



Effects of Invasive Plants on Arthropods

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Abstract: *Non-native plants have invaded nearly all ecosystems and represent a major component of global ecological change. Plant invasions frequently change the composition and structure of vegetation communities, which can alter animal communities and ecosystem processes. We reviewed 87 articles published in the peer-reviewed literature to evaluate responses of arthropod communities and functional groups to non-native invasive plants. Total abundance of arthropods decreased in 62% of studies and increased in 15%. Taxonomic richness decreased in 48% of studies and increased in 13%. Herbivorous arthropods decreased in response to plant invasions in 48% of studies and increased in 17%, likely due to direct effects of decreased plant diversity. Predaceous arthropods decreased in response to invasive plants in 44% of studies, which may reflect indirect effects due to reductions in prey. Twenty-two percent of studies documented increases in predators, which may reflect changes in vegetation structure that improved mobility, survival, or web-building for these species. Detritivores increased in 67% of studies, likely in response to increased litter and decaying vegetation; no studies documented decreased abundance in this functional group. Although many researchers have examined effects of plant invasions on arthropods, sizeable information gaps remain, specifically regarding how invasive plants influence habitat and dietary requirements. Beyond this, the ability to predict changes in arthropod populations and communities associated with plant invasions could be improved by adopting a more functional and mechanistic approach. Understanding responses of arthropods to invasive plants will critically inform conservation of virtually all biodiversity and ecological processes because so many organisms depend on arthropods as prey or for their functional roles, including pollination, seed dispersal, and decomposition. Given their short generation times and ability to respond rapidly to ecological change, arthropods may be ideal targets for restoration and conservation activities.*

Keywords: community composition, detritivores, functional groups, herbivores, insects, literature review, non-native species, phytophagous, predators

Efectos de las Plantas Invasoras sobre los Artrópodos

Resumen: *Las plantas no-nativas han invadido casi todos los ecosistemas y representan un gran componente del cambio ecológico global. Las invasiones de plantas cambian frecuentemente la composición y la estructura de las comunidades vegetales, lo que puede alterar a las comunidades animales y a los procesos ambientales. Revisamos 87 artículos publicados en la literatura revisada por colegas para evaluar las respuestas de las comunidades de artrópodos y de los grupos funcionales a las plantas no-nativas invasoras. La abundancia total de artrópodos disminuyó en 62% de los estudios e incrementó en 15%. La riqueza taxonómica disminuyó en 48% de los estudios e incrementó en 13%. Los artrópodos herbívoros disminuyeron en respuesta a las plantas invasoras en 48% de los estudios e incrementaron en 17%, probablemente debido a los efectos directos de la diversidad disminuida de plantas. Los artrópodos depredadores disminuyeron en respuesta a las plantas invasoras en 44% de los estudios, lo que puede reflejar efectos indirectos debido a reducciones en la cantidad de presas. El 22% de los estudios documentaron incrementos en los depredadores, lo que puede reflejar cambios en la estructura vegetal que mejoraron la movilidad, la supervivencia o la construcción de telarañas de estas especies. Los detritívoros incrementaron en 67% de los estudios, probablemente en respuesta al aumento de basura y vegetación en descomposición; ningún estudio documentó disminuciones en la abundancia de*

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este grupo funcional. Aunque muchos investigadores han examinado los efectos de las invasiones de plantas sobre los artrópodos, todavía existen vacíos considerables de información, específicamente con respecto a cómo las plantas invasoras influyen los requerimientos de dieta y hábitat. Además de esto, la habilidad de predecir los cambios en las poblaciones de artrópodos y en las comunidades asociadas con las invasiones de plantas podría mejorarse al adoptar una estrategia más funcional y mecánica. Entender las respuestas de los artrópodos a las plantas invasoras informará críticamente a la conservación de toda la biodiversidad y de los procesos ecológicos porque tantos organismos dependen de los artrópodos como presa o para sus papeles funcionales, como la polinización, la dispersión de semillas y la descomposición. Dados sus tiempos cortos de generación y su habilidad de responder rápidamente al cambio ecológico, los artrópodos pueden ser objetivos ideales para las actividades de conservación y restauración.

Palabras Clave: composición de la comunidad, depredadores, detritívoros, especies no-nativas, fitófago, grupos funcionales, herbívoros, insectos, revisión de literatura

Introduction

The introduction and spread of invasive plants is a conservation concern worldwide (Vitousek et al. 1996). Plant invasions can alter vegetation communities, disturbance regimes, and nutrient cycling (Vitousek et al. 1996). Such changes can alter the quantity and quality of habitat for animal species at multiple trophic levels, including arthropods.

Increased dominance by invasive plants typically results in decreased diversity of native plants (Vilà et al. 2011). Changes in composition resulting from plant invasions may be especially detrimental for arthropods because many species require specific plants as food or sites for reproduction (Bernays & Graham 1988). Native arthropods may not recognize or be able to use novel plants (Strong et al. 1984; Tallamy 2004), which could lead to changes in presence and abundance of some arthropod species.

Changes in vegetation composition may lead to changes in structural characteristics, including cover, plant height, and concomitant changes in bare ground (e.g., Toft et al. 2001; Standish 2004; Spyreas et al. 2010). Structural changes may affect arthropod movement and modify temperature, light intensity, and soil moisture, which are important determinants of the distribution and reproductive success of certain arthropod taxa (Wolkovich et al. 2009; Schirmel et al. 2011; Talley et al. 2012).

Invasive plants also can alter characteristics of the litter and soil (Standish 2004; Kappes et al. 2007; Wolkovich et al. 2009). Increases in dominance by invasive plants often are associated with increases in the amount and depth of litter and changes in chemical composition of litter, characteristics important for detritivores (Lambrinos 2000; Talley et al. 2012; Alerding & Hunter 2013). Invasive plants may contribute to changes in soil nutrients, moisture, salinity, and pH, and these changes may affect reproduction and composition of arthropods belowground (Witkowski 1991; Gratton & Denno 2005).

To improve understanding of changes resulting from plant invasions, we reviewed the scientific literature on the effects of invasive plants on arthropods. We sought to synthesize existing research and reveal general patterns in documented effects of invasive plants on arthropods, overall and within functional and taxonomic groups, while considering the life form of the invading plant and plant community.

