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SURFACE-ACTIVE ARTHROPOD COMMUNITIES IN NATIVE AND EXOTIC RIPARIAN VEGETATION IN THE MIDDLE RIO GRANDE VALLEY, NEW MEXICO

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ABSTRACT—The rapid naturalization of exotic saltcedar (*Tamarix*) trees in riparian ecosystems throughout the southwestern United States necessitates understanding its impacts on various ecosystem components, yet surface-active arthropod communities in these systems remain largely unstudied in spite of their importance to ecosystem structure and function. We used pitfall-trap captures to estimate taxonomic richness, abundance, and composition of surface-active arthropods in two cottonwood-dominated and two saltcedar-dominated riparian forests along the Middle Rio Grande of central New Mexico during 1991 through 1993. Arthropod communities at cottonwood sites were generally more similar to each other than to those at saltcedar sites, but similarity varied among taxonomic groups. Total richness was similar between the two saltcedar sites and one cottonwood site, but lower at the second cottonwood site. Cottonwood sites were distinguished by a greater abundance of exotic isopods (*Armadillidium vulgare* and *Porcellio laevis*), but abundance of other key taxa was generally similar or higher at saltcedar sites. Richness and abundance of spiders was greater at saltcedar sites. Predators were the most speciose trophic group at all sites, although detritivores had the greatest numbers of individuals due to the abundance of isopods. Although saltcedar has greatly altered riparian ecosystems and may be less desirable than native riparian vegetation, it does support a varied and abundant surface-dwelling arthropod community that is available as prey to vertebrate species.

RESUMEN—Los tarayes o tamariscos (*Tamarix*) son árboles exóticos que se han naturalizado en el suroeste de los Estados Unidos, especialmente en las zonas ribereñas, siendo necesario entender su impacto sobre varios componentes de este ecosistema. A pesar de la importancia de las comunidades de artrópodos terrestres en estos ecosistemas los mismos han sido estudiado muy poco. De 1991 a 1993 utilizamos trampas de copas enterradas para determinar la riqueza taxonómica, abundancia y composición de los artrópodos terrestres en cuatro bosques ribereños-dos alamedas y dos tarayales a lo largo del Middle Rio Grande en centro New Mexico. Generalmente, las comunidades de artrópodos terrestres en las dos alamedas eran más parecidas entre si que con las comunidades en los dos tarayales, pero las semejanzas variaban entre grupos taxonómicos. La riqueza taxonómica total era similar entre los tarayales y una de las alamedas, pero más baja en la otra alameda. Los bosques de álamos se distinguían por una gran abundancia de isópodos exóticos (*Armadillidium vuulgare* y *Porcellio laevis*) pero la abundancia de otros taxones claves era similar o superior en los bosques de tarayes. La riqueza y abundancia de arañas eran superior en los tarayales. Los depredadores eran el grupo trófico con más especies en todos los sitios, mientras que los detritívoros eran más numerosos debido a la gran abundancia de los isópodos. Aunque los tarayes han alterado enormenente los ecosistemas ribereños y pueden ser menos deseables que la vegetación nativa los mismos mantienen una comunidad variada y abundante de artrópodos terrestres disponibles como presa para las especies de vertebrados.

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Riparian ecosystems in the southwestern United States have been altered extensively since European settlement. One primary impact has been introduction of exotic plants, which have greatly changed species composition and structure of riparian forests (Ohmart and Anderson, 1982; Loope et al., 1988; Vitousek, 1990; Howe and Knopf, 1991; Brock, 1994; Busch and Smith, 1995; Crawford et al., 1996). For example, saltcedar (*Tamarix*) was first introduced into the western United States in the late 1800s (Horton, 1964). It expanded rapidly

throughout western riparian areas between 1900 and the 1960s, and saltcedar now occupies nearly 500,000 ha (Brock, 1994). Concomitant anthropogenic changes in the natural flow regimes of most western rivers have favored the spread of exotic vegetation while contributing to the decline of native riparian plants (Rood and Hinze-Milne, 1989; Rood and Mahoney, 1990; Stromberg and Patton, 1991). Along the Rio Grande in central New Mexico, decreased cottonwood regeneration combined with rapid colonization of saltcedar (*Tamarix ramosissima*) and Russian-olive (*Elaeagnus angustifolia*) suggest that, without changes in current water management strategies, the local riparian ecosystem will soon be dominated by exotic trees and shrubs (Howe and Knopf, 1991). Eradication of exotic plants and restoration of native vegetation are both costly and labor intensive, and although such restoration efforts are underway in many areas, total elimination of these invasive species will be impossible in most cases.

The southwestern United States maintains an exceptionally rich diversity of both invertebrate and vertebrate species, due to its complex geologic history and to the variety of habitats present (Parmenter et al., 1995). Riparian vegetation supports particularly high taxonomic richness and abundance of several vertebrate groups compared to drier uplands (Ohmart and Anderson, 1982; Knopf et al., 1988; Szaro, 1991), and effects of saltcedar on a number of vertebrate populations have been documented (Hunter et al., 1988; Brown and Trosset, 1989; Ellis, 1995; Konkle and Schemnitz, in litt.; Ellis et al., 1997). However, much less is known about invertebrates in these aridland riparian habitats, and arthropod communities in these exotic forests remain virtually undescribed.

Terrestrial arthropods are the most abundant and diverse group of animals on earth (Wilson, 1987, 1988), and they occupy a large variety of ecological niches and play numerous key roles in many kinds of ecosystems (Collins and Thomas, 1991; Kim, 1993). Arthropods can be important as herbivores, pollinators, predators, parasites, and detritivores, and as prey for a number of vertebrate taxa. Thus, composition of the arthropod community can influence structure and function of an entire ecosystem (Price, 1984; Williams, 1993). Although vertebrate species most often are used as biological indicators (Landres et al., 1988; Noss, 1990; Karr, 1991), the predominance of arthropods in terrestrial ecosystems suggests that identifying key arthropod groups as indicators should be a priority for inventory and monitoring in conservation planning (Refseth, 1980; Andersen, 1990; Brown, 1991; Kim, 1993; Kremen et al., 1993; Williams, 1993). Describing existing arthropod communities along southwestern rivers is particularly important now as the vegetative composition of these riparian ecosystems is rapidly changing, because changes in the arthropod community due to the presence of exotic plants such as saltcedar may directly or indirectly affect a number of native plant and animal species.

Our objectives in this study were to compare surface-active arthropod assemblages in cottonwood-dominated forests with those in monotypic saltcedar stands along the Rio Grande in central New Mexico. Here we address four questions with respect to surface-active arthropod communities in these two vegetation types: 1) does taxonomic richness differ between vegetation types, 2) does abundance of key groups differ between vegetation types, 3) does taxonomic composition differ between vegetation types, and 4) does trophic composition differ between vegetation types? Finally, we hope this paper will stimulate more extensive studies of arthropods in native and altered riparian landscapes throughout the southwestern United States to provide a foundation for monitoring ecological change.

