



Reduction of riparian arthropod abundance and diversity as a consequence of giant reed (*Arundo donax*) invasion

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Abstract

The non-indigenous perennial grass, *Arundo donax*, is an aggressive invader of riparian areas throughout California and many sub-tropical regions of the world, and is hypothesized to provide poorer quality habitat for native wildlife in riparian systems. We sampled aerial and ground-dwelling insects and other terrestrial arthropods associated with *Arundo*, native willow vegetation (*Salix* spp.), and mixtures of the two vegetation types during two seasons to determine how *Arundo* influences invertebrate composition in a low gradient stream in central California. The total number of organisms, total biomass and taxonomic richness of aerial invertebrates associated with native vegetation was approximately twice that associated with *Arundo* vegetation, while mixed vegetation supported intermediate arthropod levels. Shannon-Weaver (Weiner) diversity associated with native vegetation stands was also higher than that of *Arundo* vegetation. Ground-dwelling assemblages did not show differences as great as aerial assemblages which are more critical to foraging avian species. These results indicate that vegetation type is a significant factor reducing the abundance and diversity of invertebrates in this, and presumably in many other riparian ecosystems where this invasive species has become a dominant component. *Arundo* invasion changes the vegetation structure of riparian zones and in turn, may increasingly jeopardize its habitat value for birds and other wildlife whose diets are largely composed of insects found in native riparian vegetation.

Introduction

Terrestrial arthropods are commonly associated with characteristic vegetation types, and the loss of appropriate plant habitat can lead to declines in insect populations (Thomas 1995; Strong et al. 1984). This may be particularly the case in riparian areas, which in arid and semi-arid regions are among the most productive of ecosystems, the vegetation supporting an abundance of invertebrates far greater than that found in adjacent uplands (Gregory et al. 1991). Both aquatic and terrestrial insects use riparian vegetation for feeding, resting, refuge and reproduction, and these organisms, in turn, provide a critical resource

base for many wildlife species, including birds, fish and other vertebrates (Motroni 1984; Gray 1993; Doyle 1990).

Riparian ecosystems are among the most endangered habitats in California, with an estimated 5% of their historic extent retaining relatively natural physical and biotic structure (RHJV 2000). Many sensitive bird species depend upon these remnant habitats for foraging and nesting, including threatened species such as southwestern willow flycatcher (*Empidonax traillii extimus*), least Bell's vireo (*Vireo bellii pusillus*), and other declining migrant and resident songbirds (Gaines 1977; Humple and Geupel 2002; Yong and Finch 1997). Invertebrates are particularly

important in their diets during the spring when energetic costs of migration and reproduction are high (Skagen et al. 1998; Thomas 1995).

In these ecosystems, invasion by non-indigenous plants has the potential to alter a range of community and ecosystem properties, including the associated invertebrate assemblage and the value of this resource for other trophic levels. In other communities it has been observed that when an aggressive invader displaces native plants, one impact is to diminish arthropod assemblages. Beerling and Dawah (1993) found insect abundance and diversity to be lower on non-indigenous *Fallopia japonica* and *Impatiens glandulifera* than on adjacent native plants near riparian zones, and Slobodchikoff and Doven (1977) showed that arthropod abundance and diversity declined as the density of a non-native grass, *Ammophila arenaria*, increased. Bock et al. (1986) indicated that native vegetation supported a greater variety of grasshoppers, and in turn birds, when compared to non-native grassland vegetation.

The presence of non-indigenous plants in California's riparian ecosystems has become a major conservation concern, particularly because fully one-half of legally protected species are associated with riparian and wetland habitats (Dudley and Collins 1995). One such invader is *Arundo donax*, which the California Exotic Pest Plant Council has designated as a top priority invasive species in California (CalEPPC 1999). The increasing presence of *Arundo* in riparian areas has resulted in numerous management and ecological problems. *Arundo* transpires more water per unit land area than native species (Zimmerman 1999; Iverson 1994) and presents a fire hazard by increasing available fuel for wildfires (Scott 1994). In addition, it is believed that *Arundo* modifies the micro-climate of riparian systems by providing little shade to streams, therefore increasing water temperature and chemistry, decreases litter quality and provides poor quality habitat for native wildlife (Jackson et al. 1993; Bell 1998; Dudley 2000).

Stands of *Arundo* are present in most low elevation regions of California within riparian areas originally dominated by cottonwood/willow gallery forest (Dudley and Collins 1995), and are expanding despite local control efforts (Team *Arundo del Norte* 1999). The goals of this study were to (1) document the types of insects and other terrestrial arthropods associated with *Arundo*-infested vegetation, and (2) determine whether invertebrate abundance and taxon diversity supported by *Arundo* differed from that found within native riparian vegetation.

