THE CAUSES AND CONSEQUENCES OF ANT INVASIONS

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■ **Abstract** Invasions by non-native ants are an ecologically destructive phenomenon affecting both continental and island ecosystems throughout the world. Invasive ants often become highly abundant in their introduced range and can outnumber native ants. These numerical disparities underlie the competitive asymmetry between invasive ants and native ants and result from a complex interplay of behavioral, ecological, and genetic factors. Reductions in the diversity and abundance of native ants resulting from ant invasions give rise to a variety of direct and indirect effects on non-ant taxa. Invasive ants compete with and prey upon a diversity of other organisms, including some vertebrates, and may enter into or disrupt mutualistic interactions with numerous plants and other insects. Experimental studies and research focused on the native range ecology of invasive ants will be especially valuable contributions to this field of study.

INTRODUCTION

Ants play a diversity of roles in terrestrial ecosystems. Ants act as predators, scavengers, herbivores, detritivores, and granivores (Hölldobler & Wilson 1990) and participate in an astonishing array of associations with plants and other insects (Beattie 1985, Hölldobler & Wilson 1990, Huxley & Cutler 1991, Jolivet 1996). Ants, in turn, are preyed upon by a variety of specialist predators, including reptiles (Pianka & Parker 1975), mammals (Redford 1987), spiders (Porter & Eastmond 1982), and insects (Gotelli 1996) and are host to both dipteran (Feener & Brown

1997) and hymenopteran parasitoids (Heraty 1994). Ants also serve as important agents of soil turnover, nutrient redistribution, and small-scale disturbance (Hölldobler & Wilson 1990, Folgarait 1998, MacMahon et al. 2000). For these reasons, and because they can be sampled and identified with relative ease, ants figure prominently in ecological studies and have become a key indicator group in studies of diversity and ecosystem function (Agosti et al. 2000). The widespread success of ants stems in large part from their elaborate social behavior, which is itself a tremendously rich source of information for studies of kin selection, reproductive skew, levels of selection, foraging behavior, and self-organization (Wilson 1971, Hölldobler & Wilson 1990, Keller 1993, Bourke & Franks 1995, Crozier & Pamilo 1996).

Invasive ants form a small and somewhat distinct subset of the at least 150 species of ants introduced into new environments by humans (McGlynn 1999a). A majority of introduced ants remain confined to human-modified habitats and some of these species are often referred to as tramp ants because of their reliance on human-mediated dispersal and close association with humans generally (Hölldobler & Wilson 1990, Passera 1994). Although also largely dependent on humans to reach new environments, invasive ants differ from most other introduced ants in several key respects. Invasive ants penetrate natural ecosystems where they often reduce native ant diversity and affect other organisms both directly and indirectly. A minor caveat regarding this definition is that species invading oceanic islands with few or no native ants may exhibit patterns of invasion different from those observed in regions with indigenous ants. In Hawaii, for example, species such as *Hypoponera opaciceps* and *Solenopsis papuana* have spread into undisturbed forest (Reimer 1994), and their occurrence in natural environments on this archipelago may be due in part to the lack of native ants there (Zimmerman 1970, Cole et al. 1992, Reimer 1994).

In this review, we focus on (*a*) the causes underlying the ecological success of invasive ants (especially their interactions with native ants), and (*b*) the direct and indirect effects that occur following invasion. This perspective differs from previous reviews on introduced ants, most of which are limited to *Solenopsis invicta* and have primarily addressed urban and agricultural impacts (Vinson 1986, 1997, Vander Meer et al. 1990a, Williams 1994, Taber 2000). Here, in contrast, we highlight studies conducted in more natural ecosystems. Given their broad and steadily increasing geographical range, high local abundance, and potential to disrupt ecosystems, invasive ants are an important conservation concern. This problem is particularly worrisome given that, once established, invasive ants have proven difficult to control and virtually impossible to eradicate. Obtaining a better understanding of the causes and consequences of ant invasions remains crucial to achieving the ultimate goal of reducing problems associated with these invaders and preventing the introduction of other species that possess similar characteristics. We also submit, as have others (Ross & Keller 1995, Tschinkel 1998, Chapman & Bourke 2001), that these introductions present unique opportunities for research in ecology, behavior, and evolution.