MATERIALS AND METHODS—*Study Sites*—Study sites were established in 1991 at Bosque del Apache National Wildlife Refuge, Socorro Co., New Mexico (Fig. 1). The refuge includes over 19 km of the Rio Grande and its associated riparian vegetation, including forests dominated by Rio Grande cottonwood (*Populus deltoides wislizenii*) and extensive tracts of saltcedar (*Tamarix ramosissima*). Saltcedar was established in the refuge by the late 1930s, and expanded rapidly after floods in the early 1940s (J. Taylor, pers. comm.). All of the sites have been isolated from flooding for about 50 years.

Two 3.1 ha sites were established in cottonwood-dominated forests (Cottonwood-1 and Cottonwood-2), and two 2.9 ha sites were established in saltcedar-dominated vegetation (Saltcedar-1 and Saltcedar-2). Both cottonwood sites and Saltcedar-1 were in a strip of continuous forest, 200 to 300 m wide, west of the

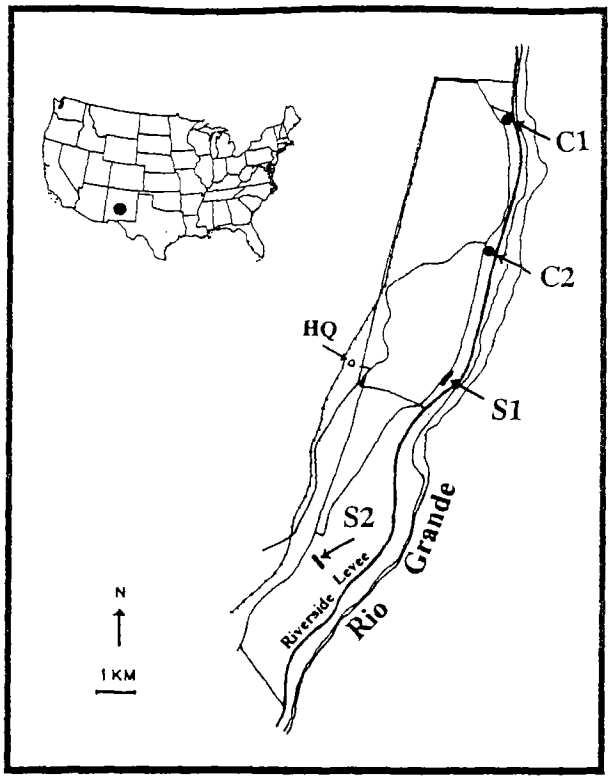

FIG. 1—Location of study sites within Bosque del Apache National Wildlife Refuge, Socorro Co., New Mexico. The four study sites are Cottonwood-1 (C1), Cottonwood-2 (C2), Saltcedar-1 (S1) and Saltcedar-2 (S2); refuge headquarters is indicated as HQ. The location of the refuge is indicated on the inset map of New Mexico.

riverside levee and ca. 0.5 km west of the Rio Grande (Fig. 1). At the time of the study, the strip varied from areas dominated by cottonwood to nearly pure stands of saltcedar. Cottonwood-2 was 3.7 km south of Cottonwood-1, and Saltcedar-1 was 3.5 km south of Cottonwood-2. West of these linear forests were agricultural fields and intermittently flooded wetland areas, with scattered cottonwood and saltcedar but without large continuous stretches of cottonwood forest. Chihuahuan upland vegetation dominated by creosote bush (*Larrea*) lies west of the fields, ca. 2 km west of these three study sites. Saltcedar-2 was isolated from the other three sites, being ca. 5.8 km south of Saltcedar-1, 1.5 km west of the river, and 0.5 km east of Chihuahuan upland vegetation (Fig. 1). The site was within an extensive stand of saltcedar that contained a few small cottonwood patches; there were no continuous cottonwood forests within at least 1 km of the study site. A large, continuously flowing water canal ran between the stand of saltcedar containing the study site and the upland vegetation.

Cottonwood sites included a canopy dominated by medium to large cottonwoods, with a subcanopy of saltcedar and Goodding willow (*Salix gooddingii*). The understory included seepwillow (*Baccharis glutinosa*), New Mexico olive (*Forestiera neomexicana*), and low densities of other shrubs. The estimated density of woody plants at the two cottonwood sites averaged 1,579 plants/ha (Ellis, 1995). Although saltcedar comprised 44% of woody stems at cottonwood sites, it was much less abundant than at saltcedar sites, where it comprised 98% of woody stems (see below and Ellis 1995), and aerial cover of cottonwood was much greater than of saltcedar. A variety of herbaceous understory species were also present, the density of which varied among years (L. M. Ellis et al., pers. obser.). The most common of these were *Conyza canadensis*, *Chamaesyce serpyllifolia*, *Ratibida tagetes*, *Solanum elaeagnifolium*, and *Sphaeralcea angustifolia*. Patchy but often deep litter layers were present at cottonwood sites (Ellis et al., 1998). Soils also varied considerably within a small spatial scale (often within meters) and within each site ranged from largely sandy to highly clayey (L. M. Ellis et al., pers. obser.).

Saltcedar sites included predominantly saltcedar with low densities of seepwillow. Saltcedar-2 had a few cottonwoods in about one-third of the site. Estimated density of woody species at the two saltcedar sites averaged 8,622 plants/ha (Ellis, 1995). Both saltcedar sites included a gradation in structure along the 500 m length of each site ranging from relatively low (<2 m), dense, shrubby clumps of saltcedar with no overstory to large (2 to 4 m) trees forming a partial to full overstory with relatively open spaces beneath; this gradation was parallel to the river at Saltcedar-1 and nearly perpendicular to it at Saltcedar-2. Herbaceous understory species were less common than at cottonwood sites, occurring primarily in openings, and litter accumulations were generally more uniform (Ellis et al., 1998). Soils were also locally quite variable, but overall Saltcedar-1 had a higher clay content compared to Saltcedar-2, which had a greater sand content (L. M. Ellis et al., pers. obser.).

