

Eating their way to the top? Mechanisms underlying the success of invasive insect generalist predators

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Abstract Insect generalist predators have been introduced outside of their native range intentionally to improve biological control, or accidentally during commerce, and can subsequently become invasive. Invasive insect generalist predators (IIGP) have widespread impacts on invaded communities because they consume both herbivores and other predators. Also, they often reach higher densities than and displace similar native species. Reflecting the complexity of their ecological roles, a wide variety of mechanisms might contribute to invasive success by IIGP. These species often drive resources to lower levels than do natives, leading to intense resource competition and sometimes competitive exclusion of other predators. The broader range of resources used by many IIGP can heighten their competitive advantage, particularly when IIGP exploit modified habitats. In either case, IIGP improve herbivore suppression by depressing prey densities below pre-invasion levels. Coexistence among native and invasive generalists is fostered when species differ substantially in their niche requirements. In this case, a larger proportion of the total prey population is subject to attack post- than pre-invasion, which strengthens prey suppression. On the other hand, some IIGP feed heavily on other predators, at times

leading to a weakening of prey suppression. Future research should continue to explore the roles of competition and niche partitioning on larger spatial scales, and in both the native and invasive ranges of IIGP. Additionally, combining data from empirical studies with theory might be an effective way to predict the spread and community impacts of IIGP invasions.

Keywords Resource competition · Interference competition · Niche partitioning · Species coexistence · Intraguild predation · Biological control

Introduction

Insect generalist predators play complex roles in terrestrial food webs, as they feed not only on herbivores but also on other predators, detritivores, and plants (Polis and Strong 1996; Snyder and Evans 2006). Many species have become invasive outside of their native range, and due to their complex trophic roles have widespread impacts on invaded communities (Snyder and Evans 2006). These impacts likely are increased because invasive insect generalist predators (IIGP) often reach densities several orders of magnitude greater than similar native species (Snyder and Evans 2006). Here, we only consider species as invasive that not only become established,

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but also spread readily in their non-native range (Elton 1958; Snyder and Evans 2006). Increased human commerce, and introduction of generalist predators for biological control, has increased the frequency of invasions by IIGP (Mack et al. 2000; Parry 2009). IIGP might strengthen herbivore suppression if they are more effective at prey capture than native predators, which can increase plant biomass through trophic cascades (Schmitz et al. 2000; Halaj and Wise 2001). However, IIGP could weaken herbivore suppression if they feed heavily on effective native predators (Polis et al. 1989; Finke and Denno 2004, 2005; Ives et al. 2005).

It is striking how often IIGP displace ecologically similar native species during the course of their invasion (Snyder and Evans 2006). IIGP compete

with native predators for shared resources and through interference mechanisms such as intraguild predation (Polis et al. 1989; Rosenheim et al. 1995; Reitz and Trumble 2002). Such competition can affect predator–prey dynamics (Polis and Holt 1992; Ives et al. 2005), and could contribute to the displacement of natives (Reitz and Trumble 2002). However, the mechanisms that drive displacement or promote coexistence more generally remain poorly understood (Holway et al. 2002; Reitz and Trumble 2002). Here, we review general theory examining competitive displacement or coexistence among species, and provide examples from several well-studied IIGP taxa (Table 1). Many of these species impact agriculture (Table 1), and the economic value of these systems means that they are well studied.

Table 1 List of well-studied IIGP that have invaded terrestrial ecosystems, their invasive range, intraguild native species that have been affected by the invasions, and their effects in agricultural ecosystems

IIGP	Common name	Invasive range	Intraguild species affected	Effects on agriculture	References
Coleoptera					
<i>Coccinella septempunctata</i>	Seven-spot ladybird beetle	NA	Predacious insects	Herbivore suppression	1
<i>Harmonia axyridis</i>	Multicolored Asian ladybird beetle	EU, NA	Predacious insects	Crop pest; herbivore suppression	2–4
<i>Pterostichus melanarius</i>	Common black ground beetle	NA	Predacious insects; spiders	Herbivore suppression	5
Hymenoptera					
<i>Anoplolepis gracilipes</i>	Yellow crazy ant	AF, AS, AU, SA	Ants; lizards; spiders	Herbivore suppression; mutualist with pests	6, 7
<i>Linepithema humile</i>	Argentine ant	AF, AS, AU, EU, NA	Ants; lizards; spiders; wasps	Herbivore suppression; mutualist with pests	7, 8
<i>Pheidole megacephala</i>	Big-headed ant	AU, EU, NA, SA	Ants; spiders	Herbivore suppression; mutualist with pests	6, 7
<i>Polistes dominulus</i>	European paper wasp	AU, NZ, NA	Wasps	Crop pest	8, 9
<i>Solenopsis invicta</i>	Red imported fire ant	AU, NZ, NA	Ants; lizards	Herbivore suppression; mutualist with pests	5, 6
<i>Vespula germanica</i>	German wasp	AU, NZ, NA	Spiders; wasps	Attacks pollinators; crop pest	10, 11
<i>Vespula vulgaris</i>	European common wasp	AU, NZ, SA	Spiders; wasps	Attacks pollinators; crop pest	11
<i>Wasmannia auropunctata</i>	Little fire ant	AF, AU, NA	Ants; scorpions; spiders	Herbivore suppression; mutualist with pests	6, 7
Mantodea					
<i>Tenodera sinensis</i>	Chinese mantis	NA	Mantids; spiders	Herbivore suppression	12

Abbreviations: AF Africa, AS Asia, AU Australia, EU Europe, NA North America, NZ New Zealand, SA South America

References: ¹Hodek and Michaud (2008), ²Koch (2003), ³Perves and Omkar (2006), ⁴Koch and Galvan (2008), ⁵Ribera et al. (2001), ⁶Holway et al. (2002), ⁷Ness and Bronstein (2004), ⁸Suarez et al. (2008), ⁹Liebert et al. (2006), ¹⁰Spradberry and Maywald (1992), ¹¹Beggs (2001), and ¹²Fagan et al. (2002)

Therefore, the literature includes several observational datasets that span pre- and post-invasion periods. Also, their small size and rapid development make IIGP ideal experimental subjects, and the results of manipulative field experiments are frequently available.

Ecological effects of IIGP have recently been reviewed elsewhere (Table 1; Snyder and Evans 2006; Kenis et al. 2009), and we do not duplicate those efforts here. Rather, we focus on two mechanisms thought, and often shown, to underlie successful invasion by our focal species: dominance in resource competition, and dominance in interference competition. We first review general theory on how each mechanism is predicted to allow species displacement or coexistence, and implications for resource (herbivore) densities. Then, we review observational and experimental studies that provide evidence of the mechanism operating in nature. Finally, we identify future research priorities that could improve our understanding of the interactions between IIGP, native generalist predators, and the communities in which they are embedded.

Dominance in resource competition

Theory

Ecologists have long focused on resource competition between species, and a large body of theory is devoted to the subject (e.g., MacArthur and Levins 1967; Levins and Culver 1971; Armstrong and McGehee 1980; Tilman 1982, 1994; Amarasekare 2002). Early experimental work demonstrated that two species sharing a single resource could not coexist indefinitely (Gause 1936). Much theoretical work has gone into reconciling such findings, which are conducted in simple experimental arenas, with the great species diversity in the world around us. Early work led to the coining of the competitive exclusion principle, which posits that two “complete competitors” cannot coexist indefinitely (Hardin 1960). This statement was refined by authors such as Debach (1966), who stated that “different species having identical ecological niches (that is, ecological homologues) cannot coexist for long in the same habitat.” Tilman (1982) expanded on these principles using models of two consumer

species that overlap completely in their use of a single limiting resource (Fig. 1a). These models showed that over time, the superior consumer depletes resources below threshold levels for the inferior competitor and displaces it.