Study organisms and sites

Commonly known as giant reed, *A. donax* is a cane-like perennial grass which forms massive clumps that expand through rhizomatous growth into dense thickets. It has a fast growth rate and can grow to as much as 8 meters in height within the growing season (Perdue 1958; Bell 1998). It is native to the Indian sub-continent and has been intentionally distributed by human transport to subtropical, tropical, and warm-temperate areas of the world (Bell 1998; Hoshovsky 1986; Dudley 2000). Giant reed was brought into California by Spanish colonists over 150 years ago for a variety of purposes, and has been planted horticulturally and used along ditches for (ill-conceived) erosion control (Hoshovsky 1986; Dudley 2000). *Arundo* apparently does not produce viable seed in North America, and reproduction occurs almost entirely from rhizomes carried by flood waters into new habitats where they readily sprout new culms in moist soils (Else 1996; Dudley 2000). Due to its fast growth rate and ability to thrive under well-developed canopy, *Arundo* may have a competitive advantage over native plant species once it is established, and can alter riparian ecosystems by inhibiting native vegetation growth and ultimately forming monocultural stands (Rieger and Kreager 1989).

This study was conducted at Sonoma Creek, a third order stream 40 km northeast of San Francisco, California. Three study sites were chosen near the town of Sonoma (Sonoma County, 38°17' N, 122°27' W), at elevations of approximately 10 to 20 m AMSL. The sites were separated by approximately 2 km. The channel gradient is ca. 1–2% slope, the channel width ranging from 8 to 30 m, with moderately incised banks 3 to 5 m high. Surrounding land use is agricultural and moderate density urban/suburban residential development, while most riparian vegetation has been retained within the high flow channel and is generally continuous through this 4 km reach.

In this Mediterranean-type climate zone, discharge varies seasonally with high flows following winter and spring rains, despite partial stream regulation above the study sites. During summer drought the stream is reduced to slow-flowing pools with numerous shallow riffles ca. 1 to 3 m. wide flowing over cobble substrates. The perennial nature of Sonoma Creek keeps soil moisture and humidity relatively high, and air temperatures within the riparian zone ranged from ca. 5–22 °C during spring sampling to summer temperatures about 12–36 °C.

The riparian zones of the three sites vary from 10 to

Table 1. Vegetation composition in riparian areas of the three study sites at Sonoma Cr., California, and relative abundance of taxa.

Site	1	2	3
Plant taxon			
<i>Aesculus californica</i> (N)	++		
<i>Acacia decurrens</i> (E)		+	
<i>Alnus rhombifolia</i> (N)	+	+	++
<i>Arctium lappa</i> (N)	+		
<i>Artemisia douglasiana</i> (N)	+	+	
<i>Arundo donax</i> (E)	+	++	++
<i>Conium maculatum</i> (E)		+	
<i>Foeniculum vulgare</i> (E)	+	++	
<i>Lunaria annua</i> (E)		+	
<i>Populus fremontii</i> (N)	+		++
<i>Rubus discolor</i> (E)		++	++
<i>Salix</i> spp. (N)	++	++	++
<i>Umbellularia californica</i> (N)	+	++	
<i>Vinca major</i> (E)	++	++	
<i>Vitis californica</i> (N)	++	++	++
<i>Rumex</i> sp. (E)		+	
<i>Stachys</i> sp. (N)		++	+
Poaceae		++	

+ indicates uncommon presence of plant species (< 5% cover); ++ indicates common presence of plant species (> 5% cover). (N) indicates species is native to the region and (E) indicates exotic plants. Included in *Salix* spp. are *S. lasiandra*, *S. hindsiana*, and *S. lasiolepis*.

30 meters wide. Soils are dominated by sandy depositional substrate. Willows (mostly *Salix lasiandra*, *S. hindsiana*, and *S. lasiolepis*) and cottonwood (*Populus fremontii*) are the dominant native species at the study areas, with substantial contribution by California bay (*Umbellularia californica*), white alder (*Alnus rhombifolia*) and other taxa (Table 1). Invasion by *Arundo* has only progressed to a moderate level at Sonoma Creek, with most patches approximately 2–8 m in diameter, surrounded by more or less continuous stands of willow and other woody species. Understory plants include species such as wild grape (*Vitis californica*), Himalayan blackberry (*Rubus discolor*) and a variety of other native and non-native herbaceous taxa.

Methods

Invertebrate populations were sampled using two types of traps in order to assess two different assemblages: pitfall traps to capture crawling insects on the forest floor, and sticky traps to sample airborne insects within the vegetative cover. Pitfall traps consisted of a plastic cup (9 cm diam mouth, 12 cm deep) containing ethylene glycol, covered with an inverted plastic funnel to inhibit escape and to restrict access

by larger animals such as reptiles. The traps were buried in the ground so that the mouth was level with the ground surface. The sticky traps were constructed with a 20 × 29 cm acetate sheet, coated with Tanglefoot™, and wrapped around a two liter soda bottle. The sticky trap was set over a 1 m stake and placed next to the pitfall trap. Three replicate traps (pitfall and sticky) were placed within each vegetation type at a site, each trap in a patch of that vegetation type separated by at least 20 m.