Pitfall Trapping Protocol—We used 30 pitfall traps at each site to monitor surface-active arthropod activity. Cottonwood sites were oriented around a mammal trapping web consisting of twelve 100-m transects radiating out from a center point (Fig. 2). Two or three pitfall traps were located 10 m apart along each transect, beginning 65 to 75 m from the center of the web. Due to the configuration of saltcedar stands, trapping grids were used at saltcedar sites instead of webs. Six pitfalls were spaced 10 m apart along each of five transects, 100 m apart, beginning ca. 15 to 20 m from the forest edge (Fig. 2). Each trap consisted of two plastic cups, 9 cm diameter and 12 cm deep, one inside the other and set into the ground so the open tops were flush with the surface; the inner cup could be removed to collect specimens while the outer cup maintained the trap lo-

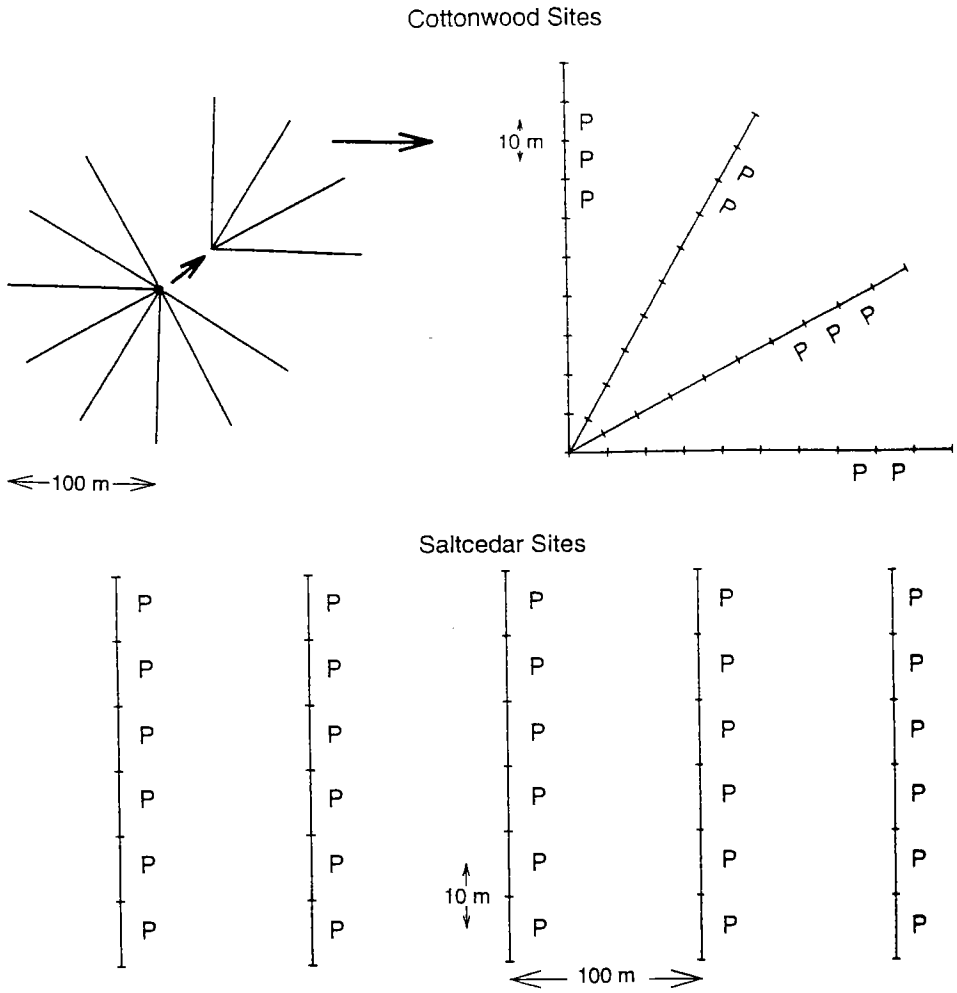

FIG. 2—Pitfall trap orientation at cottonwood and saltcedar study sites. P indicates trap location. Thirty traps were located at each site.

cation. Each trap was sheltered with a wooden cover raised ca. 3 cm over the trap when open. Traps were opened for 48 h during each trapping period, usually the third week of each of the following months: July, August, October, and December 1991, February, April, June, August, and October 1992, and February, April, and May 1993.

All arthropods captured were collected and frozen, then later identified to the lowest taxonomic level practical (ranging from family to species, depending on the group) and counted to give an estimate of taxonomic richness and abundance. Here we generally use the term taxonomic richness rather than species richness because the level of taxonomic resolution varies among groups. Identifications were made by one of us (FH) following Lindroth (1961–1969), Arnett (1975), Kaston (1972), Bland (1978), Arnett et al. (1980), MacKay et al. (1988), Bell (1990), and Hölldobler and Wilson (1990), and with reference to specimens in the Museum of Southwestern Biology, Division of Arthropods. Some additional identifications were determined or verified by specialists. Vouchers are housed in the Museum of Southwestern Biology, Division of Arthropods.

Analyses—Captures were summed across all traps and all sample periods within each site. We compared taxonomic richness and abundance at the four sites during the entire study for all taxa combined, and for spiders, all insects combined, carabid beetles (Coleoptera: Carabidae), tenebrionid beetles (Coleoptera: Tenebrionidae), and ants (Hymenoptera: Formicidae). Abundance data were standardized for differences in sample areas by expressing abundance values for each species at all sites per 2.9 ha, the smaller of the two trapping areas used.

We assessed similarity in taxonomic composition among sites for these groups by use of cluster analyses based on dissimilarity indexes. We used standardized abundance data to calculate dissimilarities using the Bray-Curtis percent dissimilarity index (PD), computed as

$$PD = 1 - [2W/(A + B)]$$

where

$$A = \sum_{i=1}^{S} X_{ij} \qquad B = \sum_{i=1}^{S} X_{ik}$$

$$W = \sum_{i=1}^{S} [\min(X_{ij}, X_{ik})]$$

and X_{ij} is the scaled abundance of species i at sample unit j, X_{ik} is the scaled abundance of species i at sample unit k, and min (X_{ij}, X_{ik}) is the smaller value of X_{ij} and X_{ik}, or the shared abundance of species i at sites j and k (Ludwig and Reynolds, 1988). Therefore W is the sum over all species of the shared abundances. For analyses dominated by very abundant species (all taxa, insects, ants), we applied an additional adjustment by dividing the abundances at each site for a given species by the maximum site abundance for that species, yielding new values scaled from 0 to 1. These values were used to calculate *PD* as described above. Distance matrices were calculated for each taxonomic group based on all pair-wise comparisons of *PD* among the four sites. We used these to perform cluster analyses with the flexible strategy to create dendrograms indicating taxonomic similarity (Ludwig and Reynolds, 1988).

For families with multiple taxa determined, individuals identified only to the family level were excluded from richness estimates and for analyses of taxonomic composition, but were included for abundance estimates. Also excluded from richness and composition estimates were member of the orders Araneae, Heteroptera, and Coleoptera for which family was not determined.

We assigned each species to one of three trophic groups (herbivore, predator, or detritivore), and compared number of taxa and number of individuals within each trophic group at the four sites. Predators included parasites (e.g., Pulicidae, Chalcidoidea) whereas detritivores included scavengers and fungivores. Ants were excluded from these trophic summaries because these taxa are not easily classified into one of the three categories (e.g., Brian, 1983; Hölldobler and Wilson, 1990).