However, the theory underlying the competitive exclusion principle is based on assumptions that rarely are satisfied in nature, as species typically differ in their use of shared and limiting resources (Armstrong and McGehee 1980; Fig. 1b, c). Indeed, it has been pointed out that if enough traits are measured, it is inevitable that some difference between species will be found (Strong et al. 1979; Lewin 1983). So, a more refined question might be, how big of a difference between species is necessary for coexistence (e.g., MacArthur and Levins 1967)? Haigh and Smith (1972) showed that two predators attacking different life stages of a prey species could coexist when the predator feeding on the earlier stage does not kill all of the prey, and enough survive to provide adequate resources for the predator feeding on the later stage (see also Wilby and Thomas 2002). Koch (1974a) showed that two competitors could coexist by exploiting a shared resource at different points in time, as long as the species that grows faster when the environment has plentiful resources grows slower when resources are limiting. In this case, population fluctuations of the two species, one that performs better when growth is density-independent, and the second that performs better when growth is density-dependent, can lead to stable coexistence. Koch (1974b) demonstrated that two species sharing a resource could coexist when the detrimental effects of intraspecific competition are strong relative to the effects of interspecific competition. The mechanism underlying all of these results is roughly the same: species that are specialized on attacking a particular subset of resources experience intense intraspecific competition for preferred resources, but relatively weak interspecific competition for the full range of available resources (Vandermeer 1972; Chesson 2000). Weak interspecific competition in turn encourages co-existence. Thus, the outcome of resource competition depends on the degree of resource-niche overlap between species, with sufficiently large differences in resource use in space and/or time permitting coexistence (Hutchinson

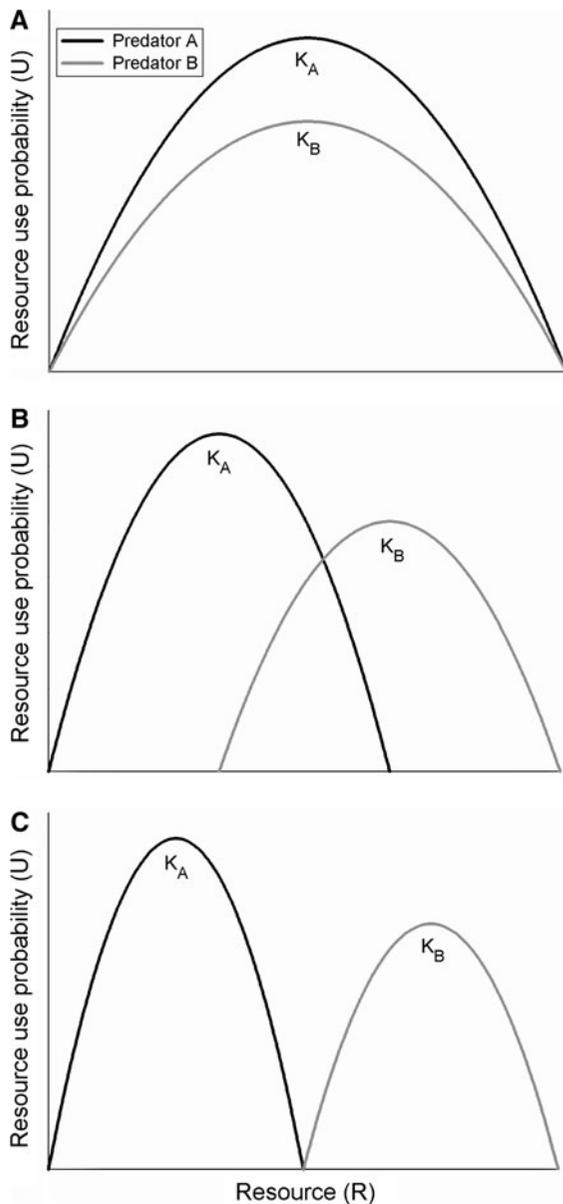


Fig. 1 Niche overlap between species. For each predator (A and B), U is the probability that the resource R will be used in a unit time (MacArthur and Levins 1967). The total resource use by each predator is the area under the curve (K). **a** Two predators overlap completely in resource consumption. Over time, predator A is expected to decrease resource levels below thresholds to support predator B and will displace it. **b** Two predators with incomplete overlap in resource consumption. The two species compete in the shared niche, but can coexist through niche partitioning. **c** Two predators with no overlap in resource consumption. The two predators are expected to coexist by exploiting fully complementary niches

1959; Armstrong and McGehee 1980; De Roos et al. 2008).

Thus, because IIGP exploit multiple resources, niche partitioning affects resource competition between IIGP and native predators. We use the term niche partitioning broadly to indicate differences between species in resource or habitat use. Niche partitioning between species can foster coexistence by increasing costs associated with intraspecific competition relative to interspecific competition, or by providing refuges from competition (Schoener 1974; Chesson 2000; Amarasekare 2003; Finke and Snyder 2008). Species coexistence is fostered when species have narrow niche breadths with limited or no overlap, or when a species subject to the most intense resource competition is the most effective at increasing when rare (MacArthur and Levins 1967). In contrast, increasing niche breadth can lead to competitive exclusion, as the most effective resource exploiter will displace species with considerable niche overlap (MacArthur and Levins 1967). Further, species that exploit multiple resources or habitats are expected to reach higher densities than could be supported on a single resource or in a single habitat (Polis et al. 1997), which could increase the rate of competitive displacement. At the same time, species displaced into widely scattered habitats presumably would experience extinction risks typical of other forms of habitat fragmentation (Fahrig 2002).

In summary, theory predicts that if competitive exclusion is a key mechanism underlying IIGP invasions, we would expect to see several types of ecological effects following these invasions. First, IIGP would be superior competitors for resources (prey), such that prey densities would decline following invasion. Second, native species would be displaced (locally or entirely), with species that are most ecologically similar to the invader most affected, and those with clear niche differences with the invader least affected. Indeed, these patterns have been recorded for several of our focal IIGP species, as we next discuss.

Evidence that IIGP are superior resource competitors

There is substantial evidence that IIGP commonly outcompete natives for common resources (Fig. 2).

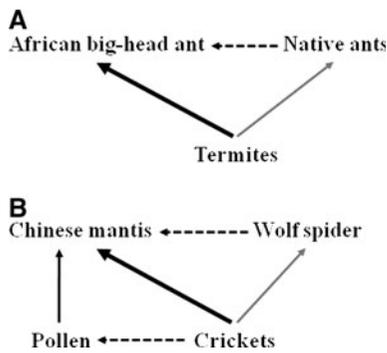


Fig. 2 Impact of superior resource exploitation by IIGP on native predators and prey. *Solid lines* indicate direct interactions, with *arrows* indicating the direction of energy flow. The *width* of the *arrows* indicates the strength of the interaction. *Dashed lines* indicate indirect interactions, with the *arrow* pointing away from the species that is negatively affected. **a** In Mexico, the invasive African big-head ant *Pheidole megacephala* is a more effective predator of termites than 13 native ant species (Dejean et al. 2007). In sympatric regions, suppression of termite populations by *P. megacephala* below thresholds needed to support the native species can drive competitive displacement of the natives. **b** In Virginia, invasive populations of the Chinese mantis *Tenodera sinensis* can supplement their diets with pollen (Beckman and Hurd 2003). Pollen-supplemented populations can reach high densities even when other prey resources are scarce, leading to greater suppression of cricket prey, which reduces resources available to native wolf spiders

Holway (1999) showed that the invasive Argentine ant, *Linepithema humile*, located and recruited to food baits more rapidly and in greater numbers than seven native ant species, contributing to the displacement of the natives from food resources. Dejean et al. (2007) showed that the invasive African big-headed ant, *Pheidole megacephala*, was more effective at capturing termite prey than 13 native ant species in Mexico. In sympatric regions, *P. megacephala* reduced termite prey resources below levels sufficient to support the native species (Fig. 2a). Similarly, studies of invasive carabids (e.g., Prasad and Snyder 2006b), lady beetles (e.g., Michaud 2002; Gardiner and Landis 2007), mantids (e.g., Moran et al. 1996), and wasps (e.g., Toft and Rees 1998), have shown that IIGP are more effective resource competitors than native predators.

