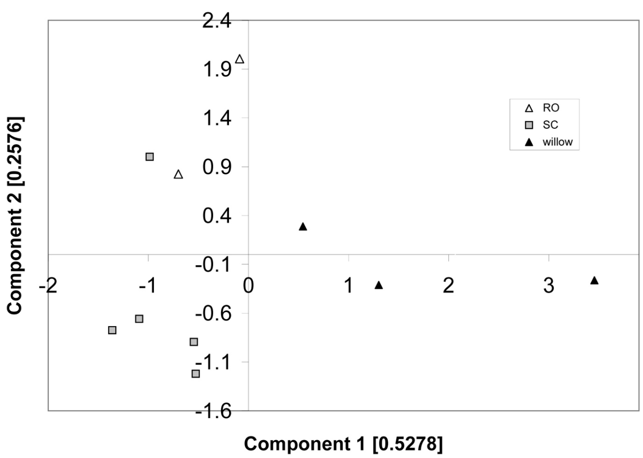

Figure 2—Results from principal components depicting differences in insect assemblages collected from willow, Russian olive and saltcedar.

Soft-winged flower beetles comprised the bulk of coleopterans collected, however a number of other beetle families were also collected. Six beetle families were collected from Russian olive, seven from saltcedar, and ten from willow (appendix 1). All families collected, with the exception of ladybird beetles (*Coccinellidae*) and fireflies (*Lampyridae*), have at least some species commonly found on flowers (Borror and White 1970) or implicated in pollination (Pollinator Conservation Digital Library). Therefore, we considered beetles in the remaining 11 families to be potential pollinators. The preponderance of soft-winged flower beetles makes them particularly important as potential pollinators, especially for Russian olive and saltcedar (figure 3A).

Lepidopterans comprise the second largest order of insects, but very few were collected in this study. Those collected were either geometer moths (*Geometridae*), noctuid moths (*Noctuidae*), or unidentified caterpillars (appendix 1). All nine adults of the two moth groups can be considered potential pollinators, and these were found exclusively on willow.

Flies are among the most frequent insect visitors to flowers (Kearns 2001) and are more important as pollinators than is commonly recognized. We collected ten families of flies from Russian olive, 15 from saltcedar, and 22 from willow (appendix 1). We found reports of nectar consumption and/or flower visitation for nearly all fly families collected in this study. The single exception was picture-winged flies, *Otitidae* (now *Ulidiidae*), for which we could find no information on adult feeding behavior. Non-biting midges comprised the bulk of dipterans collected from willow (figure 3B). Most adult non-biting midges (*Chironomidae*) do not eat. However, the family is listed as nectar feeders on arctic plants, including willows, in several sources (Gilbert and Jervis 1998; Kevan and Baker 1983; Larson and others 2001). Consequently, we have included all flies as potential pollinators, although the non-biting midges are questionable. Dance flies comprised the bulk of dipterans collected from Russian olive, whereas saltcedar hosted midges, frit-flies, and a smattering of other families (figure 3B).

Hymenopterans consist of ants, wasps and bees. Four families were collected from Russian olive, four from saltcedar, and ten from willow (appendix 1). The vast majority were ants and parasitoid wasps. Although a few specialized cases of ant pollination have been documented, ants are rarely effective as pollinators because antibiotic body excretions render pollen inviable (Wagner 2000). Parasitic (chalcidoid, ichneumon, braconid) and predaceous (sphecid, vespid) wasps are known to pollinate, as adults feed on rich sugar sources, including floral nectaries. Parasitic wasps, especially chalcidoids, made up the bulk of hymenopterans collected from all three species (figure 3C). Bees, however, are the most important and effective of all pollinators. Their mouthparts and bodies are well adapted to make use of floral resources (Kevan and Baker 1983), which they use both as food and to provision their nests. The total number of bees collected in this study was relatively small, possibly due to their quickness in flight. Twenty-eight bees in four families (*Andrenidae*, *Apidae*, *Colletidae*, and *Halictidae*) were collected from willow, compared with two bees in one family (*Halictidae*) from saltcedar. No bees were collected from Russian olive. The proportions of potential pollinators by order are shown in figure 4. Dipterans are the most abundant visitors for all three plant species. In willow, most of these are non-biting midges. If midges are excluded, hymenopterans and dipterans are about equal in abundance on willow, whereas dipterans and coleopterans make up the bulk of visitors on Russian olive and saltcedar.