RESULTS—*Taxonomic Richness*—Total number of taxa present was similar among the two saltcedar sites (66 and 65 taxa at Saltcedar-1 and Saltcedar-2, respectively) and Cottonwood-1 (65), but lower at Cottonwood-2 (55; Fig. 3, Table 1). More spider taxa were present at the saltcedar sites (22 and 16 at Saltcedar-1 and Saltcedar-2, respectively) than at the cottonwood sites (13 at each; Fig. 3, Table 1). Richness of all insects combined and of ant taxa was highest at Cottonwood-1 (48 and 12, respectively) followed by Saltcedar-2 (43 and 10, respectively). Cottonwood-1 also had the greatest number of tenebrionid beetle species (8), but had only 1 species of carabid beetle compared to 4 or 5 carabid species at each of the other three sites.

Abundance—The two species of isopods combined (*Armadillidium vulgare* and *Porcellio laevis*) made up the most abundant group present at all sites, with number of isopods exceeding combined totals of all other species for three of the four sites (Table 1). Isopods were more abundant at cottonwood sites than at saltcedar sites, and the high total abundance (all taxa) at cottonwood sites was driven primarily by the large numbers of isopods (Fig. 4). Spiders were more abundant in saltcedar than in cottonwood (Fig. 4). High insect abundance at Saltcedar-1 primarily reflected large numbers of ants captured there (Fig. 4). Abundance of insects other than ants was greater at cottonwood sites. Carabid beetles were most abundant at Saltcedar-1, but more tenebrionid beetles were captured at Saltcedar-2 than at each of the other three sites (Fig. 4).

Taxonomic Composition—When all taxa were considered, community composition of surface-active arthropods was more similar between the pairs of sites within vegetation types than across vegetation types (Fig. 5). However, this pattern changes when particular arthropod groups were considered separately (Fig. 5). Similarity among all sites was highest for spiders compared to other taxonomic groups, with cottonwood sites most similar in spider composition. The pattern for insects was similar, but with less congruence among all sites and with Saltcedar-1 more similar to the cottonwood sites than Saltcedar-2. Ant communities generally were similar between sites in each vegetation type. These patterns were affected particularly by species such as *Tapinoma sessile,* which was abundant at saltcedar sites but absent from cottonwood sites, *Crematogaster cerasi,* which was present at both cottonwood sites but only at Saltcedar-1, and *Monomorium minimum,* which was abundant at all sites, but much less so at Saltcedar-2 (Table 1). There was very little overlap in carabid species among sites, with the similarity between Cottonwood-2 and Saltcedar-1 driven by the presence of *Calathus opaculus* (Fig. 5 and Table 1). Tenebrionids were more abundant than carabids, particularly at Saltcedar-2 which therefore differed most from the other three sites in tenebrionid composition (Fig. 5).

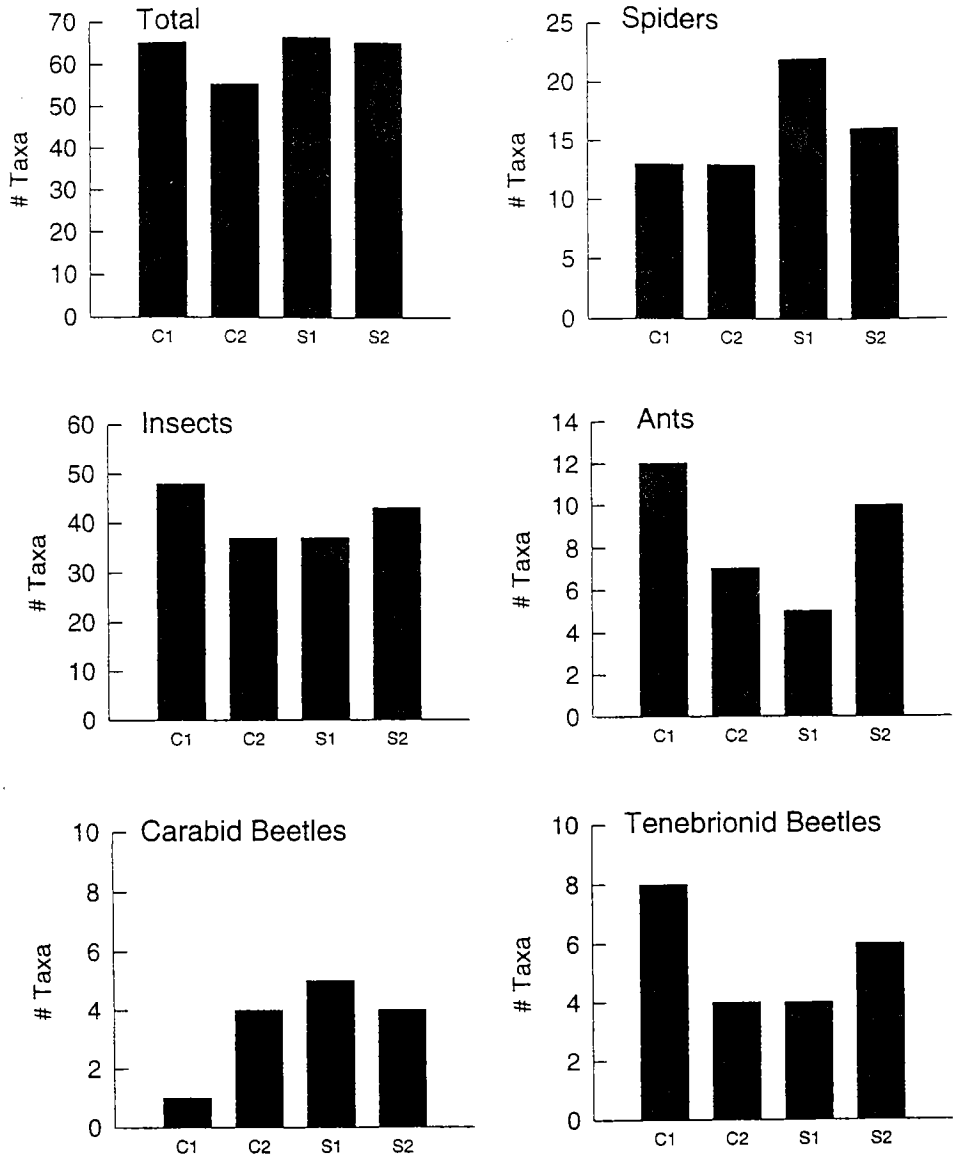

FIG. 3—Taxonomic richness for different arthropod groups captured in pitfall traps at Cottonwood-1 (C1), Cottonwood-2 (C2), Saltcedar-1 (S1), and Saltcedar-2 (S2) between July 1991 and May 1993, inclusive. Total includes all arthropods captured.

Trophic Composition—Predators were the most taxon-rich trophic group at all sites (Fig. 6), followed by detritivores and herbivores. Saltcedar sites had slightly more predaceous taxa than cottonwood sites, which reflects the greater number of spider taxa at the former. Most individuals in collections were detritivores, reflecting the high numbers of isopods. Excluding isopods, the remaining individuals were dominated by predators. Herbivores were much less common at all sites, both in the number of taxa and number of individuals, but were especially underrepresented at Saltcedar-1.