Samples were collected during two periods to represent different seasons during the study. In spring, when greater insect and bird utilization of the riparian habitat is expected (Gray 1993), traps were in place for one week and collected on 26 March 1997. During the summer insect activity was lower so traps were left in the sampling sites for two weeks, and were collected on 9 July 1997. While set up, all traps were monitored and cleaned of debris every two days.

At each site, traps were placed into three common vegetation types which commonly occur in Sonoma Creek: pure *Arundo* stands, native-dominated vegetation with no *Arundo* present, and mixed *Arundo*-native vegetation stands. An *Arundo* stand is defined as a setting in which the *Arundo* forms a 'clump' at least two meters in diameter, and no native vegetation is found within two meters of the sampling apparatus. Mixed *Arundo*-native consisted of *Arundo* clumps with native vegetation less than one meter away, allowing easy movement by insects between native and non-native plants. Native stands contain primarily willows, along with other native trees and shrubs and no *Arundo* within 30 meters, although non-native understory species were generally present.

Invertebrates were collected at the end of each sampling period and preserved in 95% ethanol. For insects collected in sticky traps, only those greater than one mm were retained as the smallest insects were assumed not to be major contributors to avian diets. Insects and spiders were then identified to family level in most cases, although some families included more than one operational taxon, and body length measured under a dissecting scope to the nearest mm. Myriapods, and ground dwelling invertebrates smaller than 2 mm, were identified to order.

The biomass of invertebrates in each vegetation type was calculated from abundance of each size class, with a curvilinear length-weight regression fitted using the formula: $\text{weight} = e^{b(x)^a}$, where x = length and constants a and b have a published numerical value depending on the insect order (Sample et al. 1993). Taxon diversity was also estimated from the

number of taxa found in each sample. All data were log-transformed before statistical analysis, and analyzed by ANOVA using vegetation type and site as independent variables to test for differences in invertebrate abundance, biomass, and taxon diversity; 'site' did not yield a significant interaction so is not included in the results. The spring and summer sample dates were analyzed separately, as several trap locations were changed between sampling periods making repeated measures testing inappropriate. The diversity index (H') was calculated using the Shannon-Weaver (Weiner) index (Zar 1984), and these indices were compared qualitatively, rather than statistically.

A census of the vegetation composition during spring, using a point-intercept method with a vertical line from substrate to canopy to estimate percent cover at each trap location, indicated that *Salix* spp. comprised the dominant native vegetation but other important trees were present (Table 2). Overstory or canopy height was generally 4 to 10 meters above the traps, and mid-level measurements encompassed the zone from about 1 to 2 meters above the ground, which was the height where sticky traps were placed. Understory cover consisted of vegetation found at a height from 0 to 20 cm above the substrate (Table 2). Native stands contained greater understory vegetation than *Arundo* stands, albeit comprised largely of non-native herbaceous taxa such as blackberry (*Rubus discolor*), dock (*Rumex* sp.) and periwinkle (*Vinca major*).

Results

Spring

Aerial traps

Mostly insects were collected from the sticky traps, and about 89% of the individuals were aphids, various Diptera, and small Coleoptera (Table 4). The mean total number of flying insects collected in Native stands was about double that in *Arundo* patches, with mixed vegetation containing an intermediate insect abundance (Figure 1a, Table 3). Native vegetation appeared to support two times as much biomass of flying insects than did *Arundo* and mixed vegetation supported an intermediate biomass, but large variance in the data obviated statistical significance of this difference (Figure 1b, Table 3). Mean taxon richness per sample was significantly higher in native vegetation than in *Arundo*, again by a factor of two (Figure 1c, Table 3). A total of 14 taxa were found in *Arundo*, 19 in willows, and 18 taxa collected in mixed vegetation (Table 4). Native vegetation also contained the highest H' diversity index (Figure 1d).

Ground traps

Collections of ground dwelling arthropods from pit-fall traps showed a pattern similar to that found with aerial insects. A mean number of 40 individuals was in *Arundo* traps as compared to almost 80 within native vegetation, the mixed vegetation traps producing intermediate abundances (Figure 2a, Table 3).

Table 2. Mean percent cover (\pm 1 S.E. unless recorded only once) of riparian vegetation adjacent to trap locations in three vegetation types at Sonoma Creek, California.