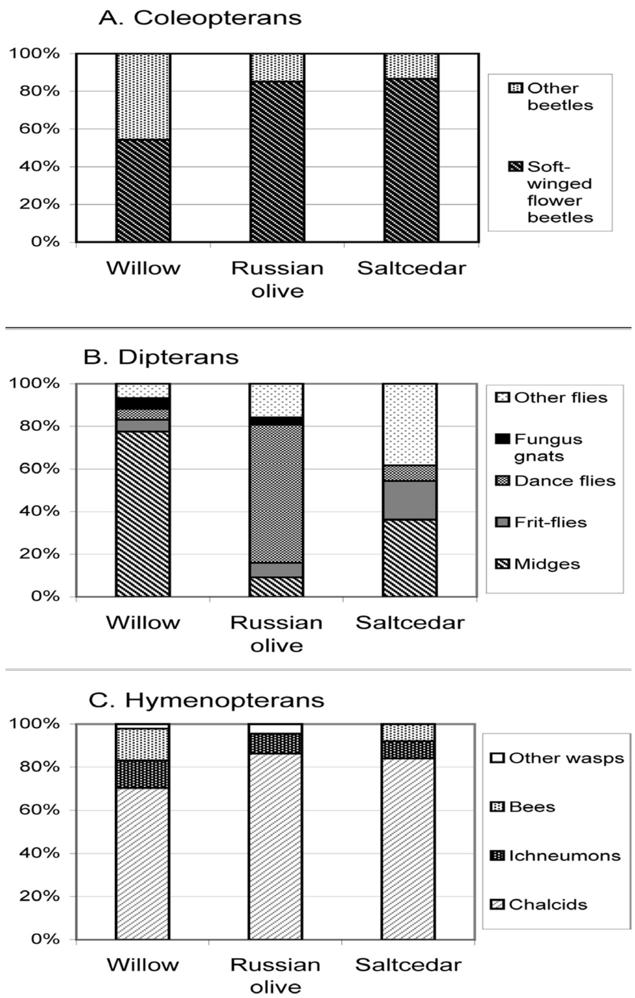

Figure 3--Family make-up of three of the four principal pollinating insect orders by woody plant species. Lepidopterans are not shown because adults were collected only from willow.

DISCUSSION

Arthropods

In this study, we found willows to have a greater abundance and diversity of arthropods than did either saltcedar or Russian olive. Findings from previous studies on arthropod communities of exotic and native vegetation have been mixed. Shafroth and others (2005; p. 236) cite several Master's theses (Liesner 1971; Miner 1989; Stevens 1985) that found saltcedar to be depauperate in arthropod assemblages when compared with native vegetation. DeLay and others (1999) found spring arthropod collections from saltcedar habitat to be significantly lower in abundance than collections from either cottonwood or willow habitats. Cohan and others (1978) reported low use of saltcedar stands by insectivorous bird species, which correlated with their finding of significantly less insect biomass in saltcedar as compared with other riparian vegetation types, including willow. Other researchers have also reported greater avian density and diversity in cottonwood-willow communities than in saltcedar (see Kerpez and Smith 1987). Arthropod abundance is a better predictor of insectivorous bird density than either foliage height or volume (Brush and Stiles 1986).

Existing studies of insects and insectivorous birds on Russian olive show a similar pattern to that depicted above for saltcedar. Waring and Tremble (1993) studied insect herbivores of native and exotic woody species along the San Juan River in Utah. They found richness and density of insect herbivores to be lowest on Russian olive and highest on coyote willow. Brown (1990) found willow sites to have higher bird species richness, relative abundance, and density, and more foraging guilds and nesting guilds than Russian olive sites. All foraging guilds (herbivore, insectivore, granivore, omnivore) preferred willow over Russian olive. She attributed differences in bird use to the relatively low abundance of insects found in Russian olive stands. Knopf and Olson (1984) also reported a lower richness and diversity of bird species in Russian olive sites than in native riparian communities.