INVASIVE ANTS AND THEIR GENERAL CHARACTERISTICS

Table 1 lists characteristics of six of the most widespread, abundant, and damaging invasive ants. A great disparity exists with respect to how much is known about each of these species. For example, the red imported fire ant (*S. invicta*) ranks as one of the most well studied social insects (Ross & Keller 1995, Tschinkel 1998), whereas *Anoplolepis gracilipes* remains poorly studied by comparison, so much so that its native range is not even known. As an inevitable result of this difference, we devote more attention to the relatively well-known *S. invicta* and the Argentine ant (*Linepithema humile*) than to other species but caution against drawing the conclusion that other invasive ants resemble *L. humile* and *S. invicta* or pose less

TABLE 1   Characteristics of the six most widespread, abundant, and damaging invasive ants

| Species | Subfamily[a] | Geographical Range[b] | | Poly-morphic workers | Colony Structure[c] | | Diet[d] |
		Native	Introduced		Native Range	Introduced Range	
Anoplolepis gracilipes Long-legged ant, crazy ant	F	AF? (1), AS? (2)	AF, AS, AU, CAR, IO, PO (3)	N	?	U (4,5)	OM (4,5)
Linepithema humile Argentine ant	D	SA (6,7)	AF, AO, AS, AU, ME, NA, PO, SA (6)	N	M-V (8)	U (8)	OM (9–11)
Pheidole megacephala Big-headed ant	M	AF (1)	AF, AU, NA, CAR, IO, ME, PO, SA (3)	Y	?	U (5,12)	OM, GR (5,12)
Solenopsis invicta Red imported fire ant	M	SA (13)	CAR, NA (14), AU (15), NZ (16)	Y	V (17)	V (17,18)	OM (19)
Solenopsis geminata Tropical fire ant	M	CA, NA, SA (20)[e]	AF, AS, AU, PO, CAR (?), IO (21)	Y	V (22)	V (?)	OM, GR (19,23)
Wasmannia auropunctata Little fire ant	M	CA, SA (3)	AF, CAR, PO, SA, NA (3)	N	?	U (24)	OM (24)

[a]D = Dolichoderinae, F = Formicinae, M = Myrmicinae.

[b]AF = Africa (subsaharan), AO = Atlantic Ocean (islands), AS = Asia, AU = Australia, CA = Central America, CAR = Caribbean, IO = Indian Ocean (islands), ME = Mediterranean, NA = North America, PO = Pacific Ocean (islands), SA = South America.

[c]M = Multicolonial, U = Unicolonial, V = Variable (see text).

[d]OM = omnivorous, GR = granivorous.

[e]The native range of *S. geminata* is disputed, in part because the species is continuously distributed from the SE United States to northern South America. Some of these populations (including those in the Caribbean) may be the result of human introductions. See Ross et al. 1987 for more information.

1. Wilson & Taylor 1967; 2. Wheeler 1910; 3. McGlynn 1999a; 4. Haines & Haines 1978a; 5. Greenslade 1972; 6. Suarez et al. 2001; 7. Tsutsui et al. 2001; 8. Tsutsui et al. 2000; 9. Newell & Barber 1913; 10. Markin 1970a; 11. Human et al. 1998; 12. Hoffmann 1998; 13. Ross & Trager 1990; 14. Williams et al. 2001; 15. http://www.dpi.qld.gov.au/fireants/; 16. http://www.maf.govt.nz/biosecurity/pests-diseases/animals/fire-ants/; 17. Ross & Keller 1995; 18. Tschinkel 1998; 19. Tennant & Porter 1991; 20. Ross et al. 1987; 21. Taber 2000; 22. MacKay et al. 1990; 23. Torres 1984; 24. Clark et al. 1982.

serious threats. Our focus on the species listed in Table 1 is not meant to dismiss the potential importance of other, less well known or more locally distributed ants; some of these may emerge as problematic invaders in the future. In this section, we provide an overview of the general characteristics of invasive ants; we return to many of these same topics later in our review.

Invasive ants originate in both the New and Old Worlds but now occur in many areas outside their original ranges (Table 1). For all species, the climate of the introduced range approximately matches that of the native range. *L. humile*, for example, is native to sub-tropical and mild-temperate portions of Argentina and surrounding regions and is not known to invade tropical and cold-temperate regions but is widespread in areas with mild-temperate climates (e.g., Mediterranean-type ecosystems) (Suarez et al. 2001). *S. invicta*, also from central South America, likewise prevails as an invader primarily in areas of the southeastern United States with mild-temperate or subtropical climates (Tschinkel 1983, Korzukhin et al. 2001). The remaining invasive ants are from the tropics or subtropics and have primarily invaded regions with similar climates. In Hawaii, where several invasive ants now occur, tropical species (e.g., *Pheidole megacephala* and *A. gracilipes*) occur at low to mid elevations, while *L. humile* occurs at intermediate to high elevations (Fluker & Beardsley 1970, Reimer 1994). Cold-temperate climates appear unsuitable for the invasive ants listed in Table 1; in areas with such climates these ants occur only around human habitation (Ulloa-Chacon & Cherix 1990, Taber 2000, Suarez et al. 2001).