Literature Review

We examined scientific papers quantifying the effects of invasive plants on arthropod communities and functional groups. We searched for studies in scientific databases (BIOSIS Citation Index, Web of Science, and Zoological Record), Google Scholar, and cited references within papers. We used diverse search terms to maximize the number of studies considered for review: *invasive*, *invaded*, *invasion*, *nonnative*, *non-native*, *exotic*, and *alien* with the words *plant* and *vegetation*, in combination with *arthropod*, *insect*, or *invertebrate*. We included papers that examined changes in arthropod abundance, biomass, richness, or diversity because these responses can be compared among taxa and functional groups.

Analyses

We extracted data from papers and computed relative changes in each response variable in areas dominated by native plants relative to invaded areas as

$$\text{relative change (\%)} = [(\text{invasive} - \text{native})/\text{native}] * 100$$

to provide common units for comparison. Where researchers sampled at multiple points along a gradient of the plant invader, we used the sites most dominated by the invasive plant and sites most dominated by native vegetation to compute relative change. We averaged results for studies occurring over multiple sampling periods if the directionality of responses did not change.

When we had insufficient information to compute relative changes, we indicated the direction or presence of documented effects. We also noted cases in which authors explored differences in the response variable between native and invaded areas but did not detect statistically significant effects. Non-significant differences can result when the response truly did not differ between native and invaded areas or because the study had insufficient statistical power to detect differences. Because we could not distinguish between these distinctly different outcomes, we suggest our finding of “no effect” be interpreted with caution.

We organized results in tables based on different levels of ecological organization. We considered responses at the level of ecological community, functional group (where defined explicitly in the study), and taxonomic class or order (presented alphabetically in tables). Because arthropod classes and orders often are comprised of diverse functional groups, we did not impose an alternative organization on these findings in tables unless the functional group was clear from the study. Instead, we aimed to discuss the functional aspects within the text. Finally, we documented the life form of the invading plant, invaded plant community, and location of the study to assess potential patterns.

Reviewed Papers

We summarized the results presented in 87 peer-reviewed scientific papers and graduate theses that examined effects of invasive plants on arthropod communities, functional groups, and taxa (Supporting Information). The studies examined various life forms of invasive plants (grasses, 38%; forbs, 33%; woody plants, 34%); some studies considered multiple species and life forms. Research focused on many vegetation communities: 22% of studies in forests, 26% in grasslands, 14% in shrublands, and 30% in communities associated with water (e.g., salt marsh, riparian areas). Studies spanned the world, but were concentrated in the United States (44%), with substantial research also in Europe (16%), South Africa (11%), New Zealand (10%), and Australia (10%). When considering functional groups, we incorporated studies that focused on specific arthropod taxa, where appropriate.

Effects on Arthropod Communities

When a single species of plant invades and dominates a system, the quantity and quality of habitat change for some species, altering the overall community (Breytenbach 1986; Haddad et al. 2001; Samways & Sharatt 2010). Forty-nine percent of studies compared arthropod communities between areas dominated by invasive and native plants (Table 1). Thirty-four of these 43 stud-

ies examined total abundance of arthropods; 62% documented decreases in abundance with invasive plants, whereas only 15% documented increases and 18% did not detect changes (Table 1). Thirty-one studies examined overall richness of arthropods; 48% documented decreased richness with invasive plants, 13% documented increases, and 32% did not detect differences (Table 1). We did not find clear patterns with respect to the life form of the invasive plant where overall abundance or richness of arthropods increased, but most of these studies examined forests or shrublands.

Vegetation changes associated with invasive plants can affect arthropods differently depending on specific habitat requirements of functional groups, taxa, and life stages. Because community-scale measures are relatively coarse, they may not capture fully the effects of invasion, given that changes in species identity and composition may be masked entirely. This result is especially likely for species richness because the entire community could change without altering the number of taxa; relatively few studies examined indices of similarity or community overlap.

Effects on Herbivores

When herbivores do not share an evolutionary history with a plant, they may not be able to use the plant as food (Strong et al. 1984; Tallamy 2004). At least 90% of all insect herbivores feed on plants in only a single family or a few genera (Bernays & Graham 1988). Abundance, biomass, or richness of herbivores decreased in response to plant invasions in 48% of studies and increased in 17%; no changes were detected in 26% (Table 2).

Specialist herbivores may be affected most by loss of native forbs and other plants associated with invasions if they cannot feed on the novel plant (Strong et al. 1984). If the invasive plant is related closely to native species, herbivores may have adaptations to counteract chemical defenses. Abundance and richness of larval Lepidoptera (moths, butterflies, and skippers) decrease in response to non-native plants that are both congeners and noncongeners of native plants, but declines are most pronounced for noncongeneric plants, especially for specialist lepidopterans (Burghardt et al. 2010). The relatedness of native and invasive plants was not always discussed in the papers we reviewed, but this information might be especially helpful to understand variation in responses.

Many species in the orders Hemiptera (true bugs) and Lepidoptera and a few Thysanoptera (thrips) and Coleoptera (beetles) species are considered host specific during some or all life stages (Triplehorn & Johnson 2005), and these species may be greatly affected by increased abundance of novel plants (Tables 3–5). When an invasive plant dominates the vegetation community, hemipterans may be less abundant (e.g., Spireas

Table 1. Summary of changes in abundance, biomass, and species richness, diversity, and composition of arthropods shown in scientific articles included in a review of the effects of invasive plants on arthropods ($n = 43$ studies).

Reference	Invasive plant	% change ^a				Composition ^b
		Abundance	Biomass	Richness	Diversity	
Bateman & Ostoja 2012	<i>Tamarix</i> spp.	-43		no Δ order	no Δ Simpson	
Belnap & Phillips 2001	<i>Bromus tectorum</i>	varied with grassland type		varied with grassland type		
Cord 2011	<i>Dichanthium annulatum</i>	-~11		-10 order, -17 family		
Dávalos & Blossey 2004	<i>Alliaria petiolata</i>	no Δ				
deHart & Strand 2012	<i>Alliaria petiolata</i>			no Δ spp.		
Derraik et al. 2005	<i>Agrostis capillaris</i> & <i>Anthoxanthum odoratum</i>	+80		+25		
Douglas & O'Connor 2003	<i>Urochloa mutica</i>			varied over time		
Ellis et al. 2000	<i>Tamarix ramosissima</i>	-		+9		
Ernst & Capuccino 2005	<i>Vincetoxicum rossicum</i>	-20-94				
Fork 2010	<i>Conium maculatum</i> & <i>Phalaris aquatica</i>			no Δ order		
Gerber et al. 2008	<i>Fallopia</i> spp.	-40	-45-60	-20-30 m spp. ^c		
Gratton & Denno 2005	<i>Phragmites australis</i>	-63		-57 spp.	-51 spp.	