Height	Understory			1.5 m			Canopy		
	A	AN	N	A	AN	N	A	AN	N
Plant species									
<i>Acacia decurrens</i> (E)								20	
<i>Aesculus californica</i> (N)								40	5
<i>Alnus rhombifolia</i> (N)			30			20		15	40
<i>Arundo donax</i> (E)	35 (2)	15 (2)		40 (7)	24 (2)		34 (5)	8 (2)	
<i>Salix</i> spp. (N)			9 (1)		5	15		12 (2)	37 (7)
<i>Populus fremontii</i> (N)								14 (6)	
<i>Umbellularia californica</i> (N)						10			80 (10)
<i>Vinca major</i> (E)		9	20 (7)						
<i>Rubus discolor</i> (E)		5 (3)	8 (4)						
<i>Rumex</i> sp. (E)	8								
Poaceae		8							

A = *Arundo*, AN = *Arundo*-Native mix, and N = Native. The three height levels are: Understory = primary cover species below ca. 0.2 m; 1.5 m = plants present at intercept between 1–2 m high; and Canopy = any overstory species above 4 m. (N) indicates species native in this region and (E) indicates exotic species. Bare area was not tabulated but is approximately the total from each column in the Understory component subtracted from 100.

Table 3. ANOVA results for invertebrate abundance, biomass, and taxon diversity in three vegetation types; see Figures 1 and 2.

Date	Spring			Summer		
	<i>P</i>	<i>F</i>	<i>R</i> ²	<i>P</i>	<i>F</i>	<i>R</i> ²
Aerial						
Abundance	0.007	6.66	0.59	0.002	9.13	0.67
Biomass	0.15	2.12	0.50	0.20	1.77	0.44
Taxon Richness	0.036	6.05	0.67	0.004	16.50	0.85
Ground						
Abundance	0.02	4.89	0.64	0.64	0.46	0.54
Biomass	0.10	2.58	0.55	0.95	0.05	0.36
Taxon Richness	0.16	2.59	0.46	0.68	0.41	0.12

Table 4. Families of invertebrates collected from pitfall and sticky traps during the study.

Taxon	Ground-dwelling			Aerial		
COLEOPTERA						
Carabidae*	N	M	a	N		
Chrysomelidae	N	m		N		
Cleridae	–			N	m	
Curculionidae	N	m	A	–		
Dermestidae	N		a	–		
Elateridae*	N	m		N	M	a
Nitidulidae	N	m	a	–		
Scarabaeidae*	N	m	A	N	M	
Scolytidae*	N	m		N	M	a
Staphylinidae*	N	m	a	N	M	a
Tenebrionidae	N	m	a	–		
DIPTERA						
Mycetophilidae/Sciaridae	–			N	m	a
Chironomidae	–			N	m	a
Muscidae	n	m	A	N	m	a
Phoridae	n	M		N	m	a
HEMIPTERA						
Miridae	N	m	a	N	m	
Reduviidae	N	m		–		
HOMOPTERA						
Aphididae*	N	m		N	m	a
Cicadellidae*	n	m	A	N	m	A
HYMENOPTERA						
Formicidae	N	m	a		M	
Braconidae	–			N	m	A
Ichneumonidae	–			N	m	a
ARANEAE						
Clubionidae*	N	m	a	N	m	a
Lycosidae*	N	m	a	N	m	a
ISOPODA						
Armadillidae*	n	M	A	–		
Porcellionidae*	n	M	A	–		
Trichoniscidae	N	M	A	–		
DIPLOPODA						
Spirobolida*?	N	M	a	–		
ACARI						
Oribatidae	–			n	M	a
Trombididae	N	M		–		

Asterisks denote common organisms comprising > 5% of individuals found within any vegetation type or sampling type. Letters indicate that the family was collected from a given vegetation type, a capital letter indicating the type or pair of vegetation types in which it was most abundant (N, n = Native; M, m = Mixed; A, a = Arundo treatments).