Invasive ants exhibit both phylogenetic and morphological diversity (Table 1). Although both the Ponerinae and Pseudomyrmicinae contain widespread tramps (McGlynn 1999a), the invasive ants listed in Table 1 derive from the three most species-rich subfamilies of ants: Dolichoderinae, Formicinae, and Myrmicinae. Although *Solenopsis*, *Wasmannia*, and *Pheidole* are all Myrmicines, these genera are placed in different tribes (Brown 2001). The fire ants, however, include three invasive species, *S. invicta*, *S. richteri*, and the widely distributed *S. geminata*. Compared to ants as a whole, invasive ants are small to medium-sized; workers range in length from 1–2 mm (*Wasmannia auropunctata*) to >5 mm (*A. gracilipes*). Across species, invasive ants also vary in the extent of physical polymorphism among workers, ranging from monomorphism (*L. humile*, *W. auropunctata*, *A. gracilipes*) to pronounced dimorphism (*P. megacephala*) and polymorphism (*Solenopsis*) (Table 1). Although McGlynn (1999b) argued that introduced ants are smaller than congeners that tend not to be introduced, he excluded *A. gracilipes* (monomorphic but with polymorphic congeners), *P. megacephala*, *S. invicta*, and *S. geminata* from his analysis because of caste polymorphism. It is unclear whether these ants are smaller than their non-invasive congeners.

A striking feature shared by many invasive ants is the tendency for introduced populations to be unicolonial, that is, to form expansive and polygynous (multiple-queened) supercolonies that lack distinct behavioral boundaries among physically separate nests. Unicoloniality appears to be over-represented among invasive ants (Table 1) given that only a tiny minority of ant species exhibits this form of colony

structure. Hölldobler & Wilson (1977) suggested that unicoloniality allows species such as *L. humile*, *W. auropunctata*, and *P. megacephala* to attain high local abundances and consequently to dominate entire habitats. Like these species, introduced populations of *A. gracilipes* maintain populous supercolonies within which intraspecific aggression is largely absent (Haines & Haines 1978a). The situation for fire ants, however, is more complex. In North America, *S. invicta* colonies now occur in both monogyne and polygyne forms (Ross & Keller 1995, Tschinkel 1998), although it should be noted that the monogyne form appears responsible for the initial and rapid invasion of most of the southeastern United States. Monogyne colonies defend territories against neighboring conspecifics (Tschinkel et al. 1995, Adams 1998), whereas polygyne colonies exhibit reduced intraspecific aggression (Morel et al. 1990, Vander Meer et al. 1990b) and maintain high densities of interconnected nests (Bhatkar & Vinson 1987, Porter et al. 1988, Porter & Savignano 1990, Greenberg et al. 1992, Macom & Porter 1996). *Solenopsis geminata* also occurs in both monogynous and polygynous forms (Banks et al. 1973, Adams et al. 1976, MacKay et al. 1990, Williams & Whelan 1991). Although little is published concerning the extent to which polygynous *S. geminata* defends territories intraspecifically, like polygyne *S. invicta*, polygynous *S. geminata* can reach high densities (MacKay et al. 1990, Way et al. 1998).

Another characteristic shared by invasive ants is omnivory. Like many aboveground foraging ants (Hölldobler & Wilson 1990), invasive ants opportunistically scavenge dead animals, prey upon small invertebrates, and harvest carbohydrate-rich plant and insect exudates. Differences exist, of course, in the proportional representation of different food items in the diets of each species. *S. geminata* (Tennant & Porter 1991) and perhaps *P. megacephala* (Hoffmann 1998), for example, commonly include a high proportion of seeds in their diets. *S. geminata*, *S. invicta*, and *W. auropunctata* all possess a venomous sting that may give these species a greater ability to subdue vertebrate and large invertebrate prey. In Argentina, *L. humile* is commonly referred to as the sugar ant, a fitting name given its strong preference for sweet substances (Newell & Barber 1913). Because invasive ants feed extensively on liquid food (Markin 1970a, Tennant & Porter 1991, Human et al. 1998), it is often difficult to obtain an understanding of the composition and seasonal variability of the diets of invasive ants and how these diets might differ from those of native ants.