Continued

Table 1. Continued.

Reference	Invasive plant	% change ^a				Composition ^b
		Abundance	Biomass	Richness	Diversity	
Greenwood et al. 2004	<i>Salix × rubens</i>	≥67 canopy spp., -flying spp. no Δ no Δ		+28-203 spp. no Δ spp.	-83 mspp.	Δ
Harris et al. 2004 Hedge & Kriwoken 2000	<i>Ulex europaeus</i> <i>Spartina anglica</i>	no Δ no Δ				Δ
Heleno et al. 2008	Multiple species	no Δ	-	+83		
Heleno et al. 2010	Multiple species	+148	+233	-50 tax ^d aerial spp.	-Shannon	
Herrera & Dudley 2003	<i>Arundo donax</i>	-50 aerial spp.	-50 aerial spp.			
Hickman et al. 2006	<i>Botriochloa ischaemum</i>		-25			
Holland-Clift et al. 2011	<i>Salix × rubens</i>	-96		-67 order		
Holmquist et al. 2011	<i>Phoenix dactylifera</i> & <i>Washingtonia filifera</i>	-83		-50 family, -67 spp.		
Jonas et al. 2002	<i>Bromus inermis</i>	varied by trap type		varied by trap type	varied by trap type	Δ
Lambrinos 2000	<i>Cortaderia jubata</i>	-				Δ
Levin et al. 2006	<i>Spartina alterniflora</i> X <i>S. foliosa</i>	-75	-57			Δ
Lindsay & French 2006	<i>Chrysanthemoides monilifera</i>	no Δ				
Litt & Steidl 2010	<i>Eragrostis lehmanniana</i>	-45		-18 family, -23 mspp., no Δ order		
Magoba & Samways 2010	Multiple tree species			-benthic macroinvertebrates no Δ family	no Δ Shannon	
Marshall & Buckley 2009	<i>Microstegium vimineum</i>	no Δ				
McGrath & Binkley 2009	<i>Microstegium vimineum</i>	+161				
Palmer et al. 2004	<i>Carpobrotus actinaciformis</i>			no Δ	-39	no Δ

Continued

Table 1. Continued.

Reference	Invasive plant	% change ^a					Composition ^b
		Abundance	Biomass	Richness	Diversity	Composition ^b	
Parr et al. 2010	<i>Andropogon gayanus</i>	–		–family			
Pawson et al. 2010	<i>Pinus nigra</i>			–spp.	–spp.	Δ	Δ
Samways et al. 1996	Many shrubs/trees						
Sax 2002	<i>Eucalyptus globulus</i>	+86		no Δ	+Shannon	Δ	
Schreck et al. 2013	<i>Brassica nigra</i>	–39		no Δ		Δ	
Simao et al. 2010	<i>Microstegium vimineum</i>			–19 RTUs ^c	no Δ	Δ	
Slobodchickoff & Doyen 1977	<i>Ammophila arenaria</i>	–			–spp.		
Spyreas et al. 2010	<i>Phalaris arundinacea</i>	–		–			
Standish 2004	<i>Transcendentia fluminensis</i>	–(weak)		–RTUs (weak)		Δ	
Talley et al. 2012	<i>Phoenix canariensis</i>	–40		–~30	–~20	Δ	
Tang et al. 2012	<i>Microstegium vimineum</i>	+		no Δ	+		
Wolkovich et al. 2009	<i>Brachypodium distachyon</i> , <i>Bromus madritensis</i> , others	–					
Wu et al. 2009	<i>Spartina anglica</i>	–40		–18 family, –18 spp.		Δ	

^aWe computed relative change; percent change = [(invasive – native) / native] * 100.

^bDominant species in arthropod community.

^cMorphospecies.

^dTaxonomic richness.

^eRecognizable taxonomic unit.

Table 2. Direction and magnitude of change^a in functional groups of arthropods ($n = 29$ studies) associated with invasive plants in studies of the effects of invasive plants on arthropods.

Reference	Invasive plant	Functional group ^b		
		Herbivores	Predators	Detritivores
Alerding & Hunter 2013	<i>Alliaria petiolata</i>			+134 density
Almeida-Neto et al. 2011	Several grass species	spp. rich highest at intermediate levels of invasion		
Bartomeus et al. 2008	<i>Opuntia stricta</i> & <i>Carpobrotus affine acinaciformis</i>	no Δ pollinator rich		
Bartomeus et al. 2010	<i>Impatiens glandulifera</i>	no Δ pollinator rich		
Baskett et al. 2011	<i>Gypsophila paniculata</i>	-300 pollinator abund		
Bassett et al. 2011	<i>Alternanthera philoxeroides</i>		no Δ abund (beetles)	none in native (beetles)
Bassett et al. 2012	<i>Alternanthera philoxeroides</i>	Δ spp. comp		
Burghardt et al. 2010	Multiple species	-larval spp. rich & abund		
Carvalho et al. 2010a	<i>Gaultheria shallon</i>	-abund specialists, no Δ abund generalists	parasitoids: -abund specialists, no Δ abund generalists	
Ellis et al. 2000	<i>Tamarix ramosissima</i>		+tax rich (slight)	
Ernst & Capuccino 2005	<i>Vincetoxicum rossicum</i>	-abund many herbivores & pollinators, no Δ seed/sap feeders	-abund	little Δ
Gerber et al. 2008	<i>Fallopia</i> spp.	-abund & mspp. rich	-abund & mspp. rich (spiders)	
Ghazoul 2004	<i>Bromolaena odorata</i>	no Δ pollinator abund		
Gratton & Denno 2005	<i>Phragmites australis</i>	Δ spp. comp	-abund	+abund, no Δ comp
Hansen et al. 2009	<i>Centaurea maculosa</i>		Δ comp ^c	
Harris et al. 2004	<i>Ulex europaeus</i>	+abund ^d	-rich ^c	
Heleno et al. 2010	Multiple species	+80 spp. rich, +101 abund	parasitoids: +100 spp. rich, +448x abund	
Herrera & Dudley 2003	<i>Arundo donax</i>	few spp. in invasive		
Holmquist et al. 2011	<i>Phoenix dactylifera</i> & <i>Washingtonia filifera</i>	-93 abund	no Δ	
Kappes et al. 2007	<i>Reynoutria</i> spp.	-abund	+abund	+abund
Levin et al. 2006	<i>Spartina alterniflora</i> X <i>S. foliosa</i>	-63 biomass	no Δ	
Lindsay & French 2006	<i>Chrysanthemoides monilifera</i> ssp. <i>rotundata</i>			+abund
Samways & Sharratt 2010 ^d	<i>Acacia mearnsii</i>		-55 abund, -48 rich	
Schreck et al. 2013	<i>Brassica nigra</i>	+110 abund, +8 rich	no Δ abund, no Δ rich	
Simao et al. 2010	<i>Microstegium vimineum</i>	-31 abund, -15 rich	-61 abund, -32 rich (w/parasitoids)	no Δ
Tang et al. 2012	<i>Microstegium vimineum</i>	no Δ abund	no Δ abund	no Δ abund
Topp et al. 2008 ^e	<i>Reynoutria</i> spp.	-abund	-abund	+abund
Wolkovich 2010 ^f	Several grass species	+abund	+abund	
Wu et al. 2009	<i>Spartina anglica</i>	Δ herbivore spp. comp		