In contrast, Ellis (1995) reported that insectivorous birds readily used saltcedar for foraging. Both Ellis and others (2000) and Mund-Meyerson (1998) concluded that saltcedar communities often have diverse and abundant arthropod assemblages. Tepedino and Griswold, working in Grand Staircase-Escalante National Monument recorded a total of 210 species of bees occurring on tamarisk (Tery Griswold, personal communication 3/20/09). Ellis and others (2000) reported a greater abundance of surface-dwelling arthropods under cottonwood than saltcedar, but attributed this solely to the high number of exotic isopods caught in the cottonwood habitat. Mund-Meyerson (1998) found no difference in either abundance or diversity of arboreal arthropod communities of cottonwood, saltcedar, and Russian olive. Shafroth and others, in their 2005 review paper, state that the abundances of several common insect families may be comparable or greater on saltcedar than on most natives (Anderson and others 2004; as cited in Shafroth and others 2005). Carothers and others (1976) reported higher arthropod abundance but lower diversity for spring collections on saltcedar compared with willow. In this case, high numbers of thrips contributed to the overall abundance. Stevens (1989) commented on the "astonishing abundance" of thrips on saltcedar flowers.

Table 3—Loadings for eigenvectors from principal components analysis.

	Component				
Response	**1**	**2**	**3**	**4**	**5**
Coleopterans	-0.1022	0.9337	-0.2313	0.2239	0.1185
Dipterans	0.5832	0.0534	0.5715	0.5551	0.1493
Hymenopterans	0.6305	0.2766	0.0456	-0.6506	-0.3171
Lepidopterans	0.1186	-0.0261	-0.0210	-0.3502	0.9285
Other orders	0.4877	-0.2193	-0.7857	0.3095	0.0304

What might be reasons for the above disparity in results? Most comparison studies of arthropods in exotic and native riparian vegetation have been done in the context of a food source for insectivorous fauna. As such, they have compared arthropod abundance on a community basis. Local plant species composition is a better predictor of arthopod assemblages than either vegetation structure or environmental conditions (Schaffers and others 2008). Cottonwood areas may or may not retain a mixed native mid-story containing willows. The presence or absence of herbaceous understory plants may also influence results. Our data directly compare the two exotic plants with a native willow species. Willows are known to have one of the richest and most diverse insect faunas of all tree families (Southwood 1961). Most of the previous reports did not specifically examine the importance of willows.

The second reason involves a time lag as insects and other arthropod species adapt to a novel food source. Southwood (1961) documented associations between insect assemblages and various tree species. He determined that the number of insect species associated with a tree species was influenced by both the amount of time the plant has been in a given area (introduction history) and its general abundance or scarcity within that region. It is therefore likely that the numbers of insect species associated with saltcedar and Russian olive have increased since their introduction into the United States. It would be interesting to compare insect assemblages in areas of recent expansion with those areas of the first early introductions.

Pollinators

While several studies have examined the effects of exotic woody introductions on arthropods in general, little attention has been given to their effects on pollinating insects. We know of only a few papers on saltcedar (Nelson and Andersen 1999; Tepedino and others 2008; Wiesenborn and others 2008) and none on Russian olive. Interest in pollinator conservation has grown in recent years as our understanding of their importance has grown. It is estimated that over 67 percent of flowering plants, including many crop species, depend on insects for pollination (Tepedino 1979). Current threats to native pollinators include excessive use of pesticides, habitat fragmentation, habitat loss, and introductions of exotic plant and animal species (Kearns and Inouye 1997). Inclusion of a variety of forb and flowering shrub species in revegetation efforts is worth consideration.

As previously indicated, the majority of pollinators are found in one of four main insect orders; Coleoptera (beetles), Diptera (flies), Lepidoptera (butterflies and moths), and Hymenoptera (bees, wasps and ants). Beetles make up the largest group of pollinating insects and are considered to be the most primitive (Kevan and Baker 1983). Pollination occurs as they move from flower to flower, chewing their way through the floral parts, becoming covered with pollen. This is often referred to as "mess and soil" pollination. Many are also considered pests of economic importance, as they damage the flowers and plants upon which they feed. Mawdsley (2003) identified 11 beetle families as important pollinating groups, seven of which were collected in this study. The *Buprestidae*, *Curculionidae*, *Mordellidae*, *Scarabaeidae*, and *Staphylinidae* were poorly represented in our study, but the *Chrysomelidae* (leaf beetles) and *Melyridae* (soft-winged flower beetles) were the two most common families collected. The flower beetles were common on all three woody plants and have been reported as pollinators of both saltcedar and willow species (Mawdsley 2003). Leaf beetles were primarily collected from willow, suggesting that willow species may be important in the conservation of this family of pollinators. Several leaf beetle species are herbivore specialists on willow leaves (Sandra Brantley, personal communication).