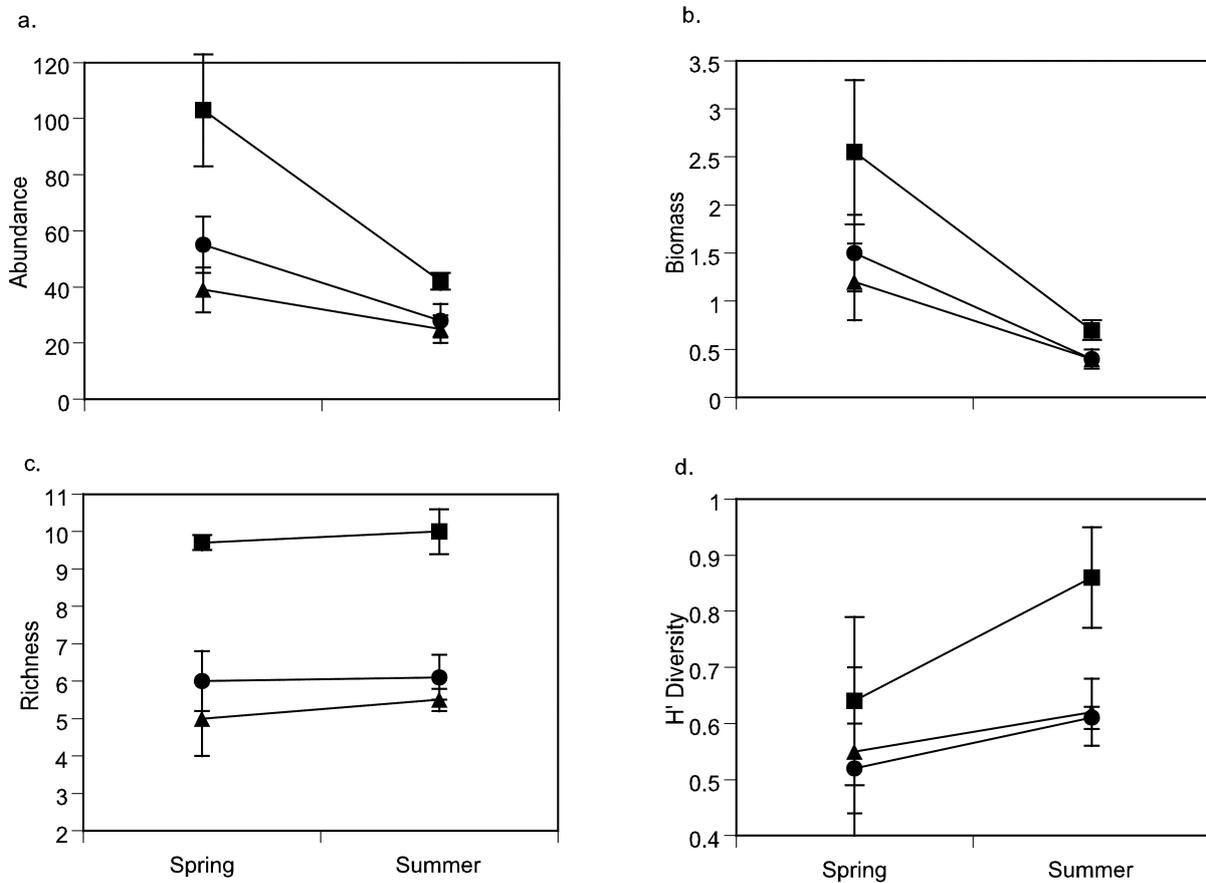


Figure 1. Aerial arthropod assemblage collected from sticky traps during spring and summer sampling periods. 1a is the mean total abundance of all individuals > 2 mm for each vegetation type across sampling sites; 1b is the estimated biomass of those organisms; 1c is the mean number of taxa collected; 1d represents the average Shannon-Weaver (Weiner) diversity index calculated for each site; error bars indicate 1 S.E. Symbols are as follows: ■ = Native vegetation sites, ▲ = *Arundo* and ● = Mixed vegetation sites.

Coleoptera species comprised the majority of individuals and biomass in these samples (Table 4). Scarab (Scarabeidae) and rove beetles (Staphylinidae) were evenly distributed among the three vegetation types, while ground and click beetles (Carabidae and Elateridae, respectively), wolf spiders (Lycosidae) and millipedes were disproportionately found in vegetation which included native plants; isopods were most common in mixed vegetation (Table 4). There were no significant differences among the three vegetation treatments in the biomass of invertebrates in traps (Figure 2b, Table 3). Diversity of ground associated arthropods appeared greater within native vegetation, both as taxon richness (Figure 2c) and H' dominance-diversity (Figure 2d), although differences were not possible to distinguish statistically (Table 3).

Summer

Sticky traps

By summer, arthropod assemblages were largely dominated by the same flying insects as in spring but had declined substantially in numbers and biomass; nonetheless, abundance was still significantly greater in the native vegetation, while *Arundo* and mixed stands supported approximately equal abundances (Figure 1a, Table 3). Biomass of aerial insects had declined to roughly a third of that collected in spring, and did not differ among stands (Figure 1b, Table 3). On the other hand, diversity seemed to increase slightly over spring, reflecting greater evenness than spring samples which were dominated by Diptera and aphids. There were twice as many taxa present in native vegetation samples as compared to *Arundo* and