^aWe computed relative change: percent change = [(invasive - native) / native] * 100.

^bAbbreviations: rich, richness; abund, abundance; comp, composition; tax, taxonomic; mspp., morphospecies.

^cExamined only Carabidae.

^dExamined only dragonflies (Odonata).

^eExamined only beetles (Coleoptera).

^fExamined only leafhoppers (herbivores) and spiders (predators).

et al. 2010; Holmquist et al. 2011; Bassett et al. 2012) or absent (e.g., Samways et al. 1996; Derraik et al. 2001, Table 4), resulting in changes in composition. Although little research has focused on nonagricultural systems, Thysanoptera also may be less abundant or absent in areas dominated by invasive plants (e.g., Derraik et al. 2001; Lindsay & French 2006; Holmquist et al. 2011, Table 5). Relatively few researchers considered responses of specialist Coleoptera to invasive plants, particularly Curculionidae (weevils), although Cord (2011) documented reduced presence of weevils with invasive grass, Harris et al. (2004) found this group only on specific plants, and Marshall and Buckley (2009) did not detect changes in abundance.

Other arthropod groups, such as lepidopterans, require specific plants for reproduction, in addition to the plants they use for food (Thompson & Pellmyr 1991). Preferences for certain plant species may be based on chemical cues for oviposition or characteristics that maximize larval growth and development, such as plant size, proximity to other host plants, and specific microclimate conditions (Thompson & Pellmyr 1991). Relatively few plant species may provide conditions appropriate for successful reproduction; some invasive plants are even toxic to larvae (Graves & Shapiro 2003). Therefore, plant invasions likely are detrimental for lepidopterans and similar taxa (Tallamy & Shropshire 2009); no study focused on Lepidoptera documented increases with plant invasions (Table 5).

Although generalist species comprise <10% of insect herbivores (Bernays & Graham 1988), this group may be more likely able to use a novel plant (Strong et al. 1984; Tallamy 2004). In practice, however, generalist herbivores still may prefer to forage on native plants because invasive plants often have high lignin and starch content and low tissue nitrogen (Haddad et al. 2001). Further, generalists may not be able to thrive on invasive plants if they have not evolved with related species (Tallamy et al. 2010). When reared on invasive plants with no shared evolutionary history, generalist Lepidoptera larvae die or grow very slowly in comparison with larvae reared on native plants. Generalist herbivores may be more affected by plant invasions than hypothesized and may be unable to compensate for the loss of specialists (Tallamy et al. 2010). Decreases in herbivores will be problematic for higher trophic levels, especially many grassland birds, because herbivorous insects can comprise more than half their diets (Wiens & Rotenberry 1979).

Arthropod families that include generalist herbivores, such as Tenebrionidae (darkling beetles) and Elateridae (click-beetles), decrease in areas dominated by certain invasive plants (e.g., Slobodchikoff & Doyen 1977; Herrera & Dudley 2003; Litt & Steidl 2010). We found relatively few studies (Marshall & Buckley 2009) that examined potential effects of invasive plants on Chrysomeli-

dae, another common group of generalists. Responses of Orthoptera were better documented, but they differed. Orthoptera decrease in areas dominated by some invasive plants (e.g., Lambrinos 2000; Standish 2004; Litt & Steidl 2010; Yoshioka et al. 2010), but researchers also report increases (e.g., Samways & Moore 1991; Marshall & Buckley 2009, Table 5). Such variable responses may result from different life forms of invasive plants and the degree of diet specificity. For example, some Orthoptera species feed on dead plant material and live prey (Triplehorn & Johnson 2005) and may benefit from structural changes associated with invasive grasses, such as increased detritus. Knowing how long the invasive plant has been established also could provide important insights (Siemann et al. 2006) because novel plants can become associated with local herbivores over time (Strong et al. 1984).

Effects on Pollinators

The distribution and abundance of pollinators also may be affected by invasive plants because native flowering plants may be less abundant (Lopezaraiza-Mikel et al. 2007). For example, Hymenoptera (sawflies, bees, wasps, and ants) include many pollinators, and their abundance decreases as abundance of invasive plants increases (e.g., Morón et al. 2009; Fork 2010; Hanula & Horn 2011, Table 4). Changes in vegetation composition can alter functional relationships between pollinators and plants (Breytenbach 1986), especially given that many invasive plants are pollination generalists (Aizen et al. 2008). Even if native and invasive plants share pollinators, movement between plant species can increase the chances for heterospecific pollen transfer and further reduce reproduction and dominance of native plants (Brown et al. 2002). Plant invasions also may facilitate colonization by non-native pollinators (Morales & Aizen 2002).