Flies are the second most important order of flower visitors (Larson and others 2001). At least 71 families of flies (dipterans) are known to contain common visitors to flowers (Kearns 2001). These range from opportunistic feeders to specialized nectarivores and vary significantly in their effectiveness as pollinators. Important flower-visiting families include the larger *Bombyliidae*, *Syrphidae*, *Anthomyiidae*, *Tachinidae*, *Calliphoridae*, as well as the smaller *Bibionidae*, *Chironomidae*, *Culicidae*, *Empididae*, *Mycetophilidae*, and *Cecidomyiidae* (Kearns 2001). Most of the flies collected in this study were small flies of the familes *Chironomidae*, *Empididae*, *Mycetophilidae*, and *Chloropidae* that feed on exposed nectaries. These small flies are generally considered to be inefficient pollinators, as their small size precludes carrying heavy pollen loads. Nevertheless, numerous visits to flowers by small inefficient pollinators may still result in significant pollination, especially in the absence of more efficient pollinators. We collected few large flies of the families indicated above. Those that were collected came from either saltcedar or willow. As yet, our understanding of flies and fly pollination is limited. Far more research on fly pollination, community composition, and conservation status is needed (Kearns 2001).

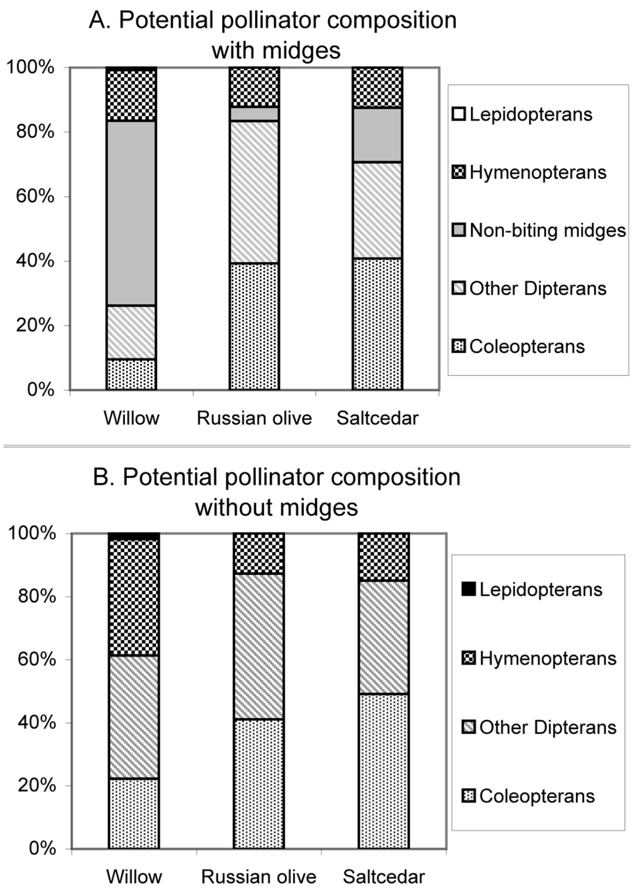

Figure 4—The proportions of potential pollinators by order for willow, Russian olive and saltcedar when non-biting midges are included (A) and excluded (B).

Adult butterflies and moths feed extensively on nectar and pollen (Kevan and Baker 1983), and so have an intimate relationship with flowers. They have been proposed as ecological indicators of riparian quality in the western United States (Nelson 2007). In this study, we collected few moths and no butterflies. What moths we did collect were all from willow and belonged to the families *Geometridae* and *Noctuidae*. Geometers and noctuids, along with sphinx moths, are considered to be the most efficient of moth pollinators (Montana State University Extension website). Nelson and Andersen (1999) found that saltcedar and restored riparian habitats along the lower Colorado River lacked the nectar and larval resources needed for butterflies historically found in cottonwood/willow vegetation. These findings suggest that willows may be an important plant resource for lepidopteran pollinators.