Other introduced species not listed in Table 1 also possess attributes of invasive ants, but are either poorly studied or currently exhibit localized distributions. Some of these species may become troublesome invaders. For example, Boomsma et al. (1990) and Van Loon et al. (1990) describe the species *Lasius neglectus* from urban areas of central Europe (see also Seifert 2000). *L. neglectus* resembles other invasive ants in that it forms populous, unicolonial supercolonies and appears to outcompete other ants, at least in urban environments. The black imported fire ant (*Solenopsis richteri*) was introduced into the southeastern United States from Argentina several decades prior to the introduction of its more notorious congener, *S. invicta*, but is now confined to only a small portion of northern Alabama and

Mississippi, where it hybridizes with *S. invicta* (Shoemaker et al. 1996). The impact of *Solenopsis richteri* on ants and other organisms native to the southeastern United States is poorly known. Native to Brazil, *Paratrechina fulva* has invaded the Magdalena Valley of Colombia where it reduces native ant diversity (Zenner-Polania 1994); this species is also reported from Cuba (Fontenla Rizo 1995). Another potentially invasive species is *Anoplolepis custodiens*. Native to southern Africa, this species has invaded Zanzibar where it reaches extremely high densities and displaces the native weaver ant *Oecophylla longinoda* (Way 1953). *Technomyrmex albipes* is likewise highly invasive in edge habitats in Mauritius and Madagascar and is associated with substantially reduced ant species richness in these areas (P.S. Ward, unpublished observation). The African *Paratrechina longicornis* is a widely distributed tramp that is sometimes considered invasive (McGlynn 1999a, Wetterer et al. 1999), but few studies have documented its effects on native ants, and in no case is it known to be a competitive dominant (Levins et al. 1973, Torres 1984, Banks & Williams 1989, Morrison 1996). Successful identification of future invaders will be greatly facilitated by careful regional studies that document new introductions and incipient invasions (e.g., Deyrup et al. 2000).

DISPERSAL AND COLONIZATION

All the ants listed in Table 1 have been introduced—most of them worldwide—as a result of human commerce. Species differ, however, in the importance of human-mediated dispersal versus natural dispersal in determining large-scale patterns of spread. In introduced populations of some invasive ants, winged dispersal of female reproductive forms is rare or absent and colonies often reproduce by budding. Colony reproduction by budding alone greatly limits rates of spread: 37–402 m/yr for *A. gracilipes* in the Seychelles (Haines & Haines 1978a), 10–40 m/yr for the polygyne-form of *S. invicta* in central Texas (Porter et al. 1988), 15–270 m/yr for *L. humile* in northern California (Suarez et al. 2001), and approximately 15 m/yr for *P. megacephala* in northern Australia (Hoffmann et al. 1999). In the absence of human-mediated dispersal, introduced populations of *Wasmannia auropunctata* are also believed to spread predominantly by budding (Clark et al. 1982). Because rates of spread by budding are so low [i.e., on the low end for terrestrial organisms (Grosholz 1996)], species that undergo colony reproduction solely by budding depend largely on human-mediated dispersal to colonize new and distant locations (Suarez et al. 2001). Moreover, budding limits the initial spread of invasive ants to areas adjacent to points of introduction or to source habitats. In such cases, invasive ants occur as localized edge effects (Suarez et al. 1998, Human et al. 1998, Bolger et al. 2000, Holway et al. 2002).

Important exceptions to the above pattern include *S. geminata* and the monogyne form of *S. invicta*, two species for which winged dispersal of female reproductive forms is common (see De Heer et al. 1999 and Goodisman et al. 2000 for discussions of dispersal in the polygyne form of *S. invicta*). In such cases, regional-scale patterns of spread may be driven both by human-assisted transport and by the

winged dispersal of female alates, which can travel kilometers from natal nests during mating flights (Wilson & Brown 1958, Vinson & Greenberg 1986, Porter et al. 1988). In contrast to colony reproduction by budding, winged dispersal of female reproductive forms enables new beachheads to be established in areas distant from the colony of origin.

Nesting behavior also influences the importance of human-assisted transport. Invasive ants exhibit general and somewhat flexible nesting habits, allowing them to associate closely with humans. Incipient colonies occupy an especially wide range of nesting substrates, including nursery stock and other products of commerce. Some invasive ants readily relocate nests in response to physical disturbance or to exploit favorable but ephemeral sites (Hölldobler & Wilson 1977, Passera 1994). *L. humile*, for example, which often uses ephemeral nest sites, engages in nest relocation in response to changes in the physical environment (Newell & Barber 1913, Markin 1970b, Passera 1994, Gordon et al. 2001) and the distribution of food resources (Newell & Barber 1913, Holway & Case 2000, Silverman & Nsimba 2000). For species with budding, such opportunistic nesting behavior must play a key role in distributing nests to locations where they are likely to be transported by humans. Lastly, the ability of colonies of both *S. invicta* (Morrill 1974, Tschinkel 1983) and *L. humile* (Barber 1916) to raft in response to flooding may pre-adapt them to live in disturbed or well-watered urban environments.