In some cases, IIGP may be more effective at capturing resources because prey lack the ability to recognize and effectively avoid IIGP. The best example comes from an invasive terrestrial arthropod that is not an insect. Pallini et al. (1999) showed that

spider mites, *Tetranychus urticae*, avoided habitat patches occupied by the native specialist predator *Phytoseiulus persimilis*, but not patches occupied by the invasive predator *Neoseiulus californicus*. This suggests that previous experience with a native predator selected for predator avoidance behavior, but that such behaviors were not triggered in the presence of the invader. In such cases invaders are not themselves exceptionally capable at capturing prey; rather, the prey are particularly ineffective at avoiding the invasive predators.

There is also some evidence that IIGP may outcompete native predators for exotic prey resources (Snyder and Evans 2006). One of the best examples comes from the case of the invasive lady beetle *Harmonia axyridis*, in soybean fields in the Midwestern US. Prior to the introduction of the invasive soybean aphid, *Aphis glycines*, *H. axyridis* was not abundant in soybean fields (Schmidt et al. 2008). The soybean aphid is a key prey item of *H. axyridis* in both species' native ranges in Asia, where the two often co-occur. Once provided with this familiar food resource, *H. axyridis* rapidly invaded US soybean fields and became the dominant predator species there (Rutledge et al. 2004; Schmidt et al. 2008; Gardiner et al. 2009a, b). These results suggest that the invasion of *A. glycines* into soybean aided in the establishment and spread of *H. axyridis*, because *H. axyridis* was able to outcompete native predators for soybean aphid prey.

The competitive advantage for IIGP in resource exploitation can be magnified when the exotics have broad diets that completely overlap, and reach beyond, those of the natives. In this case there is no niche space into which the native can retreat to escape competition with the IIGP. Also, a broad diet may open additional resources to be exploited by exotic species that are not available to otherwise-similar native species, during periods when preferred prey densities are low. Kasper et al. (2004) showed that the diet of the invasive generalist wasp *Vespula germanica* completely overlapped the diet of the native wasp *Polistes humilis*, a specialist on lepidopteran prey, in New Zealand, while also including additional prey not used by the native. The authors concluded that densities of the invasive species were augmented by these additional foods, bolstering densities of the invasive relative to the native wasp. Similarly, Le Breton et al. (2005) showed that native

ants exploited 45–65% of available food resources in Canada, while invasive colonies of *Wasmannia auropunctata* that were displacing them used over 90% of available resources. By exploiting vacant niches not used by the native species, *W. auropunctata* was able to successfully invade and reached significantly higher population densities than similar native ants. Beckman and Hurd (2003) showed that nymphs of the invasive mantid *Tenodera sinensis* can supplement their diets with pollen, unlike wolf spiders, the most ecologically-similar native species (Fig. 2b; e.g., Moran et al. 1996). Pollen-supplemented *T. sinensis* survived longer in food limited environments, and produced the same number of eggs with less cricket prey, than non-supplemented mantids. In each of these cases, the broader diets of IIGP presumably allowed them to increase their densities relative to native predators, and to better weather scarcity of particular preferred prey, to their competitive advantage.

Evidence for a link between resource exploitation and displacement of natives

Several long-term datasets provide evidence for a link between superior resource exploitation and the displacement of native predator species. For example, Evans (2004) sampled alfalfa fields in Utah both prior to and following invasion by the lady beetle *Coccinella septempunctata*. Prior to invasion, several species of native lady beetles were abundant in alfalfa fields. After introduction of *C. septempunctata*, these species were largely displaced from alfalfa habitats, coinciding with a reduction in aphid densities. However, when aphid densities were experimentally restored, the native lady beetles returned to alfalfa fields. This clever experiment suggests that resource competition drove native lady beetles out of the alfalfa habitat, but that alternative hosts in the landscape maintained native lady beetle populations elsewhere. Presumably, either native lady beetles displayed a competitive advantage when attacking prey in these refuge habitats, or the refuges were outside the habitat niche of the invasive lady beetle.

Similarly, Alyokhin and Sewell (2004) analyzed a community of lady beetles inhabiting potato crops over 31 years in Maine. Prior to invasion by *C. septempunctata*, *H. axyridis*, and *Propylea quatordecimpunctata*, the native species *Coccinella*

transversoguttata and *Hippodamia tredecimpunctata* were dominant members of the community. However, after introduction of the three exotics, the two native species declined in abundance, coinciding with increased abundance of the invaders. As with the Evans (2004) study, successive waves of lady beetle invasion led to a stepwise decline in aphid densities. This suggests that each invader displaced the previous species by lowering prey densities. Thus, in both cases, aphid biological control was improved by lady beetle invasion, albeit at a cost to native lady beetle biodiversity.

Invasions by exotic ants are also associated with declines in prey abundance, with some of the most dramatic examples coming from agroecosystems (Holway et al. 2002). For example, Eubanks (2001) investigated the effects of the invasive red imported fire ant, *Solenopsis invicta*, on pests and beneficial species in cotton and soybean fields in Texas. Increasing fire ant densities were associated with reduced abundance of all 16 pest taxa examined in cotton, and 13 of 16 pest taxa examined in soybean. Additionally, the abundance of *S. invicta* was negatively associated with 22 of 24 natural enemy taxa in cotton and 14 of 16 natural enemy taxa in soybean. However, the reduced abundance of the natural enemy species was not solely caused by reduced resource abundance, but also resulted from intraguild predation by *S. invicta*. Thus, like the lady beetle systems, invasion by *S. invicta* reduced both pest densities and native predator diversity.

Niche overlap and species displacement

There is abundant evidence that some native species are displaced from some habitats following invasion by IIGP (Holway et al. 2002; Koch 2003; Snyder and Evans 2006; Harmon et al. 2007). However, invaders rarely cause the complete extirpation of natives over their entire former range (DeBach 1966; Reitz and Trumble 2002). Rather, competitive displacement typically occurs in a subset of the available habitats a species can occupy (Reitz and Trumble 2002). For example, Elliott et al. (1996) showed that densities of a few native lady beetle species declined 20- to 30-fold in abundance following invasion by *C. septempunctata* in South Dakota alfalfa, corn, and small grain fields. The species in starkest decline was *C. septempunctata*'s native congener *C. transversoguttata*, a species quite

similar in size and feeding habits to *C. septempunctata*. In contrast, a few native species increased slightly in abundance following *C. septempunctata* invasion, suggesting a degree of competitive release following the displacement of other native species. This pattern suggests that niche overlap among natives and invasives is rarely complete. However, even *C. transversoguttata* has not been extirpated entirely, and is still dominant in other parts of its range (Snyder et al. 2004). Similarly, other native lady beetle species that have been displaced from some habitats persist elsewhere in the landscape (Harmon et al. 2007).