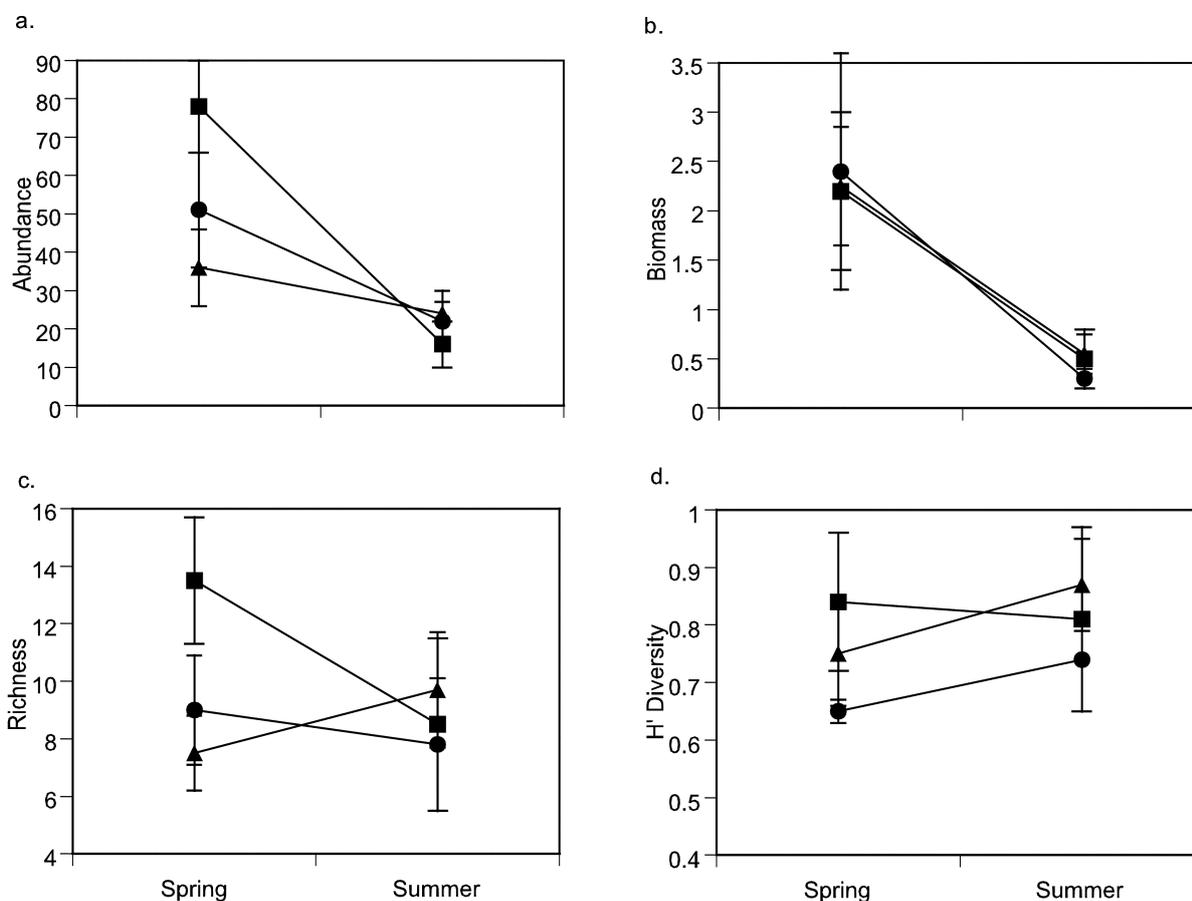


Figure 2. Ground-dwelling arthropods collected from pitfall traps during spring and summer sampling. 2a is the mean total abundance of all individuals > 2 mm for each vegetation type across sampling sites; 2b is the estimated biomass of those organisms; 2c is the mean number of taxa collected; 2d represents the average Shannon-Weaver (Weiner) diversity index calculated for each site; error bars indicate 1 S.E. Symbols are as in Figure 1: ■ = Native vegetation sites, ▲ = *Arundo* and ● = Mixed vegetation sites.

mixed collections, and H' diversity was clearly greater than in either vegetation type containing *Arundo* (Figure 1c and d, Table 3).

Ground traps

Overall arthropod abundance in summer pitfall traps also declined to about one-third the numbers collected in the spring (Figure 2a). The ANOVA results revealed that ground-dwelling invertebrate abundance (Figure 2a), biomass (Figure 2b), and taxon richness (Figure 2c) did not differ significantly in the summer among the three vegetation types (Table 3). H' diversity of arthropods, however, appeared to increase slightly over this time period (Figure 2d), again as a consequence of reduced dominance by any particular taxon. The pitfall traps at this time of year contained

mostly spiders, and carabid beetles were the only insects commonly found in all three vegetation types.

Discussion

The results of arthropod collections among the 3 vegetation types demonstrated that during the spring, where native woody plants dominate the riparian vegetation, associated invertebrate assemblages were both more diverse and approximately double the abundance of those found in patches dominated by the invasive grass, *Arundo donax*. Biomass of aerial insects may have been similarly greater in native willow stands, but variation masked the effect, while ground-dwelling insects showed no differences in biomass. In the summertime, there was a marked

decline in arthropod abundance and no relationship with vegetation, with the exception that flying insect assemblages remained substantially more diverse. In stands where willows were in close contact with *Arundo*, there was a tendency toward intermediate abundance, but generally the nearby presence of willows provided only moderate augmentation to *Arundo*-associated insects.