Plant invasions and pollinators have been the focus of numerous studies and reviews (e.g., Traveset & Richardson 2006; Bjerknes et al. 2007; Bartomeus et al. 2008; Morales & Traveset 2009; Montero-Castaño & Vilà 2012). These authors have explored changes in plant-pollinator networks, visitation and pollination rates, plant reproductive output, competition and facilitation, and other variables, revealing conflicting patterns. However, considering the phylogeny, phenology, and phenotypic similarities of invading plants relative to native floral resources should help advance understanding and predict effects (Morales & Traveset 2009). In many cases, a more complete understanding of the nature and specificity of plant-pollinator relationships also would improve prediction (Tallamy & Shropshire 2009).

Removing the invasive plant may facilitate a fairly rapid return of native pollinators (Baskett et al. 2011; Hanula & Horn 2011); planting native vegetation in human-dominated landscapes also may be a viable

Table 3. Direction and magnitude of effects^a of invasive plants on 4 arthropod taxa (*n* = 39 studies).

Reference	Invasive plant	Taxa ^b			
		Acari	Aranae	Coleoptera	Collembola
Alerding & Hunter 2013	<i>Alliaria petiolata</i>				+134 density
Bassett et al. 2011	<i>Alternanthera philoxeroides</i>			fungivores: +3x spp. rich, +11x abund ^c	
Bassett et al. 2012	<i>Alternanthera philoxeroides</i>		-64% abund		
Bateman & Ostoja 2012	<i>Tamarix</i> spp.		no Δ abund	+93 abund	
Bultman & DeWitt 2008	<i>Vinca minor</i>		no Δ spp. rich, -density, -Shannon		
Cord 2011	<i>Dichanthium annulatum</i>	-52 abund	-27 abund	-41 abund	-abund ^c
Crisp et al. 1998	Several grass species			Δ comp	
Dávalos & Blossey 2004	<i>Alliaria petiolata</i>			Carabidae: no Δ spp. rich, no Δ captures	
de Groot et al. 2007	<i>Solidago canadensis</i>			Carabidae: -abund, no Δ spp. rich, no Δ Shannon	
Derraik et al. 2005	<i>Agrostis capillaris</i> & <i>Antboxanthum odoratum</i>	+100 tax rich, no Δ abund	no Δ tax rich, no Δ abund	no Δ tax rich, no Δ abund	
Ellis et al. 2000	<i>Tamarix ramosissima</i>		+46 tax rich, +abund		
Fork 2010	<i>Conium maculatum</i> & <i>Phalaris aquatica</i>			no Δ family rich	
Gerber et al. 2008	<i>Fallopia</i> spp.		-mspp rich, abund		
Gratton & Denno 2005	<i>Phragmites australis</i>		web builders: -80 abund		
Gu et al. 2008	<i>Ageratina adenophora</i>			Carabidae: +spp. rich, -abund	
Hansen et al. 2009	<i>Centaurea maculosa</i>			Carabidae: no Δ spp. rich	
Herrera & Dudley 2003	<i>Arundo donax</i>			Δ comp	
Holmquist et al. 2011	<i>Phoenix dactylifera</i> & <i>Washingtonia filifera</i>	-99 abund	no Δ abund		
Jonas et al. 2002	<i>Bromus inermis</i>			+abund, -family div	
Lambrinos 2000	<i>Cortaderia jubata</i>		+abund		
Lindsay & French 2006	<i>Chrysanthemoides monilifera</i>	-abund	-abund		no Δ
Litt & Steidl 2010	<i>Eragrostis lehmanniana</i>			-64 abund, -abund 1 family	
Marshall & Buckley 2009	<i>Microstegium vimineum</i>			Chrysomelidae: -74 abund, Curculionidae: no Δ abund	Entomobryidae: no Δ abund
McGrath & Binkley 2009	<i>Microstegium vimineum</i>	+abund		no Δ abund	no Δ abund

Continued

Table 3. Continued.

Reference	Invasive plant	Taxa ^b			
		Acari	Aranae	Coleoptera	Collembola
Mgobozi et al. 2008	<i>Chromolaena odorata</i>		–31 abund, –32 spp. rich		
Parr et al. 2010	<i>Andropogon gayanus</i>		no Δ abund		
Pawson et al. 2010	<i>Pinus nigra</i>		no Δ in capture rate	no Δ in capture rate	–capture rate
Pearson 2009	<i>Centaurea maculosa</i>		+45–74x abund some spp.		
Robertson et al. 2011	<i>Opuntia stricta</i>		no Δ spp. rich, no Δ abund	no Δ spp. rich, +1.4x abund, Δ comp	
Samways et al. 1996	Many shrubs/trees			1 sp. only in invasive 5 families only in native	
Schirmel et al. 2011	<i>Campylopus introflexus</i>		–26 spp. rich, –63 abund, Δ comp	Carabidae: –28 spp. rich, no Δ abund, Δ comp	
Simao et al. 2010	<i>Microstegium vimineum</i>		–45 abund	–76 abund 1 sp. (seasonal)	
Slobodchickoff & Doyen 1977	<i>Ammophila arenaria</i>			–abund of 1 sp.	
Standish 2004	<i>Transcendentia fluminensis</i>			Δ comp	
Steenkamp & Chown 1996	<i>Prosopis glandulosa</i>			Scarabaeinae: –17 spp. rich, –10 Shannon, Δ comp	
Toft et al. 2001	<i>Transcendentia fluminensis</i>			no Δ abund/comp	
Topp et al. 2008	<i>Reynoutria</i> spp.			–≥9 abund, –≥19 spp. rich	
Wolkovich 2010	Several grass species		+abund/spp. rich		
Wolkovich et al. 2009	<i>Brachypodium distachyon</i> , <i>Bromus madritensis</i> , other grasses	–abund 1 family			+abund 1 family, –2 families

^aWe computed relative change: percent change = [(invasive – native) / native] * 100.

^bAbbreviations: rich, richness; abund, abundance; comp, composition; tax, taxonomic; mspp., morphospecies; Shannon, Shannon's diversity index; div, diversity.

^cWith increased rainfall.

conservation strategy (Burghardt et al. 2010b). Even small patches of native plants could be important in invaded areas because the number of pollinators typically decreases as distance from native vegetation increases (Carvalho et al. 2010b). Such fragmentation could cause patches of native vegetation surrounded by invasive plants to become isolated and largely unvisited by pollinators.