DISCUSSION—Cottonwood- and saltcedar-dominated sites did not support distinct surface-active arthropod communities that clearly reflect differences in vegetation. There was variation in richness and abundance of different taxonomic groups both within and between vegetation types, suggesting that other, site-specific factors beyond the dominant vegetation type may be important in determining which arthropod species are present. Saltcedar-1 shared its most common species with the nearby cottonwood sites, but the more isolated saltcedar site differed more in terms of overall species composition. This may reflect simple proximity among sites, or proximity to the river. However, the most dominant species over-

TABLE 1—Arthropod species list for all study sites. Values are actual total number of individuals captured between July 1991 and May 1993, inclusive; note that values used for analyses were standardized for area. Values in parentheses are the total number of trapping periods during which each taxon was captured.

	Trophic group[1]	C1	C2	S1	S2
ARACHNIDA					
Pseudoscorpionida					
Family undetermined	P	15 (11)	6 (5)	6 (5)	4 (3)
Araneae					
Family undetermined	P				1 (1)
Agelenidae	P	1 (1)			
Araneidae	P			1 (1)	
Clubionidae	P			1 (1)	
Dictynidae	P			1 (1)	4 (4)
Dictyna subulata	P				1 (1)
Mallos sp.	P			1 (1)	
Gnaphosidae	P			3 (3)	1 (1)
Drassyllus sp.	P	6 (3)	3 (3)	1 (1)	2 (1)
Gnaphosa sp.	P			1 (1)	
Haplodrassus sp.	P	1 (1)	3 (2)	1 (1)	2 (2)
Poecilochroa sp.	P				1 (1)
Zelotes anglo	P		1 (1)		
Zelotes laslanus	P			1 (1)	2 (1)
Zelotes sp.	P	6 (4)	8 (6)	37 (8)	23 (6)
Linyphiidae					
Subfamily Erigoninae	P	45 (5)	56 (6)	28 (4)	71 (8)
Subfamily Linyphiinae	P	2 (2)	3 (3)	10 (5)	2 (2)
Lycosidae	P	2 (1)		21 (1)	
Allocosa sp.	P			1 (1)	
Alopecosa sp.	P	2 (2)	1 (1)	2 (1)	
Trochosa sp.	P	43 (11)	65 (11)	59 (9)	78 (7)
Pardosa sp.	P			1 (1)	
Pirata sp.	P	1 (1)	3 (2)	2 (2)	4 (2)
Pholcidae	P				1 (1)
Physocyclus sp.	P				1 (1)
Psilochorus sp.	P	1 (1)		1 (1)	4 (2)
Salticidae	P			2 (2)	1 (1)
Habrocestum sp.	P		2 (1)		
Habronattus sp.	P		4 (1)		1 (1)
Sitticus sp.	P	1 (1)	1 (1)	4 (2)	
Theridiidae	P			4 (3)	4 (3)
Euryopis sp.	P			1 (1)	
Latrodectus sp.	P			1 (1)	
Steatoda borealis	P			1 (1)	
Thomisidae	P	1 (1)			
Misumenops sp.	P	6 (5)	7 (3)		1 (1)
Xysticus sp.	P	1 (1)			
Acari					
Family undetermined	P	38 (3)	65 (4)	22 (4)	29 (7)
MALACOSTRACA					
Isopoda					
Armadillidiidae					
Armadillidium vulgare	D	2,564 (11)	5,059 (11)	118 (7)	1,595 (12)
Porcellionidae					
Porcellio laevis	D	1,288 (12)	247 (10)	399 (12)	46 (5)

TABLE 1—Continued.

	Trophic group[1]	C1	C2	S1	S2
CHILOPODA					
Scolopendromorpha					
Scolopendridae	P			2 (2)	2 (1)
Lithobiomorpha					
Family undetermined	P		1 (1)	1 (1)	1 (1)
Lithobiidae	P			1 (1)	
INSECTA					
Thysanura					
Lepismatidae	D	7 (4)	7 (3)		
Orthoptera					
Gryllidae					
Gryllus alogus	D	20 (6)	4 (3)	10 (4)	
Raphidophoridae					
Ceuthophilus sp.	D	5 (3)	4 (3)		1 (1)
Isoptera					
Rhinotermitidae					
Reticulitermes sp.	D		3 (1)		
Psocoptera					
Family undetermined	D		6 (2)	3 (3)	4 (2)
Ectopsocidae	D			1 (1)	
Thysanoptera					
Family undetermined	H				1 (1)
Heteroptera					
Family undetermined				1 (1)	
Lygaeidae	H				5 (1)
Cymus coriacipennis	H			1 (1)	
Peritrechus fraternus	H		1 (1)		
Reduviidae	P			1 (1)	
Barce sp.	P				2 (2)
Empicoris orthoneuron	P	1 (1)			
Gardena elkinsi	P				1 (1)
Pseudometapterus sp.	P			1 (1)	
Homoptera					
Family undetermined	H	1 (1)			
Cicadellidae	H		1 (1)		
Delphacidae	H	1 (1)			
Coleoptera					
Family undetermined		11 (3)	10 (4)	30 (5)	6 (4)
Anobiidae					
Ptinus fur	D	6 (1)	8 (2)	7 (3)	
Carabidae	P	2 (2)	1 (1)		4 (3)
Amara carinata	P				1 (1)
Amara littoralis	P				1 (1)
Amara sp.	P		2 (1)		3 (2)
Calathus opaculus	P	1 (1)	9 (3)	5 (2)	
Chlaenius sp.	P		1 (1)		
Cyclotrachelus sp.	P				2 (1)
Harpalus pennsylvanicus	P		1 (1)		
Poecilus chalcites	P			7 (2)	
Scarites sp.	P			4 (3)	
Selenophorus planipennis	P			1 (1)	
Stenolophus sp.	P			1 (1)	

TABLE 1—Continued.