Invertebrate associations with exotic plants

Invertebrates may show positive associations with vegetation for a variety of reasons, including direct herbivory, use of plant surfaces for resting, refuge, or reproduction, and acquisition of other resources (e.g., prey) from this substrate (Strong et al. 1984). We observed little feeding on *Arundo* during the course of this study, except by small numbers of aphids, while substantial feeding by various Homoptera, Coleoptera (and other insects, particularly larval stages, not collected by our sticky traps) on willows was readily observed, so it is likely that most of the invertebrates sampled were using giant reed for physical structure and indirect resources. The architectural structure of *Arundo* patches is much simpler than that in willow stands, both because of the lack of layering of the canopy plants as well as the simpler composition and lower density of the understory assemblage. The reed culms are unbranched in their first year, and second year culms only produce sparse and simple secondary branching from nodes. Furthermore, culm density is very high, resulting in significantly lower light penetration (P. Zimmerman, San Francisco State University, personal communication), restricting light resources necessary to support a diverse understory plant assemblage and associated fauna. In a nearby riparian zone, similar reduction in vegetative structure and diversity (and increased abundance of other non-indigenous plants) was also associated with *Arundo* presence (Gaffney and Gledhill 2003).

This diminution of habitat heterogeneity is likely a major cause of the reduction in arthropod presence in *Arundo* patches. Slobodchikoff and Doven (1977) also found that insect abundance and diversity declined as the density of another non-native rhizomatous grass, *Ammophila arenaria*, increased. *A. arenaria* also forms near monocultures with low representation of other plants and simplification of physical structure. The moderate tendency towards insect enhancement if willows are nearby suggests a graded relationship with plant diversity and structural complexity, and further indicating that as spatial

dominance by non-native plants increases invertebrates will become even more reduced in abundance and diversity. Other riparian areas have become dominated to a much greater extent than has Sonoma Creek (Bell 1998; Dudley 2000), and comparative studies in more degraded communities would be useful to show what the eventual implications of vegetative change would be for associated animal species.

It has long been indicated that non-indigenous plants lack the associated diversity of herbivores that are present in their ecosystems of origin (Strong et al. 1984). Presumably this is a factor in the reduction of invertebrate abundance and diversity in relatively intact European riparian areas invaded by *Fallopia japonica* and *Impatiens glandulifera* (Beerling and Dawah 1993). Likewise, in the southwest US relatively few insects feed on invasive saltcedar (*Tamarix* spp., which often co-occurs with *Arundo*), while numerous herbivores are present in its natural Eurasian habitats (DeLoach et al. 1996). The assemblage associated with *Arundo* in its native habitat on the Indian sub-continent is poorly known, but records suggest that it is substantially greater than that found in California (Tracy and DeLoach 1999). In the Mediterranean region, where it has been present for over 2000 years, insect usage is relatively low but several taxa are known to feed on giant reed (Tracy and DeLoach 1999). Attack by cosmopolitan aphid species can reduce plant vigor under greenhouse conditions, but rarely have we seen such herbivory under field conditions (Dudley, unpublished data). There is interest in the foreign fauna of *Arundo* because of the potential for introduction of natural enemies to control weed abundance, and preliminary exploration indicates numerous apparently selective insects do feed on this plant (Stelljes 2001). Given that native grasses can have their own associated herbivorous fauna (Tscharntke and Greiler 1995), it is likely that suitable, monophagous biological control agents may be present among the worldwide distribution of this globally invasive plant (Tracy and DeLoach 1999).

A tangential, but economically important issue is the prevalence in California vineyards of Pierce's disease, a pathogen carried by 'sharpshooters' and other Homopterans, and sustained by suitable overwintering host plants in riparian areas (Purcell and Saunders 1999). While *Arundo* does not support large insect populations, it remains photosynthetically active in winter and is a suitable host for both sharpshooters and the *Xylella fastidiosa* bacterium (A. Mogi, University of California, Berkeley, unpub-

lished data). The blue-green sharpshooter, *Graphocephala atropunctata* (Cicadellidae), is an important vector of *Xylella*, and was regularly present in our samples (Table 4). With increasing dominance by *Arundo*, its use by sharpshooters and other disease vectors may also increase as other hosts decline, resulting in continued risks to vineyards.