Effects on Predators

Although arthropod predators do not rely on plants for food, they may be affected by invasions indirectly, through changes in prey items or vegetation structure (Gratton & Denno 2005; Pearson

2009). Predaceous arthropods decreased in response to plant invasions in 44% of studies and increased in 22%; no change was detected in 33% (Table 2). Aranae (spiders), Odonata (dragonflies), some Opiliones (harvestmen), most Neuroptera (lace-wings), some Coleoptera, Acari (mites), and Hymenoptera, and a few Diptera (flies) are predaceous (Triplehorn & Johnson 2005).

Variation in prey preferences may govern diverse responses of arthropod predators. Some hymenopteran families, such as Pompilidae (spider wasps), may be less abundant because their main food resource is less abundant (e.g., Samways et al. 1996) (Table 4), whereas other families, such as Vespidae (social wasps), that feed on a variety of arthropods can persist in areas dominated

Table 4. Direction and magnitude of effects^a of invasive plants on 3 arthropod taxa ($n = 34$ studies).

Reference	Invasive plant	Taxa ^b		
		Diptera	Hemiptera	Hymenoptera
Bassett et al. 2012	<i>Alternanthera philoxeroides</i>		-86 abund	
Bateman & Ostoja 2012	<i>Tamarix</i> spp.	no Δ abund	+7x abund	ants: -64 abund; bees & wasps: no Δ abund
Breytenbach et al. 1984, in Breytenbach 1986	<i>Hakea sericea</i>	+div		ants: -div
Cord 2011	<i>Dichanthium annulatum</i>	-24 abund	-79 abund	-43 abund ^c
de Groot et al. 2007	<i>Solidago canadensis</i>	Syrphidae: no Δ abund, no Δ spp. rich, no Δ Shannon		
Derraik et al. 2001	<i>Agrostis capillaris</i> & <i>Anthoxanthum odoratum</i>		many spp. only in native	no Δ spp. rich
Derraik et al. 2005	<i>Agrostis capillaris</i> & <i>Anthoxanthum odoratum</i>	+1.2x tax rich, +7.4x abund	+1.1x tax rich, +1.9x abund	+1.3x tax rich, +1.7x abund
Fork 2010	<i>Conium maculatum</i> & <i>Pbalaris aquatica</i>			ants: -spp. rich
French & Major 2001	<i>Acacia saligna</i>			ants: -80 abund, Δ spp. comp (+granivores)
Gratton & Denno 2005	<i>Phragmites australis</i>	-abund 1 sp.		
Harris et al. 2004	<i>Ulex europaeus</i>	Δ spp. comp, +spp. rich & 1 family		
Hanula & Horn 2011	<i>Ligustrum sinense</i>			bees: -spp. rich, -spp. div, -abund, no Δ evenness
Holmquist et al. 2011	<i>Phoenix dactylifera</i> & <i>Washingtonia filifera</i>	-79 abund	-92 abund	-90 abund
Lambrinos 2000	<i>Cortaderia jubata</i>		-abund	-abund
Lenda et al. 2013	<i>Solidago</i> spp.			ants: -spp. rich, -colony density, -colony size
Lescano & Farji-Brener 2011	<i>Cadus thoermeri</i> & <i>Onopordum acanthium</i>		aphids: +28x abund	tending ants: +51x activity
Lindsay & French 2006	<i>Chrysanthemoides monilifera</i>	-abund		-abund
Litt & Steidl 2010	<i>Eragrostis lebmänniana</i>	-45 abund, -abund 1 family, +abund 1 family	-39 abund, -abund 2 families	no Δ abund
Marshall & Buckley 2009	<i>Microstegium vimineum</i>		Cicadellidae: +4.5x abund, Lygaeidae: no Δ abund	ants: no Δ abund
Moroñ et al. 2009	<i>Solidago canadensis</i> & <i>Solidago gigantea</i>	Syrphidae: -75 spp. rich, -80 abund, -67% Shannon		bees: -78 spp. rich, -87 abund, -70 Shannon
Ostojca et al. 2009	<i>Bromus tectorum</i>			ants: +10x abund, +fg div, -spp. div, no Δ spp. rich
Osunkoya et al. 2011	<i>Macfadyena unguis-cati</i>			ants: (aboveground) -20 spp. rich, -33 abund; (subterranean) +14 spp. rich, no Δ abund
Parr et al. 2010	<i>Andropogon gayanus</i>			ants: no Δ spp. rich, abund

Continued

Table 4. Continued.

Reference	Invasive plant	Taxa ^b		
		Diptera	Hemiptera	Hymenoptera
Pawson et al. 2010	<i>Pinus nigra</i>	+capture rate	–capture rate	ants: no Δ capture rate; other groups: –capture rate
Samways et al. 1996	many shrubs/trees		only in native	ants: some spp. only in native
Schoeman & Samways 2013	<i>Pinus</i> spp.			ants: –46 spp. rich, –62 abund
Simao et al. 2010	<i>Microstegium vimineum</i>		–540 abund 1 sp. (seasonal)	
Spyreas et al. 2010	<i>Phalaris arundinacea</i>		–abund/spp. rich	
Toft et al. 2001	<i>Transcendentia fluminensis</i>	fungus gnats: no Δ spp. rich/abund, +abund 1 fam		
Webb et al. 2000	<i>Ammophila arenaria</i>	+102 abund		ants: no Δ mspp. rich
Wheeler 1999	<i>Eragrostis curvula</i>		+abund 2 spp.	
Wilkie et al. 2007	<i>Chrysanthemoides monilifera</i>		Δ spp. comp	
Wolkovich 2010	several grass species		+abund/spp, rich 1 family	
Wolkovich et al. 2009	<i>Brachypodium distachyon</i> , <i>Bromus madritensis</i> , other grasses			ants: –abund 2 spp., +1 sp.

^aWe computed relative change: percent change = [(invasive – native) / native] * 100.

^bAbbreviations: rich, richness; abund, abundance; comp, composition; tax, taxonomic; mspp., morphospecies; Shannon, Shannon's diversity index; div, diversity; fg, functional group.

^cExcluding ants.

by an invasive plant. Hansen et al. (2009) documented a shift in composition of the carabid beetle community in areas dominated by an invasive forb—generalist predators decreased and omnivores and specialist predators increased. Parasitoids were examined in only one study (Simao et al. 2010); abundance (mainly Hymenoptera) decreased in areas dominated by invasive grass, likely because of a lack of the host species (Simao et al. 2010).