	Trophic group[1]	C1	C2	S1	S2
Chrysomelidae					
Eumolpinae	H	1 (1)	1 (1)		
Corylophidae	D				2 (1)
Arthrolips decolor					1 (1)
Cryptophagidae					
Cryptophagus sp.	D	13 (3)	21 (5)	7 (5)	
Cucujidae					
Undetermined species 1	P				1 (1)
Undetermined species 2	P				3 (3)
Curculionidae				1 (1)	
Otiorhynchus ovatus	H	1 (1)			
Rhypodillus brevicollis	H	1 (1)			
Dermestidae	D	2 (2)	15 (3)	30 (3)	
Elateridae					
Aeolus livens	H	1 (1)	16 (5)		
Athous sp.	H	1 (1)			
Eucnemidae	D		2 (1)		
Histeridae					
Euspilotus assimilis	P		1 (1)		
Lathridiidae					
Undetermined species 1	D			1 (1)	
Undetermined species 2	D			1 (1)	
Ptiliidae	D				1 (1)
Scarabaeidae				1 (1)	
Ataenius sp.	D		1 (1)		2 (1)
Scraptiidae					
Anaspis sp.	D	1 (1)		1 (1)	
Silphidae					
Nicrophorus sp.	D			2 (1)	
Staphylinidae	P	3 (3)	5 (3)	3 (2)	10 (4)
Aleocharinae	D	1 (1)		1 (1)	
Olisthaerus sp.	P				1 (1)
Paederinae	P	1 (1)		2 (1)	1 (1)
Platydracus sp. 1	P	2 (1)	3 (1)	2 (1)	6 (1)
Platydracus sp. 2	P	20 (1)	10 (1)	13 (1)	11 (1)
Quedius sp.	P			2 (1)	
Reichenbachia sp.	P	1 (1)	2 (2)		1 (1)
Staphylinus sp.	P	3 (3)	17 (5)	3 (3)	
Trichophyini	P				1 (1)
Tenebrionidae	D	1 (1)		1 (1)	
Asidopsis opaca	D	1 (1)			
Blapstinus fortis	D	1 (1)	1 (1)	8 (2)	19 (2)
Blapstinus sp.	D	1 (1)		4 (1)	16 (3)
Eleodes extricatus	D	2 (2)		3 (1)	30 (4)
Eleodes fusiformis	D		1 (1)		
Eleodes longicollis	D	1 (1)			4 (3)
Eleodes obsoletus	D	1 (1)			
Eleodes sponsus	D	1 (1)			
Eleodes suturalis	D	24 (7)	11 (6)	12 (3)	13 (3)
Embaphion sp.	D		2 (1)		
Metoponium sp.	D				5 (3)

TABLE 1—Continued.

	Trophic group[1]	C1	C2	S1	S2
Trogidae					
Trox punctatus	D	7 (5)	14 (5)	3 (1)	5 (3)
Trox tuberculatus	D			1 (1)	
Lepidoptera					
Family undetermined	H	9 (4)	4 (2)		5 (4)
Diptera					
Family undetermined		9 (1)	8 (2)	20 (8)	8 (7)
Siphonaptera					
Pulicidae	P	1 (1)			
Hymenoptera					
Andrenidae	H	1 (1)			1 (1)
Chalcidoidea	P				1 (1)
Diapriidae	P	1 (1)			
Formicidae					
Dolichoderinae					
Dorymyrmex insana	A	16 (4)			25 (5)
Tapinoma sessile	A			75 (6)	33 (9)
Ecitoninae					
Neivamyrmex nigrescens	A		8 (3)		
Neivamyrmex sp.	A	7 (1)			
Formicinae					
Camponotus vicinus	A	2 (1)			
Formica sp.	A				3 (2)
Lasius sp.	A				3 (1)
Myrmicinae	A	2 (1)		1 (1)	2 (1)
Crematogaster cerasi	A	98 (9)	18 (8)	17 (4)	
Leptothorax pergandei	A	3 (1)	2 (1)		1 (1)
Leptothorax sp.	A	2 (2)	2 (1)		
Monomorium minimum	A	255 (6)	332 (8)	621 (5)	60 (6)
Pheidole sp.	A	1 (1)			
Pogonomyrmex occidentalis	A	48 (5)			1 (1)
Solenopsis sp.	A	71 (2)	5 (2)		7 (2)
Ponerinae					
Hypoponera sp.	A	1 (1)	2 (1)	1 (1)	1 (1)

[1] H = Herbivore, P = Predator, D = Detritivore, A = Ant.

all, *Armadillidium vulgare,* was more common at Saltcedar-2 than at Saltcedar-1, suggesting that something other than proximity among sites determines the composition of species present.

The greater abundance of *A. vulgare* at cottonwood sites was the biggest difference between arthropod communities in the two vegetation types. These exotic isopods are dominant macrodetritivores in riparian forests along much of the Middle Rio Grande, where they feed extensively on decomposing leaf tissue (Heinzelmann et al., 1995; Crawford et al., 1996). Some research indicates that terrestrial arthropods exhibit feeding preferences for different types of leaf litter or litter quality (Bultman and Uetz, 1984; Hassall and Rushton, 1984; Dudgeon et al., 1990; Szlávecz and Maiorana, 1991), and both growth rate and survival may differ on different types of food (Rushton and Hassall, 1983; Heinzelmann et al., 1995), but other evidence suggests that food may be of limited importance in habitat selection (Warburg et al., 1984; Hornung et al., 1992; Heinzelmann et al., 1995). Little information is available on whether isopods eat saltcedar, but captures of *A. vulgare* were sufficiently high at Saltcedar-2 to suggest that they do. Although native crickets, (*Gryllus alogus*),