As predicted by theory, there are many examples where niche differences seem related to the persistence of native generalist predators following invasion. In field experiments with the invasive ant *Anoplolepis gracilipes*, and native ants, Sarty et al. (2007) tested recruitment to three types of food bait with varying nutritional value (tuna, jam, and peanut butter). Although *A. gracilipes* dominated tuna and jam baits and excluded most other species at these resources, they did not recruit in high numbers to peanut butter baits, allowing four species of native ants to coexist on this resource. Similarly, Matos and Obrycki (2006) showed that coexistence between the green lacewing *Chrysoperla carnea* and the invasive *H. axyridis* was promoted by the ability of *C. carnea* to feed on prey that did not support *H. axyridis*. Harris et al. (1991) showed that differential foraging patterns promoted coexistence between the invasive German wasp *V. germanica* and a subsequent invader, *Vespula vulgaris*, in New Zealand (Fig. 3a). Although both species were generalists, *V. germanica* commonly foraged for protein resources on the forest floor, while *V. vulgaris* foraged on shrubs and tree saplings. Although these foraging differences promoted coexistence of the two invasive wasps, both species competed aggressively for honeydew resources produced by native scale insects, which allowed the superior interference competitor *V. vulgaris* to displace *V. germanica* in certain habitats. Thus, in all of these cases, species differed in some preferred foods, preventing total niche overlap and allowing coexistence (Fig. 3a).

Spatial niche partitioning can also promote coexistence of native predators with IIGP. Menke and Holway (2006) used field experiments to show that elevated levels of soil moisture increased the

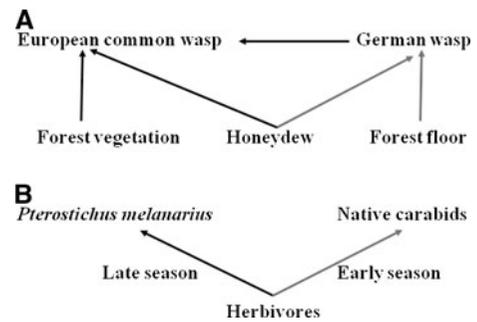


Fig. 3 Impact of niche partitioning between predators on species coexistence. Arrows indicate the direction of energy flow. **a** Two wasp species that have invaded New Zealand, the European common wasp, *Vespula vulgaris*, and the German wasp, *Vespula germanica*, compete for honeydew resources produced by scale insects (Harris et al. 1991). *V. vulgaris* is a superior interference competitor that can kill *V. germanica* individuals competing for honeydew. However, for non-honeydew resources, *V. vulgaris* forages mainly on forest vegetation, while *V. germanica* forages mainly on the forest floor. This spatial niche partitioning allows the two species to coexist. **b** The invasive ground beetle, *Pterostichus melanarius*, and native carabid beetles prey on similar herbivore species in agroecosystems of the northwestern United States and Canada (Niemela et al. 1997; Hatten et al. 2007). However, *P. melanarius* populations are active later in the season than native beetles, which allows these species to coexist through temporal niche partitioning

abundance of *L. humile* and the likelihood that native ants would be displaced. However, *L. humile* did not invade areas with lower levels of soil moisture, allowing survival of native ant species in these habitats. Additionally, *L. humile* colonies withdrew from invaded areas when soil moisture levels were experimentally decreased, allowing native ants to recolonize, demonstrating that coexistence was mediated by spatial heterogeneity in soil moisture.

Species that occupy the same niche at different points in time (temporal niche partitioning) can also coexist (Fig. 3b). Niemela et al. (1997) found that invasion by the ground beetle *Pterostichus melanarius* had no significant effects on six native species of carabid beetles. Using field cage experiments, they showed that *P. melanarius* was active mainly from June to August, whereas the native species were active mainly from April to early June. For this reason the invader never competed simultaneously with the natives for resources. Similarly, Hatten et al. (2007) found that *P. melanarius*, a summer breeder, coexisted with four native species of carabids that were spring breeders in Idaho agricultural systems.

In other cases, species coexist through niche partitioning in both space and time. One example comes from the lady beetle community in New York sweet corn and corn fields (Musser and Shelton 2003). In this system, the native lady beetle *Coleomegilla maculata* has a distinctly different temporal and spatial distribution from the invasive *H. axyridis*. *C. maculata* adults are present earlier in the season than *H. axyridis* adults, and forage lower on plants than *H. axyridis* adults, which forage higher on plants near aphid aggregations. The spatial and temporal separation of these species minimizes both resource competition and intraguild predation, contributing to their coexistence. Similarly, Rathet and Hurd (1983) showed that spatiotemporal niche partitioning allows for the coexistence of three invasive mantid species in Delaware. Two of these invaders, *T. sinensis* and its congener *Tenodera angustipennis*, occupy the same parts of vegetation but hatch at different points of the season. Because prey selection is related to body size, staggered hatch dates could minimize competition for prey throughout development. In turn, both of the *Tenodera* species occupied different parts of vegetation from a third invasive, *Mantis religiosa*, which was also segregated temporally from the two *Tenodera* species. Thus, spatiotemporal separation may have contributed to coexistence of the three mantids.

Environmental variability heightens niche separation

Variability in the environment or other abiotic factors can affect resource and habitat use, and the ability of species to tolerate variability in climate or anthropogenically produced conditions such as insecticide use can alter patterns of niche partitioning (Reitz and Trumble 2002; Menke et al. 2007). As species functional traits are often highly correlated with environmental characteristics (Ribera et al. 2001), increased environmental variability can lead to increased niche partitioning and greater species diversity. In contrast, anthropogenically altered habitats such as agricultural fields often have lower degree of variability and support the fewer species that are adapted to these conditions (Ribera et al. 2001). In such landscapes, dispersal among patchy and frequently disturbed habitats could affect competitive interactions between species (Thies et al.

2003; Tschardt et al. 2005; Rand et al. 2006). Additionally, native predators that diminish resource levels can decrease the probability that propagules of invaders will establish and spread in patchy habitats (Tilman 2004). As invaders, including IIGP, often require repeated introductions to successfully establish in a new environment (Suarez et al. 2005), such interactions are crucial for predicting the distribution, spread, and ecological consequences of invasions.

The bulk of studies on the effects of environmental variability on invasions by IIGP have been conducted with ants. Todd et al. (2008) investigated the role of forestry practices on the invasion success of *S. invicta* and corresponding effects on native predators. They found that the ability of *S. invicta* to invade increased with habitat disturbance and lower environmental variability. As a corollary, salamanders were killed by *S. invicta* in disturbed habitats, but suffered no mortality in heterogeneous (unharvested) plots, where increased vegetative ground cover provided refuges from predation. In a similar study, Bos et al. (2008) showed that *A. gracilipes* did not occur in natural rainforests of Indonesia, but was abundant in managed cacao agroforests. They showed that management practices in agroforests reduced environmental variability, which disrupted the foraging behavior and nesting sites of native ants, resulting in a decrease in native ant species richness. In turn, decreased native ant species richness in the heavily managed agroforests facilitated invasions by *A. gracilipes* by reducing competition for food resources and nesting sites. Sarty et al. (2006) showed that coexistence among native and invasive ant species was a function of both body size and environmental variability. In flat areas without rocks, or in areas with only large pieces of coral rubble (low rugosity), the large *A. gracilipes* was the most effective resource exploiter. However, smaller native ant species were more effective resource exploiters in environments containing small pieces of coral rubble (high rugosity), suggesting that a correlation between resource exploitation in variable environments was mediated by body size, and that differing resource acquisition abilities in variable environments provided a mechanism for coexistence.