Ground-dwelling arthropods did not exhibit the strong vegetation preference of aerial insects, but native vegetation still provided the more frequent habitat for a majority. Most were either detritivorous taxa (e.g., isopods, mites and several of the Coleoptera) or predators (Carabidae, spiders), and were not using live *Arundo* directly as a substrate. As with the aerial component of the arthropod assemblage, this preference was probably due to greater habitat structure, as well as a more complex and massive litter layer amongst native vegetation. Bare soil comprised a larger portion of primary substrate underneath *Arundo* secondary canopy, resulting in both reduced resource availability for soil fauna and greater likelihood of desiccation. In addition, we have observed elsewhere that *Arundo* litter decomposes in riparian environments at rates roughly similar to native litter, but forms a more 2-dimensional layer without interstitial spaces suitable for invertebrate colonization (B. Lichtman, unpublished data). These are not conditions favorable to ground-dwelling organisms.

Still, physical conditions are expected to be more similar on the ground surrounding riparian plants than within the live canopy. This appeared to be the case, and ground-dwelling arthropods also tended to be larger and more generalized in their resource use, leading to finer-grained associations with vegetation. Lovich et al. (2001) also found that the invertebrates associated with *Arundo* rootwads in southern California were opportunistic forms, very few of which utilize the plant tissue directly; the majority were also exotic. In our site the detritivorous isopods *Armadillidium vulgare* and *Porcellio* sp. were also most abundant in association with giant reed, illustrating a common relationship whereby opportunistic, non-indigenous taxa that tolerate modified conditions are often found together (e.g., King et al. 1985; Aplet 1990) in a loose association or 'invasion complex' including exotic plants and animals (D'Antonio et al. 1999; see Ellis et al. 2001 for contrary results).

Implications of exotic plants for riparian wildlife and ecosystems

The seasonal decline of invertebrate abundance from

spring to summer is an expected pattern, related to natural phenology of plants and insects in Mediterranean ecosystems (reflecting precipitation primarily in winter and early spring), and greater resource availability or suitability when environmental conditions are mesic and mild (Bosh et al. 1997; Braman and Beshear 1994). The spring maximum in insect diversity coincides with use of woody riparian plants by many migrating and/or nesting songbirds, and the time of high caloric needs for reproduction (Laymon 1984; Morrison et al. 1994). While some food resources for birds come from emerging aquatic insects, the bulk of their needs is generally met by terrestrial insects associated with riparian vegetation (Gray 1993). The displacement of native vegetation by *Arundo* potentially alters the use of critical riparian ecosystems by wildlife through reduction of this intermediate trophic level. Bock et al. (1986) found that native vegetation supported a greater variety of grasshoppers, and in turn birds, when compared to non-native grassland vegetation. Wilson and Belcher (1989) also showed that the presence of non-native plants produced a shift in the species composition of native birds and in some cases species declined significantly, in part attributable to the decline in food supply (insects). Birds appear to favor use of mature cottonwoods (*Populus* spp.), willows (*Salix* spp.) and other native plants over non-native riparian plants such as *Arundo*, *Tamarix* and other riparian weeds (Hunter et al. 1988; Morrison et al. 1994; Ellis 1995; Lynn 1998); while architectural suitability for nesting is involved in this preference, food resource quality and availability are certainly critical elements that have not received sufficient attention.

Summer arthropod densities were certainly much lower than during spring, yet such resources may still be critical for a variety of wildlife species. After fledging, some birds remain as summer residents, and require access to abundant insect resources to maintain populations through the stressful summer drought period. Other trophic guilds, particularly reptiles such as *Sceloporus* lizards, are also sensitive to reduction in invertebrate resources (Tinkle 1993; Abell 1999). Despite the lack of clear differences in ground-dwelling arthropods and only moderate reductions in flying insect abundances in summer, overall low abundances mean that even minor reductions resulting from invasion of poor quality vegetation may be important when wildlife are closer to marginal food levels for survival (Yong and Finch 1997; Skagen et al. 1998). Some of the taxa which maintained similar levels between seasons, e.g., millipedes and isopods, are not

considered to be typical food sources for birds anyway, while declines in Coleoptera, for which birds are known to forage (Gray 1993), may be more critical.

Densities of *Arundo* in Sonoma Creek are still far lower than in other riparian areas, especially in southern California where *Arundo* has become a dominant plant in many floodplain ecosystems (Bell 1998; Jackson et al. 1993). It is increasingly common in northern California systems, including the Russian River (also in Sonoma County) and many low gradient tributaries of the Sacramento River (Gaffney and Gledhill 2003; Dudley 2000). Several other invasive species of woody riparian plants are also increasing in the region, including saltcedar (*Tamarix ramosissima* and *T. parviflora*), tree-of-heaven (*Ailanthus altissima*), castor bean (*Ricinus communis*) and *Eucalyptus*, all of which are also considered detrimental to riparian ecosystems (Dudley and Collins 1995). With the increasing dominance of riparian vegetation by non-indigenous species, the potential for cumulative effects to regional biodiversity is ratcheted upwards and the capacity to recover the integrity of these critical ecosystems is diminished. Such concerns justify the acknowledged need to control invasive taxa and promote restoration of key elements of native riparian assemblages (CALFED 2001).

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