Hymenopterans are the most important order of flower visitors (Kevan and Baker 1983; Tepedino 1979). Parasitic wasps were the most common group of potential pollinators collected. They appear to be generalized flower visitors and were found on all three woody plant species (Kevan and Baker 1983). Bees, however, are the most efficient and important of all pollinator groups. Their life histories are intimately linked with those of flowering plants, as they depend completely on floral resources. Both generalist and specialist foragers exist. It is estimated that less than two-thirds of bee species have been described (Kearns and Inouye 1997). Other than two halictids collected on saltcedar, all of the bees and bee families collected in this study occurred on willow, indicating its importance as a floral resource, both for nectar and the copious amounts of pollen produced.

Willows are primarily insect pollinated but wind may also play a role, depending on the species (Sacchi and Price 1988). Willows have one of the highest numbers of insect species occurring on trees, even when the effects of introduction history and geographic abundance are removed (Southwood 1961). A large number of insect species have been identified as floral visitors or pollinators of willow (Kevan and Baker 1983; Pollinator Conservation Digital Library website). Our results support these observations. Willows supported the greatest diversity and abundance of arthropods, potential pollinators, and bees.

Little is known of the pollination needs of woody exotics. Stevens (1989) reported that saltcedar requires insect pollinators to successfully produce seed. The most commonly mentioned pollinators are honeybees (Shrader 1978). Wiesenborn and others (2008) collected a total of 17 families and four orders of floral-visiting insects from saltcedar flowers in Arizona. Relative pollen loads indicated that honey bees were the most important pollinators. A number of native bees of the *Apidae*, *Halictidae*, and *Megachilidae* also carried pollen, but were found in low numbers. The authors also indicated that syrphid flies may be important pollinators due to the high frequency of visits. Our data suggest that small flies and flower beetles may supply the majority of saltcedar pollination in our study area, as honeybees are relatively rare.

The pollination needs of Russian olive in North America are virtually unknown, although the consensus is that they are insect pollinated (Olson and Barbour 2008). As with saltcedar, the majority of potential pollinators we collected were flower beetles and small flies. No lepidopterans or bees were collected, although Russian olive has been promoted for the production of honey (Hayes 1976). Clearly, pollination studies are needed for this species.

The value of woody exotics to major arthropod communities in general, and to pollinator groups in particular, is largely relative and depends on the associated plant species. While we demonstrated that replacement of willow understory by woody exotics has a detrimental effect on the pollinator community, especially bees, this may not be true for all plant/pollinator associations. The presence of an herbaceous layer can have a profound effect on the abundance and richness of floral visiting insects (Campbell and others 2007). In addition to food for adults, insects require suitable larval hosts and nesting sites to complete their life cycle. Wiesenborn and others (2008) attributed the lack of butterflies to a lack of larval host plants. They also observed that saltcedar did not readily form hollow stems for cavity nesting bees and wasps. Parasitic wasps require other insects as larval food sources, and saltcedar supports a low diversity of insect herbivores (Wiesenborn and others 2008).

Nevertheless, the effects of exotics on insect populations are not all negative. The addition of saltcedar in mixed stands may, in some cases, actually increase the abundance of native bees. Again, this depends on the structure and composition of associated vegetation. Exotic species, such as tamarisk, may be most attractive when native species are not available or are not in flower (Terry Griswold, personal communication 3/20/09). Tepedino and others (2008) compared bee assemblages visiting exotic and native flowering plants in Capitol Reef National Park. They found that exotic species, including saltcedar, were host to a number of native generalist bee species and concluded that exotics could potentially increase the carrying capacity and population size of generalist bees. Saltcedar provides an early source of pollen for overwintering bees (Kerpez and Smith 1987) and may also be a refugia for bees when nearby agricultural fields are being sprayed (Horton and Campbell 1974).

CONCLUSIONS

This study highlights the importance of maintaining willows in the riparian community. When compared head-to-head with woody invasives, willows appeared to be more important to pollinating insects, especially bees. Approximately 73 percent of the world's cultivated crops are pollinated by some species of bee (Food and Agriculture Organization of the United Nations 2004). The effect of woody exotics on native bee populations is therefore of considerable importance. Cohan and others (1978) suggested that a reduction in density of pure saltcedar stands and subsequent replacement with mesquite and willow would be of benefit to wildlife. This report suggests additional benefits to native pollinators, especially bees, of maintaining or restoring willow species in southwestern riparian zones.

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APPENDIX 1—Numbers of arthropods by family that were collected from each of the three woody plant species.