However, not all studies on the effects of environmental variability have been conducted with ants. Carmona and Landis (1999) found that carabid beetle diversity was greater in Michigan agricultural fields when habitat strips with high variability were planted

next to commercial fields, and in agricultural areas with cover crops. In both years of the study, the invasive carabid *P. melanarius* was most abundant in refuge strips, and less common in agricultural fields without a cover crop. In contrast, five native carabid species were equally distributed among habitats. Thus, increased environmental variability may have provided refuge from competition for the native species and allowed for coexistence through niche partitioning.

Metapopulation structure can affect the relationship between environmental variability and invasion success (Reitz and Trumble 2002). Inferior competitors can coexist with a superior invader by occupying portions of the habitat that have not been invaded, and native species can persist by dispersing to vacant niches more effectively than invaders (Tilman 1994, 2004; Long et al. 2007). In some cases, displacement of native species may be attributed to competition from an invader, although metapopulation structure and dispersal ability may play a role. King and Tschinkel (2006) found that populations and diversity of native ants did not increase after colonies of invasive *S. invicta* were removed from habitats, suggesting that competition from *S. invicta* did not limit native ant abundance and diversity. Rather, populations of native ants failed to recruit to habitats that had been disturbed and were ultimately displaced from these habitats.

Increased environmental variability is expected to indirectly strengthen herbivore suppression by promoting coexistence among predators and/or increasing predator abundance (e.g., Thies and Tschantke 1999). Increased environmental heterogeneity may promote predator diversity within habitats through niche partitioning, when invasive and native predators exploit different subsets of the available resources (Tylianakis et al. 2008). Further, increased environmental variability can result in increased predator densities, because greater resource diversity in heterogeneous habitats allows generalist predator populations to thrive despite reductions in any single resource (Polis et al. 1997). For example, Gardiner et al. (2009a) showed that landscape diversity was positively associated with the biological control of soybean aphid, which was primarily provided by a guild of lady beetles. Predators were less effective in landscapes dominated by monocultures of corn and soybean, and more effective in areas with significant

acreage of non-crop habitat. In a related study, Gardiner et al. (2009b) showed that the abundance of the most effect aphid predators, *H. axyridis* and *C. septempunctata*, increased in areas with high landscape diversity, resulting in greater aphid suppression as environmental variability increased. Likewise, Landis et al. (2008) showed that increased production of corn in the Midwestern US, which decreased landscape heterogeneity, weakened suppression of the soybean aphid, at an estimated cost of \$58 million per year in biocontrol services lost. Although these studies are observational, and therefore do not reflect a causal link between levels of environmental variability and biocontrol, such variability could affect predator population dynamics and therefore influence the effectiveness of predator guilds in suppressing herbivores. Although the mechanisms are often unclear, increased environmental variability has been associated with increased predator abundance.

Summary of resource competition as a mechanism underlying invasion

Evidence from studies of IIGP support predictions from theory that competitive displacement of native predators can result from IIGP's dominance in resource acquisition. IIGP often are more successful than native species at acquiring shared resources, and can drive prey or other resources below levels needed to support ecologically-similar native species. Additionally, broad diets of some generalist invaders allow them refuges from depletion of particular resource types, further heightening their competitive advantage. In contrast, although invaders often dominate shared resources, native predators can coexist by performing well on resources not shared by the invader, or by exploiting resources in different habitats or at different times in the season. These differences can be accentuated by habitat diversity, which broadens the total available niche space. Thus, the biological simplicity of agricultural monocultures and agriculture-dominated landscapes, along with the frequent disturbance typical of these systems, likely heightens competitive interactions and encourages species displacement. Nonetheless, variation in resource and habitat use likely explains why IIGP rarely entirely extirpate native predators.

Further supporting prediction of theory, when strong resource competition occurs, prey suppression

is nearly always heightened by IIGP because IIGP are more effective predators than native species. Also, when IIGP use a broader range of resources, they are able to maintain high densities even when particular food types are rare. This would maintain more consistently-strong predation pressure on prey. Finally, niche differences with natives lead to a broader total coverage of available prey resources when IIGP are present.

Dominance in interference competition

Theory

Several authors have used models that consider species which compete indirectly for resources and directly via interference competition (Case and Gilpin 1974; Armstrong and McGehee 1980; Kuno 1992; Amarasekare 2002). Interference competition occurs when species have direct, negative effect on one another through such interactions as territoriality, predation, chemical competition, and mating disruption. In predatory insects, and IIGP in particular, such interactions are often strongly asymmetrical, and various outcomes of competition are possible depending on the relative strength and direction of competitive effects through interference and resource-depletion channels (e.g., Lawton and Hassell 1981; Denno et al. 1995; Reitz and Trumble 2002; Snyder and Evans 2006). If one species is superior at resource and interference competition (Fig. 4a), competitive displacement of the inferior competitor is expected, with displacement likely to occur more rapidly than through resource competition alone (Case and Gilpin 1974; Kuno 1992; Amarasekare 2002). However, if the superior resource competitor is inferior at interference competition (Fig. 4b), several outcomes are possible (Case and Gilpin 1974; Kuno 1992; Amarasekare 2002). First, the superior resource competitor can displace the superior interference competitor by dominating the shared resource. Second, the superior interference competitor can displace the superior resource competitor through a priority effect (when the superior interference competitor has a high initial abundance), or through benefits gained from interference competition (e.g., acquiring nutrients via intraguild predation). Finally, coexistence can occur through contrasting selection

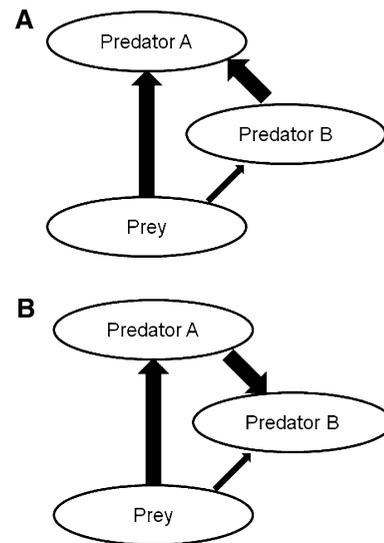


Fig. 4 Interactions between two species that engage in resource and interference competition. The *arrows* indicate the direction of energy flow, with the *width* of the *arrows* demonstrating the relative strength of the effect. **a** One species is superior at resource acquisition and interference competition. The predicted outcome is that dominant predator drives resource levels below thresholds that support the inferior predator, and limits its population growth through interference, leading to competitive displacement. For example, Holway (1999) showed that populations of the invasive Argentine ant were superior at both interference and resource competition compared to native ants. This competitive superiority led to competitive displacement of native ant species in California. **b** The superior resource exploiter is inferior at interference. Multiple outcomes are possible, including competitive displacement of either consumer or coexistence. For example, Morrison (2000) showed that the invasive red-imported fire ant was a superior interference competitor compared to native ants, but was an inferior resource competitor. These tradeoffs allow for coexistence of these species

pressures, where one species is negatively affected by its relative inability to acquire resources but benefits from interference competition (Case and Gilpin 1974; Kuno 1992; Amarasekare 2002). Thus, the combined effects of resource and interference competition among species are likely to determine the overall effects of competitive interactions.