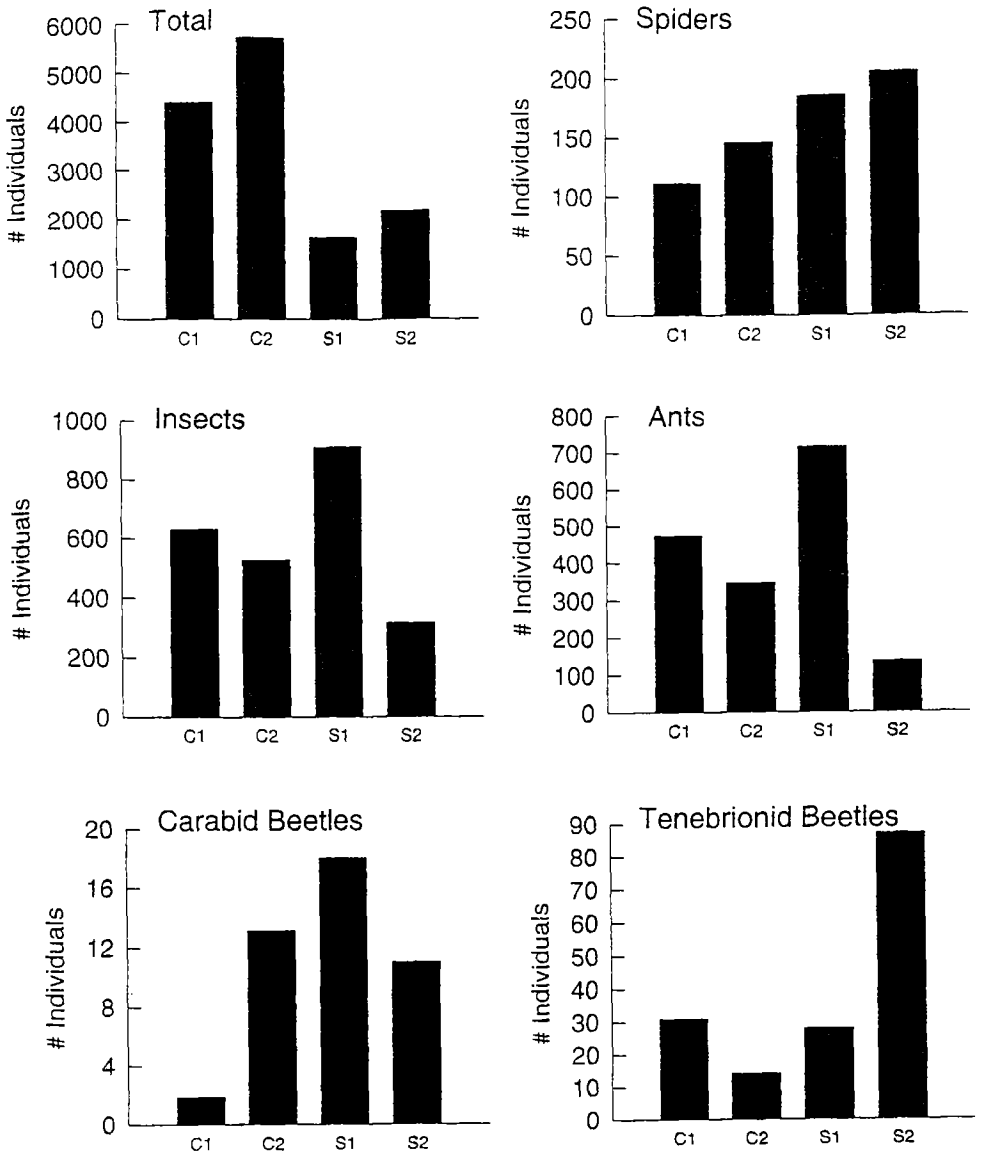

FIG. 4—Abundance of individuals in different arthropod groups captured in pitfall traps at Cottonwood-1 (C1), Cottonwood-2 (C2), Saltcedar-1 (S1), and Saltcedar-2 (S2) between July 1991 and May 1993, inclusive.

which may have been the dominant macrodetritivore in this system before the introduction of isopods, were absent from Saltcedar-2, they were present at Saltcedar-1, again suggesting that saltcedar litter may provide a sufficient food source.

Habitat variables other than leaf litter may be important in determining the distribution of isopods, particularly substrate, moisture, shelter, and climate (Warburg et al., 1984; Warburg, 1993; Heinzelmann et al., 1995). In riparian forest sites ca. 65 km north of these study sites, *A. vulgare* was captured more often in clay-loam soils than in sandy-loam soils (Heinzelmann et al., 1995). Soils varied greatly within small spatial scales at our study sites, but overall the site with the greatest abundance of *A. vulgare* (Cottonwood-2) had the highest overall sand content in the soil, and among the two saltcedar sites, the one with greater abundance of *A. vulgare* again had soils with a higher sand content (L. M. Ellis et al., pers. obser.). Substrate differences are thus also inconclusive for explaining differences in isopod abundance. More studies are needed to understand the role of these introduced detritivores and their interactions with both native and exotic vegetation.

Several arthropod groups have been identified as important biological indicators. McIver

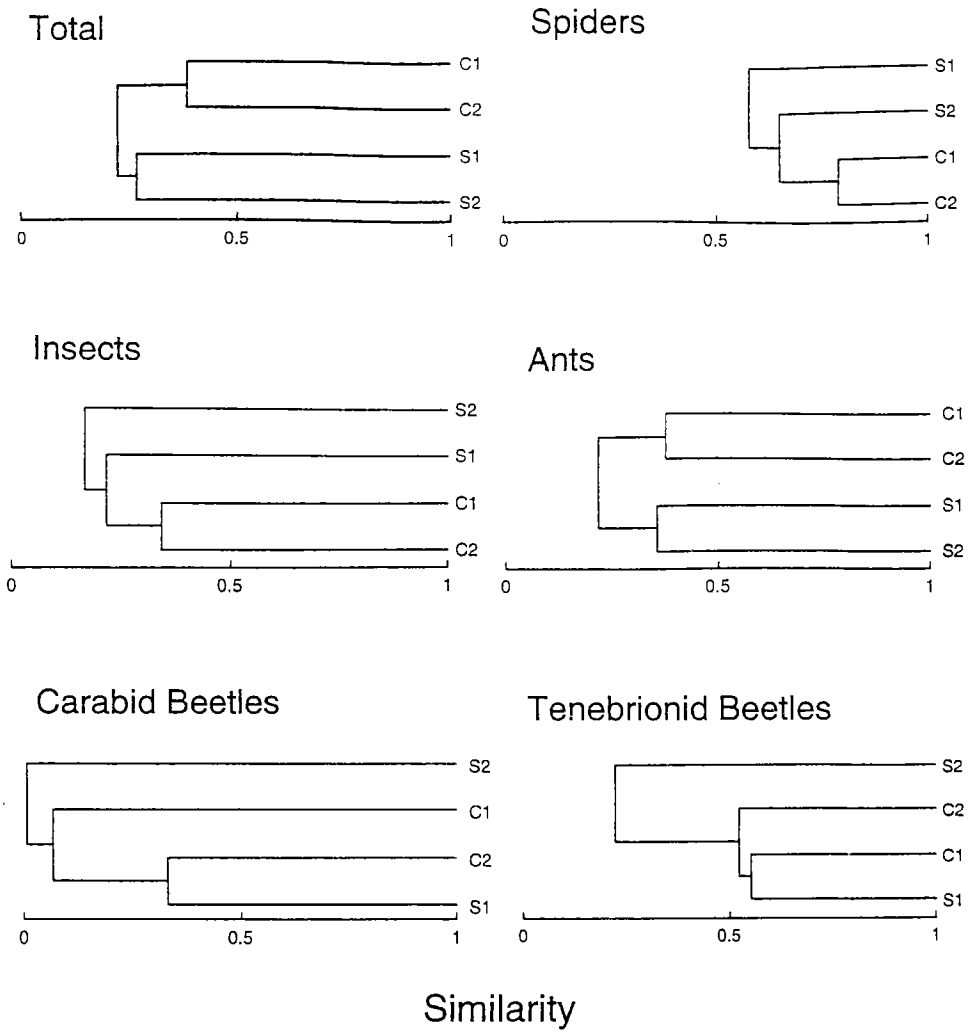

FIG. 5—Similarity in arthropod community composition among study sites, for different arthropod groups at Cottonwood-1 (C1), Cottonwood-2 (C2), Saltcedar-1 (S1), and Saltcedar-2 (S2) between July 1991 and May 1993, inclusive. Clustering along the x-axis indicates degree of similarity.

et al. (1992) note that litter spiders, as primary predators of other litter arthropods, represent strong indicators of forest habitat quality. Canopy closure, litter development, and the availability and species composition of prey directly affect variation in spider species composition (McIver et al., 1992), whereas litter depth and structure affect spider abundance (Bultman and Uetz, 1984). Forest floor litter at saltcedar sites tended to be more uniform, whereas litter at cottonwood sites was more patchily distributed, with the surface ranging from bare ground to deep accumulations of leaves and woody debris (Ellis et al., 1998). Both the greater richness and abundance of spiders at saltcedar sites may reflect litter development there, or simply the patchy nature of litter at cottonwood sites. Pursuit spiders of families Gnaphosidae and Lycosidae were common among captures at all sites throughout the study period. Their presence, particularly at saltcedar sites, indicates that substantial prey species must also have been present to support the population of predators.