Some spiders and other predators also may be affected by structural changes in vegetation associated with invasive plants (e.g., Bultman & DeWitt 2008; Wolkovich 2010) (Tables 2–4). Increases in predators may reflect changes in vegetation structure that increase mobility and survival or influence structural support for web building. For example, Pearson (2009) found that an invasion by invasive forbs into grasslands increases availability of web-building substrates and results in large increases in densities of native spiders. The more expansive architecture of the invasive forbs allows spiders to construct larger webs that double capture rates of prey. For predators that respond to changes in vegetation structure, restoring or conserving plant physiognomy characteristic of native plants may be more important than vegetation composition. Changes in predaceous arthropods associated with invasive plants are complicated, and meaningful interpretations of published work usually require more information about prey capture methods, prey preferences, and

other habitat needs, especially for nonarachnid predator groups, than is provided within the study.

Effects on Detritivores

Of all functional groups, detritivores are most likely to benefit from a plant invasion because increases in ground litter and decaying vegetation associated with many invasive plants can provide more food and preferred microclimate conditions (Longcore 2003; Levin et al. 2006, Table 2). Additionally, the rate of litter decomposition in invaded areas can be higher (Standish 2004) because dead vegetation may have different chemical properties than living plants. Detritivores are represented by species from several taxa, including Collembola (springtails), Acari, Microcoryphia (bristletails), several Opiliones, and some Coleoptera and most Diptera (Triplehorn & Johnson 2005). Detritivores increased in 67% of studies and no studies documented decreases (Table 2). Increases in abundance of detritivores in areas dominated by invasive plants could lead to ecosystem-wide shifts in trophic dynamics—from a food web based on living vegetation to a food web based on detritus (Gratton & Denno 2006; Levin et al. 2006).

Although many detritivores benefit from invasive plants, some species may decrease in abundance. For

Table 5. Direction and magnitude of effects^a of invasive plants on 4 arthropod taxa (*n* = 25 studies).

Reference	Invasive plant	Taxa ^b			
		Lepidoptera	Neuroptera	Orthoptera	Thysanoptera
Bateman & Ostoja 2012	<i>Tamarix</i> spp.	no Δ abund		no Δ abund	
Bock et al. 1986	<i>Eragrostis lehmannaiana</i> & <i>E. chloromelas</i>			-44 abund, Δ comp (8 spp ^d -, 1+, 4 no Δ)	
Burghardt et al. 2008	several non-native ornamentals	-4x larval abund, -3x larval spp. rich			
Burghardt et al. 2010	multiple species	-52-74 larval abund, -39-68 larval spp. rich			
Cord 2011	<i>Dichanthium annulatum</i>			-28 abund	
de Groot et al. 2007	<i>Solidago canadensis</i>	-spp. rich, -abund, -Shannon			
Derraik et al. 2001	<i>Agrostis capillaris</i> & <i>Antboxanthum odoratum</i>	some only in native	only in native		most only in native
Derraik et al. 2005	<i>Agrostis capillaris</i> & <i>Antboxanthum odoratum</i>	no Δ tax rich, no Δ abund			
Ghazoul 2004	<i>Chromolaena odorata</i>	no Δ abund			
Harris et al. 2004	<i>Ulex europaeus</i>	no Δ spp. rich, -32-94 abund			
Holmquist et al. 2011	<i>Phoenix dactylifera</i> & <i>Washingtonia filifera</i>	-91 abund	-86 abund	no Δ abund	only in native
Jonas et al. 2002	<i>Bromus inermis</i>			+abund, +spp. rich, +Shannon	
Lambrinos 2000	<i>Cortaderia jubata</i>			only in native	
Lindsay & French 2006	<i>Chrysanthemoides monilifera</i>				-abund
Litt & Steidl 2010	<i>Eragrostis lehmannaiana</i>			-37 abund, -abund 1 family, +abund 1 family	
Marshall & Buckley 2009	<i>Microstegium vimineum</i>			Acrididae: +4x abund, Gryllidae: +3.4x abund	
Moroñ et al. 2009	<i>Solidago canadensis</i> & <i>Solidago gigantea</i>	-60 spp. rich, -73 abund, -60 Shannon			
Pawson et al. 2010	<i>Pinus nigra</i>			-capture rate	
Samways & Moore 1991	<i>Cupressus arizonica</i> & <i>Pinus roxburghii</i>			+spp. rich/abund (<i>Cupressus</i>), -(<i>Pinus</i>)	
Samways et al. 1996	many shrubs/trees			no Δ abund, 1 sp. only in native	
Schooler et al. 2009	<i>Lythrum salicaria</i> & <i>Phalaris arundinacea</i>	moths: - spp. rich, no Δ Simpson			
Schreck et al. 2013	<i>Brassica nigra</i>				+4x abund

Continued

Table 5. Continued.

Reference	Invasive plant	Taxa ^b			
		Lepidoptera	Neuroptera	Orthoptera	Thysanoptera
Standish 2004	<i>Transcendentia fluminensis</i>			only in native	
Valtonen et al. 2006	<i>Lupinus polyphyllus</i>	no Δ spp. rich, –24 abund			
Yoshioka et al. 2010	<i>Eragrostis curvula</i>			–abund in 7–10 spp., no Δ abund in 2–5 spp.	

^aWe computed relative change: percent change = [(invasive - native) / native] * 100.

^bAbbreviations: rich, richness; abund, abundance; comp, composition; tax, taxonomic; mspp., morphospecies; Shannon, Shannon's diversity index; div, diversity; fg, functional group; Simpson, Simpson's diversity index.

example, abundance of Sminthuridae (globular springtails) increased where invasive plants were dominant, but abundance of Entomobryidae and Isotomidae (elongate-bodied springtails) decreased (Wolkovich et al. 2009) (Table 3). Cord (2011) documented decreases in abundance of collembolans with an invasive grass but only during sampling periods with increased rainfall (Table 3). Variability in responses among or within taxa is not well understood; thus, more species- and context-specific information is needed.