Among IIGP, intraguild predation is a common form of interference competition (Polis et al. 1989; Rosenheim et al. 1995). When intraguild predation occurs among two species, the intraguild prey must be superior at exploiting resources in order to coexist with the intraguild predator (Polis and Holt 1992). In contrast, if the intraguild predator is superior at

exploiting resources, competitive displacement of the intraguild prey is expected (Polis and Holt 1992). If intraguild predators feed on particularly effective consumers, prey (herbivore) densities could increase (Ives et al. 2005). However, intraguild predation can have no effect on resource densities when surviving species consume an increasing portion of the resource pool, or when intraguild predators are particularly effective consumers (Ives et al. 2005).

Evidence that IIGP are superior interference competitors

IIGP often eat native predators, with strong asymmetry in these interactions such that invasives are more likely to eat natives than vice versa. Intraguild predation has been associated with displacement of native species by invasive ants (Holway et al. 2002), carabids (Dinter 1998), lady beetles (e.g., Michaud 2002; Snyder et al. 2004; Yasuda et al. 2004), mantids (Snyder and Hurd 1995), and wasps (Toft and Rees 1998). In some cases, these interactions may be mediated by chemicals that make invasive species unpalatable to natives (Hemptinne et al. 2000; Rieder et al. 2008). However, intraguild predation is most often documented in simple laboratory arenas, and the magnitude of its impact in the field is not always clear (Snyder 2009). Recent reviews suggest that intraguild predation rarely is sufficiently strong in the field to disrupt herbivore suppression (e.g., Rosenheim and Harmon 2006; Vance-Chalcraft et al. 2007), although there are some exceptions from particular systems (e.g., Finke and Denno 2004, 2005; Rosenheim et al. 2004). Thus, it is important to note that the occurrence of intraguild predation does not necessarily mean that herbivore suppression will be irreparably harmed (Ives et al. 2005).

However, it is not necessary for predators to kill one another for interference competition to occur. Often, negative predator–predator interactions are transmitted through behavioral, rather than consumptive, channels (Schmitz 2008). Wilder and Rypstra (2004) showed that chemical cues left by the invasive mantid *T. sinensis* reduced the activity and feeding rate of wolf spiders, resulting in spiders that gained less mass. The authors inferred that chemical cues left by *T. sinensis* were similar to cues left by spider predators, which caused the spider to go into a defensive mode. Moran et al. (1996) showed that

wolf spiders emigrated significantly more often from plots containing *T. sinensis* than plots without mantids, presumably to escape predation or because prey density was lower when mantids were added. These indirect interference mechanisms allowed *T. sinensis* to competitively dominate shared resources, even though intraguild predation may not often have been successfully consummated. Likewise, IIGP can dominate native species when the natives do not recognize threats from invaders and are less aggressive towards them (Le Breton et al. 2007; Dejean et al. 2008).

Tradeoffs between resource acquisition and interference ability can promote coexistence of species (Holway 1999). For example, Morrison (2000) showed that colonies of *S. invicta* were more successful at interference competition than two native ant species, but the native ants were more successful at exploiting resources, allowing for coexistence of the species. However, IIGP often break this tradeoff, and displace native predators through simultaneously increased resource acquisition and direct interference (Snyder and Evans 2006; Fig. 4b). For example, Holway (1999) found that colonies of *L. humile* were superior at exploiting shared resources compared to several native ant species, and *L. humile* colonies were also dominant interference competitors and killed native ants (Fig. 4a). Similarly, Michaud (2002) found that the invasive *H. axyridis* was an effective intraguild predator of the native lady beetle *Cycloneda sanguine* in Florida citrus fields, and was a more voracious consumer compared to the native species; both factors presumably contributed to displacement of the native lady beetle.

There is reason to believe that intense resource competition, and thus declining resource availability, will exacerbate the intensity of intraguild predation (and perhaps other forms of predator interference). Noia et al. (2008) found that decreased aphid densities increased rates of intraguild predation between the invasive lady beetle *H. axyridis* and the native *Coccinella undecimpunctata*. Currie et al. (1996) found that interference competition between the invasive ground beetle *P. melanarius* and the native *Pterostichus adstrictus* increased with declining food resources, while Yasuda et al. (2004) found that food scarcity increased the likelihood that two invasive lady beetle species would prey upon two native lady beetle species. In these cases, decreased

prey availability increased the magnitude of interference competition, and presumably made coexistence among species less likely. For this reason, resource and interference competition present something of a “chicken and egg” problem, with the two factors feeding into one another and thus not entirely independent (Fig. 2; Snyder 2009).

Interference competition between IIGP and natives could weaken biological control if the natives are very effective predators (Ives et al. 2005). Cardinale et al. (2006a) manipulated predator diversity among a guild of lady beetles with two invasive species, *C. septempunctata* and *H. axyridis*, and the native *C. maculata*, attacking pea aphids, and found that aphid suppression weakened with increased diversity. In this case, *C. septempunctata* may have altered the foraging activity of *C. maculata*, which reduced the native’s ability to capture aphid prey. In contrast, interference competition can have no effect on biological control when a superior interference competitor is an effective resource exploiter. Costamagna et al. (2007) investigated a guild of multiple predators including *H. axyridis* and a parasitoid wasp attacking soybean aphids and found that the activity of the parasitoid was negatively affected by the predators. Yet, *H. axyridis* was such an effective predator in this system, that soybean aphid densities were reduced whenever it was present. Similarly, Gardiner and Landis (2007) showed that the exotic *H. axyridis* was an effective intraguild predator of the native predators *C. carnea* and *Aphidoletes aphidimyza*, but again the exceptional voracity of *H. axyridis* as a soybean aphid predator more than compensated for any negative effects due to intraguild predation.

Summary of interference competition

As predicted by theory, evidence from studies of IIGP suggests that asymmetrical interference competition between invasive and native predators can drive competitive displacement. Interference competition occurs when species directly compete through mechanisms such as intraguild predation, or when one species causes another to disperse away from available resources. Such interactions are often strongly asymmetrical in favor of IIGP. Tradeoffs between resource acquisition and interference competition can promote coexistence among IIGP and native predators. However, IIGP often break this tradeoff and

dominate through both superior resource acquisition and interference abilities, which can lead to the rapid displacement of native predators. Strong interference competition can weaken herbivore suppression when IIGP interfere with prey capture by particularly effective native predators. However, interference competition can have no effect on biological control when species that are superior at interference are also most effective at capturing prey, which is often the case with IIGP.

Other mechanisms

Reduced intraspecific competition

Invasive ants often form supercolonies with reduced levels of intraspecific competition, allowing these colonies to compete more effectively for resources and via interference competition (Holway et al. 2002). Holway and Suarez (2004) found that colonies of the native ant *Forelius mccoocki* produced fewer eggs and workers, and foraged less actively, when reared along with two colonies of *L. humile* that did not exhibit intraspecific aggression than with two colonies of *L. humile* that were aggressive to each other. Additionally, reduced intraspecific aggression increased the ability of *L. humile* colonies to exploit food baits in the presence of *F. mccoocki*. Holway (1999) showed that individuals of *L. humile* often did not outcompete individual native ants, but supercolonies of *L. humile* outcompeted native ant colonies. This suggests that it was the ability to form supercolonies that increased the competitive ability of *L. humile*, rather than superior competitive abilities of individual ants.