Beetles are commonly used as indicator species (Refseth, 1980; di Castri et al., 1991; Kremen et al., 1993; Lövei and Sunderland, 1996; Oliver and Beattie, 1996). Carabid beetles are particularly well suited as ecological indicators because they are distributed in terrestrial habitats, they are taxonomically well known, and because most species are both restricted to particular types of habitats but also are able to move in response to environmental changes (Refseth, 1980). The family is known to be well adapted to floodplain conditions (Siepe, 1994), so we expected to see carabid beetles well-represented at our sites. However, carabids

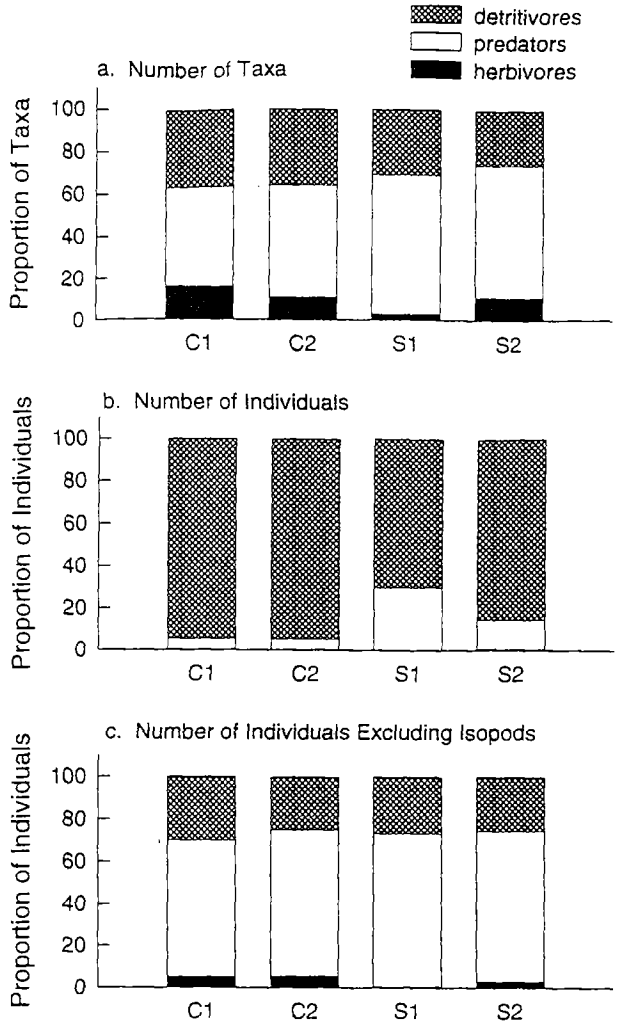

FIG. 6—Distribution of the number of taxa among three trophic levels (a), and the abundance of individuals within each trophic level both including (b) and excluding (c) isopods.

were not particularly numerous at any of our sites during the period reported here, with saltcedar sites supporting as many or more species and individuals than cottonwood sites. Both the number of carabid species present and the number of individuals increased at Cottonwood-2 beginning in June 1993, after experimental flooding designed to simulate the historic flood-pulse (Ellis, 1999). It may be that carabids have declined in the floodplain as the riparian forests have become drier following river regulation.

Staphylinid beetles (Coleoptera: Staphylinidae), another group of primarily predaceous beetles, were slightly more abundant than carabids at all sites. Staphylinids occur in almost every type of habitat, and are often abundant along shores and streams, as well as in soil litter and decaying vegetable matter (Arnett, 1975). Tenebrionid beetles, which are major detritivores in the arid Southwest (references in Crawford, 1991) were also fairly numerous. They were particularly abundant at Saltcedar-2, which may reflect the more uniform distribution of food resources (leaf litter), or the high sand content of the soil, which is preferred among at least some tenebrionids for oviposition (Allsopp, 1980; Stapp, 1997). The greater abundance of these arid-adapted beetles at Saltcedar-2 may also reflect the proximity to upland vegetation, as was suggested for the rodent community at that site (Ellis et al., 1997).

Ants have been identified as good bioindicators because of their abundance, relatively high species richness, responsiveness to environmental changes, and the presence of a variety of specialist species (Majer, 1983; Andersen, 1990). The most numerous species of ants in this study were *Monomorium minimum,* which was common at all sites, *C. cerasi,* which was most abundant at Cottonwood-1, fairly common at Cottonwood-2 and Saltcedar-1, and absent from Saltcedar-2, and *Tapinoma sessile,* which was common at both saltcedar sites but absent from cottonwood. *Monomorium minimum,* a ground-nesting species adapted to forest clearings (Wheeler, 1926), was absent from riparian sites located inside the riverside levees at Bosque del Apache, which are more directly affected by inundation from high river flow (Ellis, 1999), and were relatively uncommon at riverside sites located north of the refuge (Milford, 1996). Its abundance at these sites may reflect their isolation from flooding at the time of the study. In contrast, *C. cerasi,* is a largely arboreal species that was common in sites that were regularly flooded (Ellis, 1999) and thus may have been a dominant species in forests before river regulation. Its absence from Saltcedar-2 is not easily explained, because it is reported from upland sites dominated by juniper and sagebrush as well as from riparian sites (MacKay et al., 1988) *Tapinoma sessile* is found in a variety of habitats, typically nesting in open soil, under rocks or logs, or in dead wood (MacKay et al., 1988).

Popular belief has been that extensive saltcedar stands represent a biological desert that supports less wildlife than native riparian vegetation (Griffen, 1990; Glausiusz, 1996). Some

studies have shown abundant vertebrate species living in saltcedar (e.g., Hunter et al., 1988; Brown and Trosset, 1989; Ellis, 1995; Ellis et al., 1997), and recent comparisons of arboreal arthropods in native and exotic riparian trees at Bosque del Apache found a diverse and abundant arthropod community in saltcedar (Mund-Meyerson, 1998). This study indicates that there is an abundant surface-active arthropod community present under saltcedar, which may help to support vertebrate species using this exotic vegetation. We could not clearly identify arthropod taxa that were restricted to cottonwood-dominated sites, so the overall effect of saltcedar on surface-active arthropod communities remains uncertain. More widespread sampling of arthropod communities in southwestern riparian vegetation, in both altered and unaltered forests, is needed to understand the regional impact of saltcedar on this important ecosystem component.

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