Effects on Ants

Although effects of invasive plants on Formicidae (ants) are relatively well studied, responses are variable due to their diverse ecological roles as herbivores, predators, and detritivores (Triplehorn & Johnson 2005). Fifteen of 24 studies considering Hymenoptera focused on ants (Table 4). Abundance and richness of ants decreased with plant invasions in 47% of studies and increased in 7%. Results were mixed in 27% of studies, depending on the response variable or subgroup of ants considered, and differences were not detected in 20% of studies.

Changes in food resources or microclimate conditions resulting from invasive plants are detrimental for some ant species (e.g., Webb et al. 2000; Fork 2010) but beneficial for others (e.g., Wolkovich et al. 2009). For example, richness and abundance of seed-feeding ants decrease in invaded areas relative to native fynbos (French & Major 2001). Conversely, abundance of ants increases in invaded areas relative to native sagebrush (Ostoja et al. 2009), which may result from increases in seeds or reduced seed predation by rodents in invaded areas (Anderson & MacMahon 2001). In the Patagonia steppe, activity of tending ants increases with invasive thistles due to a concomitant increase in aphids (Lescano & Farji-Brener 2011). Because ants represent diverse functional groups and are relatively easy to identify, research on this group can provide important insights. Ants also play important roles as seed dispersers and predators, and their effects on

seed removal and predation should be considered carefully when planning seeding and restoration efforts (e.g., Ostoja et al. 2009).

Synthesis

For many arthropod groups, plant invasions resulted in decreased abundance or richness, yet conflicting patterns were still relatively numerous. Given the diversity within broad taxonomic groups and the coarse grain of many of the variables considered, perhaps it is somewhat surprising that any general patterns emerged. In the studies we considered, sample size, sampling effort, sampling method, sampling season, sampling duration, plot size, and weather condition differed greatly. Such differences could alter responses of arthropods greatly and obscure general patterns (Bjerkes et al. 2007). By incorporating more information about spatial and temporal scales and specific context of each study, we could move closer to developing a unified framework for responses.

Arthropods fill diverse niches and functional roles, and responses to plant invasions reflect the breadth of forms and functions. Assessing responses of arthropods to plant invasions at the level of class, order, or family may mask diverse genus- or species-specific responses. Although challenging, future research would best inform conservation efforts if it focused on the lowest taxonomic level possible to identify the full range of responses. Examining similarities in responses based on functional roles may contribute most to building a predictive framework because groups with tightly evolved trophic relationships with native plants, such as herbivores, could be separated from predators that respond indirectly to changes in prey or vegetation structure.

Seventy-nine percent of studies compared areas dominated by native plants with invaded areas; quantifying the degree of dominance by the invasive plants or examining changes over a gradient would help identify critical thresholds where responses change in direction and magnitude. Although few studies included information about

the size of invaded areas, connectivity of patches, and distance to native vegetation, these factors could be important predictors of the magnitude of effects of invasive plants on arthropods.

Future Directions and Implications for Restoration and Conservation

Although numerous studies have focused on invasive plants and arthropods, sizeable information gaps remain. In particular, understanding of how invasive plants actually influence habitat and dietary requirements for arthropods is limited; these requirements may not be well-understood for many species. Collecting detailed information about changes in vegetation, litter, and soil characteristics associated with plant invasions and incorporating this information directly could improve understanding of the factors that drive effects of plant invasions on life stages and activities of arthropods. Because the degree to which plant invasions affect arthropods depends largely on the degree to which invasive plants alter form and function of native vegetation communities, comparing arthropod responses to different life forms of invasive plants and different native communities also could contribute to a predictive framework and more effective conservation.

Beyond this, our understanding and ability to predict changes in arthropod communities with plant invasions would be improved by adopting a more mechanistic approach. For example, by understanding that invasion by garlic mustard (*Alliaria petiolata*) typically increases soil pH, which in turn increases reproduction in some springtails (Alerding & Hunter 2013), one can better predict effects of similar plants or explore restoration tools to alter effects. Further, quantifying changes in species interactions (e.g., food webs, pollination networks) and population-level parameters (e.g., reproduction, survival) may provide important insights into complex effects not captured by examining only presence and abundance. For example, plant invasions have resulted in increased population sizes and longer breeding seasons for some butterfly species, but invasions may reduce reproduction if the invasive plants are toxic to larvae (Graves & Shapiro 2003).

In many cases, plant invasions are only one of several factors affecting arthropod communities, given that invasions often are facilitated by disturbance (e.g., fire) or changes in land use and weather patterns (Vitousek et al. 1996). Considering multiple stressors and the potential for interactive effects on arthropod communities would be another important area for future research (e.g., Bartomeus et al. 2010).

Examining the efficacy of removal or restoration treatments can provide essential insights into whether control

measures can mitigate the effects of invasive plants on arthropods (e.g., Heleno et al. 2010; Magoba & Samways 2010; Baskett et al. 2011). Given their short generation times, arthropods can respond rapidly to activities that help conserve and restore native plant communities (e.g., Gratton & Denno 2005; Samways & Sharratt 2010; Baskett et al. 2011; Hanula & Horn 2011), which may make arthropods ideal conservation targets. Because eradication of many invasive plants is often impractical or impossible, creating or maintaining a heterogeneous mosaic of vegetation patches and microhabitats may provide a practical alternative (e.g., Samways & Sharratt 2010). Understanding the role of patch size and configuration could be essential for conservation because relatively small patches of native plants in invaded areas may be sufficient for some arthropod groups such as pollinators (Carvalho et al. 2010b). There is a need for more research on the efficacy of weed management on arthropods at higher trophic levels, how mobility of some species influences re-colonization, and the potential for restorative effects to persist over time.

Arthropods comprise a large part of the diet of many reptiles, amphibians, small mammals, and birds, including grassland birds that are declining in abundance (Wiens & Rotenberry 1979). Increasing understanding of arthropods and plant invasions will be important for conservation of species at higher trophic levels and ecosystem function. As distributions of invasive plants continue to increase or shift in response to changes in land use and climatic patterns (Bradley et al. 2009; Pauchard et al. 2009), effective conservation of arthropods will be essential for the organisms that depend on them and ecosystem processes they facilitate.

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Supporting Information

A list of the scientific papers included in this review and lists of the invasive plant species, plant life forms, vegetation communities, and study locations are available online (Appendix S1). Queries should be directed to the corresponding author.

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