Escape from natural enemies

IIGP may competitively dominate native species if they are relatively unaffected by natural enemies. Colonies of *S. invicta* displace several native ant species in part because *S. invicta* is not attacked by phorid fly parasitoids that attack native ants (Morrison 1999). Colonies of the invasive wasp *Polistes dominulus* respond more rapidly to predation by raccoons than native colonies of *Polistes fuscatus* (Gamboa et al. 2004). In addition, *P. dominulus* is not parasitized by Strepsipteran parasites that cause

significant mortality to *P. fuscatus* colonies (Gamboa et al. 2004). Similarly, the invasive lady beetle *H. axyridis* is not affected by the fungal pathogen *Beauveria bassiana*, a species that commonly infects the native lady beetle *Olla v-nigrum* (Cottrell and Shapiro-Ilan 2003). Such interactions could increase the magnitude of competitive dominance for IIGP over native species, leading to displacement.

Biodiversity manipulations provide insight on the ecological roles of IIGP

Recent years have seen growing interest in the relationship between species richness and the functioning of ecosystems. This more recent work draws on the long history of multipredator effects studies in the predator–prey literature (reviewed by Sih et al. 1998), but expands on this work by considering the individual and combined effects of >2 predator species at a time (Straub et al. 2008). This emerging field has been intensely experimental, with researchers manipulating the number of species present and measuring resulting effects on resource use and other community attributes (Hooper et al. 2005). As a general rule across studies to date, resource use increases with more consumer species (Cardinale et al. 2006b). This pattern is generally attributed to niche-complementarity among constituent species, although this mechanism can be difficult to convincingly demonstrate (Finke and Snyder 2008). Studies with predators make up a relatively small fraction of this literature (Cardinale et al. 2006b), but the studies that exist suggest that increasing predator biodiversity also generally improves herbivore suppression (Ives et al. 2005; Cardinale et al. 2006b). Fortuitously, several experimental manipulations of predator biodiversity include IIGP as community members, shedding insight into the contribution of these predators to community-wide resource exploitation.

Snyder and Ives (2001, 2003) examined species richness effects within the diverse community of predators attacking pea aphids in Wisconsin alfalfa fields. The invasive ground beetle *P. melanarius* fed voraciously on pea aphids dumped on the ground after alfalfa harvest, but was also an effective predator of pupae of the specialist aphid parasitoid *Aphidius ervi*. As alfalfa re-grew, decreased predation by *A. ervi* led to *P. melanarius* having a net negative

impact on aphid suppression (Snyder and Ives 2001). However, the disruptive effects of *P. melanarius* were not typical of the whole community. When experiments included the full diversity of generalist predator species, in particular the invasive lady beetles *C. septempunctata* and *H. axyridis*, the entire predator guild together acted to strengthen aphid suppression (Snyder and Ives 2003). This occurred because the lady beetles were particularly voracious predators of pea aphids in the foliage, but generally avoided eating parasitoid pupae (Snyder and Ives 2003). Thus, the lady beetles counteracted any negative effects of *P. melanarius*. Likewise, the invasive praying mantis *T. sinensis* disrupts feeding by native wolf spiders, but due to the mantid's large size and voracity, *T. sinensis* nonetheless strengthens herbivore suppression to the benefit of plant growth (Moran et al. 1996). Similar interactions between the invasive lady beetle *H. axyridis* and native predators and parasitoids of soybean aphid have also been reported (Costamagna et al. 2007). In each case, IIGP filled unique functional roles as the most voracious predators, with their positive direct effects on prey outweighing any negative indirect effects due to intraguild predation (at least, when within naturally-diverse communities).

There also is evidence that the greater feeding breadth of some IIGP leads to a unique contribution to prey suppression. Cardinale et al. (2003) constructed predator communities including one versus three predator species attacking aphids (pea aphid and cowpea aphid) on alfalfa plants. They drew from a species pool including the invasive lady beetle *H. axyridis*, the invasive aphid parasitoid *A. ervi*, and the native predatory bug *Nabis* sp. They found that aphid densities were lowest, and alfalfa biomass was highest, when three predator species were present. This occurred because *H. axyridis* was the only effective predator of cowpea aphid, freeing the parasitoid to concentrate its attacks on pea aphids. Thus, effective suppression of all aphids occurred only when *H. axyridis* and *A. ervi* were together. In this case, *H. axyridis* played a functionally unique role as the only predator that effectively attacked both aphid species, such that its relatively broad diet breadth was its key contribution to the community of biological control agents.

A similar case involves *P. melanarius* predators in radish fields in Washington. Here, the target pests

were fly maggots (*Delia* spp.) that attack plant roots, and the community included a diverse assemblage of native ground-active predatory beetles (Prasad and Snyder 2004, 2006a, b). *P. melanarius* was much larger than the native species, and disrupted the smaller beetles' control of maggot pests through intraguild predation and intimidation (Prasad and Snyder 2004, 2006a, b). However, aphids serve as a preferred prey for *P. melanarius*, and aphids nearly always co-occur with root maggots in the field. When aphids were included in experimental arenas *P. melanarius* hunted more vigorously, and incidental predation of root maggots more than compensated for any disruptive effects due to interference competition with the smaller native beetles (Prasad and Snyder 2006b). Thus, both its relative voracity, and inclusion of aphid prey in its broad diet, compensated for this species' negative impacts as an intraguild predator. Also notable is that, once again, disruptive effects of intraguild predation that dominated interactions among simple subsets of species, appeared unimportant when communities approached a more natural level of predator and prey biodiversity.

Biodiversity studies also provide evidence that spatial niche partitioning among predators will strengthen herbivore suppression. Losey and Denno (1998) demonstrated that the combined impacts of the invasive lady beetle *C. septempunctata* and the native ground beetle *Harpalus pensylvanicus* exceeded that of either predator species alone. This synergistic effect resulted from spatial separation of the two predators, with the lady beetles foraging in the foliage and the ground beetles on the soil surface. Lady beetle foraging caused aphids to drop to the ground as a predator-avoidance strategy, exposing them to predation by ground beetles. Snyder and colleagues (Snyder et al. 2006, 2008; Straub and Snyder 2008) report a similar example of spatial niche partitioning from the community of predators attacking green peach and cabbage aphids on collard plants. The invasive lady beetle *C. septempunctata* is an important community member that is capable of consuming more aphids per capita than any native species (Straub and Snyder 2006). However, the slippery surface wax on collard plants limits *C. septempunctata* foraging to leaf edges and stems (the beetles need to grasp edges to maintain traction on the plant). For this reason, aphid suppression was most effective when the lady beetle was paired with

predatory bugs and parasitoids that could access aphids in the center of leaves. Thus, only diverse communities pair the unique voracity of *C. septempunctata* with the ability to also attack aphids in spatial refuges that was provided by other predator species with better adherence abilities.

On the whole, biodiversity studies that include IIGP support the role of these species as unusually strong resource competitors. In many cases, resource consumption by the invasives was greater than any native generalist predator. Despite these strong individual effects, IIGP often filled unique feeding or spatial niches and complemented native species. This niche partitioning in turn leads to a broader-based attack on the entire prey population, and thus stronger herbivore suppression. Yet, these experiments were conducted on too small a spatiotemporal scale to yield much insight into species coexistence. Still, the fact that overall resource use generally is greatest when predator communities are diverse indicates that a greater breadth of resources is available to multiple rather than single species.