Order	Family	Common name	Russian olive	Saltcedar	Willow
Araneida	Araneidae	Orb-weaving spiders	5	11	15
	Anyphaenidae	Anyphaenid sac spiders		2	
	Clubionidae	Sac spiders			2
	Lycosidae	Wolf spiders			1
	Mimetidae	Pirate spiders			1
	Oxyopidae	Lynx spiders	1		2
	Philodromidae	Running spiders	1	1	5
	Salticidae	Jumping spiders	3	2	4
	Tetragnathidae	Thick-jawed orb weavers			1
	Thomisidae	Crab spiders	2	3	53
	Unknown		2	4	11
Coleoptera	Bruchidae	Seed beetles	3		
	Buprestidae	Metallic wood-borers		1	
	Chrysomelidae	Leaf beetles	2	8	34
	Cleridae	Checkered beetles			3
	Coccinellidae	Ladybird beetles		1	9
	Curculionidae	Snout beetles		1	5
	Dermestidae	Dermestid beetles	2		4
	Lampyridae	Fireflies			1
	Melyridae	Soft-winged flower beetles	52	63	57
	Mordellidae	Tumbling flower beetles		1	
	Scraptiidae	False flower beetles	11	8	9
	Scarabaeidae	scarab beetles			1
	Staphylinidae	Rove beetles	1		1
Collembola	Entomobryidae	Springtails		1	2
	Sminthuridae	Globular springtails		2	
Dermaptera	Unknown	Earwigs			1
Diptera	Asilidae	Robber flies			1
	Anthomyiidae	Anthomyiid flies			1
	Bibionidae	March flies	1		7
	Bombyliidae	Bee flies		3	5
	Calliphoridae	Blow flies			1
Diptera	Cecidomyiidae	Gall Gnats			3
	Ceratopogonidae	Punkies, biting midges	2		2
	Chironomidae	Midges	8	34	689
	Chloropidae	Frit flies	6	17	50
	Culicidae	Mosquitos		4	1
	Dolichopodidae	Long-legged flies	6	3	3
	Empididae	Dance flies	57	7	45
	Muscidae	House flies		1	2
	Mycetophilidae	Fungus gnats	3		44
	Otitidae	Picture-winged flies	1	1	6
	Phoridae	Hump-backed flies		10	8
	Pipunculidae	Big-headed flies			1
	Sciaridae	Dark-winged fungus gnats	2		3
	Sciomyzidae	Marsh flies		2	
	Syrphidae	Syrphid flies		1	

APPENDIX 1 (continued)—Numbers of arthropods by family collected from each of the three woody plant species.

Order	Family	Common name	Russian olive	Saltcedar	Willow
Diptera	Tachinidae	Tachnid flies		1	1
	Therevidae	Stiletto flies		2	1
	Tipulidae	Crane flies	2	4	6
	Trixoscelididae	Trixoscelidid flies		4	9
Hemiptera	Berytidae	Stilt bugs		5	
	Corimelaenidae	Negro bugs			1
	Lygaeidae	Seed bugs	18	149	33
	Miridae	Leaf or plant bugs		37	8
	Phymatidae	Ambush bugs			1
	Reduviidae	Assassin bugs		1	
	Thyreocoridae	Negro bugs		1	
	Tingidae	Lace bugs		6	5
Homoptera	Aphidae	Aphids	3	16	77
	Cicadellidae	Leafhoppers	2	30	837
	Dictyopharidae	Dictyopharid planthoppers		1	14
	Psyllidae	Psyllids			3
	Unknown				23
Lepidoptera	Geometridae	Geometer moths			8
	Noctuidae	Noctuid moths			1
	Unknown	caterpillars		1	4
Hymenoptera	Andrenidae	Andrenid bees			7
	Apidae	Bumble, honey bees, etc.			7
	Braconidae	Braconids		2	17
	Chalcidoidea	Unknown chalcidoids	19	21	133
	Colletidae	Yellow-faced bees			3
	Formicidae	Ants	31	56	356
	Halictidae	Sweat bees		2	11
	Ichneumonidae	Ichneumons	2		7
	Sphecidae	Sphecid wasps			3
	Vespidae	Vespid wasps	1		1
Orthoptera	Acrididae	Short-horned grasshoppers			13
	Gryllidae	Crickets			5
Plecoptera	Unknown	Stoneflies		1	2
Psocoptera	Liposcelidae	Liposcelid booklice		2	4
Thysanoptera	Thripidae	Thrips	21		36
Trichoptera	Hydroptilidae	Caddisflies			2