Directions for future research

Although significant progress has been made on the study of mechanisms that affect invasive success by IIGP and their community level impacts, many factors remain poorly understood. Considering the widespread impacts of IIGP, it is surprising that relatively little is known about the mechanisms underlying these invasions. In addition to continued studies on the effects of how niche partitioning mediates competition, we briefly review several promising avenues for future research.

Landscape factors

Anthropogenic habitat modification has pronounced effects on the structure and function of insect communities (Thies et al. 2003; Tscharrntke et al. 2007; Tylianakis et al. 2007). However, only recently have scientists begun to consider the effects of agricultural intensification on biodiversity and species abundance from a landscape perspective (Peterson et al. 1998; Tscharrntke et al. 2005; Bianchi et al. 2006). The effects of landscape structure can differ

greatly depending upon the spatial scale of analysis, and results obtained from field, laboratory, and greenhouse experiments do not always scale up in broader landscapes (Peterson et al. 1998; Tscharrntke et al. 2005; Clough et al. 2007). For example, competitive dominance among species in experimental microcosms may overestimate the likelihood of displacement if species differ in their spatial and temporal use of habitats or resources in a broader landscape (Srivastava and Vellend 2005). Additionally, the ability of species to disperse between habitats is often difficult to quantify experimentally, and the significance of dispersal among habitats may require a landscape-level approach (Thies et al. 2003; Tscharrntke et al. 2005; Rand et al. 2006). Thus, there is a clear need to examine mechanisms of competitive displacement or coexistence among IIGP and native predators not only in small-scale experiments but also at the scale of entire landscapes.

Recent advances in the use of geographical information systems (GIS), remote sensing, and spatial statistics are revolutionizing the study of landscapes and enabling researchers to test novel hypotheses from a landscape perspective (Carrière et al. 2004, 2006). Such analyses can be used to identify and quantify areas of natural and human-managed habitats on a broad spatial scale. These data, combined with field observations of arthropod abundance, can allow researchers to determine the role of habitat variability on arthropod density, the ability of arthropods to disperse between habitats, and the spatial scale of these effects (Carrière et al. 2004, 2006). However, such analyses have primarily dealt with the effects of landscape structure on agricultural pests, and only recently have similar tools been applied to study communities of invasive and native IIGP (Gardiner et al. 2009a, b). Gardiner et al. (2009a) demonstrated that the abundance of IIGP depends strongly on habitat structure, as most species were more abundant in grassland and forested habitats than in agricultural landscapes. Further, Gardiner et al. (2009b) used spatial analyses to show that grasslands with low diversity and limited forested habitat serve as a refuge from competition for native coccinellid beetles from invasive lady beetles. However, further research is needed to continue exploring the interactions between landscape structure, competition, niche partitioning, dispersal, and resource availability on competitive

displacement or coexistence between IIGP and native species at various spatial scales.

Comparative studies in native and invaded ecosystems

A growing body of work, primarily with invasive ants, has used comparative methods to investigate invasive species in their native and introduced ranges. Le Breton et al. (2007) conducted field competition experiments between *W. auropunctata* and species of the genus *Pheidole* in both French Guiana (where both are native) and in New Caledonia (where *Pheidole* is native and *W. auropunctata* is invasive). In the native range of both species, the experimental introduction of *W. auropunctata* at food resources dominated by *Pheidole* induced the recruitment of major workers of the *Pheidole* species, which were effective competitors. In contrast, *Pheidole* ants in New Caledonia lacked this behavioral response, and were therefore negatively affected by competition from *W. auropunctata*. In a similar set of field experiments, Dejean et al. (2008) showed that populations of the invasive ant *P. megacephala* raided nests of other ants in Cameroon (its native range) and Mexico (its introduced range). Eleven out of 12 species strongly resisted nest-raiding populations of *P. megacephala* in the native range, while only three of 11 species resisted nest raiding in the invasive range, demonstrating a similar lack of behavioral response of species in the invaded range that contributed to displacement.

Another factor associated with ant invasions that has been elucidated through comparative studies is mechanisms leading to reduced intraspecific aggression. Tsutsui et al. (2000) showed that a population bottleneck reduced the genetic variation of introduced *L. humile* populations in North America, and this was associated with reduced intraspecific aggression, while native populations from South America with greater genetic diversity exhibited pronounced intraspecific aggression. Errard et al. (2005) showed that reduced intraspecific aggression in invasive colonies of *W. auropunctata* was associated with high uniformity in cuticular hydrocarbons used for colony recognition, while greater variability in hydrocarbons among native colonies was associated with increased intraspecific aggression. Such studies can shed light on factors that limit the spread of IIGP

in their native range, and mechanisms that promote their negative impacts in invaded ecosystems.

Combining theory and empirical work

Research that links theory with data is critically needed to identify factors that promote the invasive spread of nonnative species and predict their impact on invaded communities (Marco et al. 2002; Cannas et al. 2003). However, despite numerous theoretical and experimental studies focused on invasions by IIGP, there remains a paucity of studies that link theory with data. Models that incorporate data from experiments can be used to examine the relative effects of multiple factors on competitive displacement or coexistence between IIGP and native species. Such investigations could be particularly effective in systems where the effects of multiple factors have been quantified in isolation, like many of the focal species reviewed here. Linking models with data could provide unique insight into the quantitative effects of multiple factors on displacement or coexistence, which would be difficult to test experimentally (Suarez et al. 2008).

Spatially-explicit models that incorporate environmental heterogeneity and stochastic variation in ecological processes could also be valuable for predicting the distribution, spread, and impacts of IIGP (Marco et al. 2002; Cannas et al. 2003; Guisan and Thuiller 2005). In particular, models are needed that incorporate both landscape variability and biotic interactions between species, as both factors can significantly influence the spread of invasive species. However, such models have rarely been applied to invasions by insects or other animals (Guisan and Thuiller 2005) and never to invasions by IIGP. In many systems with IIGP, data exist on the mechanisms of competitive displacement or coexistence with native species. Such data could be used to parameterize models that predict the spread of invaders and their community-wide impacts. Models could be fit to patterns of invasions that have already occurred in order to predict the future spread and impacts of invaders. Further, the increasing availability of precise spatial data, particularly in agricultural ecosystems (Carrière et al. 2004, 2006; Gardiner et al. 2009a, b), could be used to predict invasion dynamics over vast landscapes.

Conclusions

A myriad of factors affect competitive displacement or coexistence among IIGP and ecologically similar native predators, including resource competition, niche partitioning, and negative predator–predator interactions. Displacement can be driven by indirect competition for shared resources or through direct interference mechanisms. Coexistence is promoted through contrasting selection pressures, niche partitioning, complementary use of shared resources, and spatially heterogeneous environments. These factors do not operate in isolation, and therefore it is important to use a community level approach for studying the effects of IIGP on their native counterparts. In general, coexistence among IIGP and native predators increases biological control, because in most cases IIGP are particularly effective at exploiting prey resources. Thus, displacement of native predators generally has no harmful effect on herbivore suppression. Intraguild predation and other forms of interference competition are common, but do not often appear to strongly disrupt herbivore suppression. Thus, the contribution of interference competition to invasion success is unclear. Various theoretical and empirical approaches exist for testing hypothesis of mechanisms that promote displacement or coexistence, and corresponding impact on herbivore suppression, at various scales of interest. Such approaches will advance our knowledge of the effects of IIGP in invaded ecosystems and the mechanisms underlying these effects, and will increase our ability to manage IIGP and predict their impacts in agricultural ecosystems.

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