Following dispersal to a new environment, propagules face a host of obstacles that can impede successful establishment. As for other introduced insects (Lawton & Brown 1986, Simberloff 1989), the factors influencing the probability of successful colonization by invasive ants remain poorly known. Below, we discuss attributes that may affect colonization success but acknowledge that the colonization process itself remains inadequately studied. This discussion focuses on ants that reproduce by budding; independent colony founding by the monogyne form of *S. invicta* has been studied in detail (Markin et al. 1972, Tschinkel & Howard 1983) and is reviewed elsewhere (Tschinkel 1993, 1998; Bernasconi & Strassmann 1999).

Although little information exists on the sizes of propagules transported by human commerce, it seems likely that the probability of successful establishment increases steeply with propagule size, at least for small colonies. Propagules with no workers must commonly fail because queens in species with dependent colony founding often lack sufficient metabolic reserves to found colonies on their own (Chang 1985, Keller & Passera 1989, Ross & Keller 1995, Hee et al. 2000). For incipient colonies containing workers and at least one queen, the number of workers present is likely an important determinant of colony-level survival. Disparities in the size of incipient colonies are important since, relative to smaller propagules, larger ones may be able to better withstand stressful physical environments (Markin et al. 1973), starvation (Kaspari & Vargo 1995), and competition from established, neighboring colonies. Although much remains to be learned about the factors governing colonization success, important insights could be obtained through manipulative experiments involving founding queens or small colonies.

Such experimental approaches have been employed with great success as a means to examine the dynamics of independent colony founding in *S. invicta* (Tschinkel & Howard 1983; Adams & Tschinkel 1995a,b; Bernasconi & Strassman 1999).

For at least some species of invasive ants, propagules need not even contain queens to establish successfully (Aron 2001). Although workers of all invasive ants are sterile, in species such as *L. humile*, workers can rear eggs and early instar larvae into sexuals in the absence of queens (Passera et al. 1988, Vargo & Passera 1991). Moreover, in *L. humile*, production of sexuals does not require overwintering, queens produce haploid eggs throughout the year, and mating occurs in the nest (Aron 2001). In combination, these attributes make it possible for dequeened propagules that contain eggs and larvae to produce both male and female sexuals. There is little evidence of inbreeding in *L. humile* colonies despite intranidal mating (Krieger & Keller 2000) (probably because males disperse by flight among nests), and therefore dequeened propagules could in theory develop into reproductively viable colonies (Aron 2001). It will be of interest to determine if other invasive ants share this remarkable capability. [See Tschinkel & Howard (1978) for a discussion of queen replacement in orphaned colonies of *S. invicta*.]

CHARACTERISTICS OF INVADED HABITATS

Natural ecosystems vary greatly in the extent to which they are affected by invasive ants. An ecosystem's physical environment (Tremper 1976, Ward 1987, Holway 1998b, Holway et al. 2002) and its history of anthropogenic disturbance (Tschinkel 1988) and fragmentation (Suarez et al. 1998) all influence susceptibility to invasion. Introduced populations of both *S. invicta* and *S. geminata*, for example, often favor open and disturbed habitats (Tschinkel 1988, Morrison 1996, De Heer et al. 1999). The extent to which biotic resistance from native ants influences the vulnerability of communities to invasion appears to vary regionally. In riparian woodlands in northern California, native ant richness and rate of spread of Argentine ants were uncorrelated over a 4-year period (Holway 1998b). Majer (1994), Andersen (1997), and Hoffmann et al. (1999), however, suggest that the *Iridomyrmex*-rich fauna of Australia may be resistant to invasion owing to the strong competitive ability of ants in this genus (Andersen 1992, Andersen & Patel 1994). Moreover, the absence of native ants on Hawaii and other islands in the Pacific Ocean undoubtedly makes these areas vulnerable to invasion (Cole et al. 1992, Reimer 1994).

EFFECTS OF INVASIVE ANTS ON NATIVE ANTS

The competitive displacement of native ants by invasive ants is the most dramatic and widely reported effect of ant invasions (Hölldobler & Wilson 1990, Williams 1994). In invaded areas, the abundance of native ants can be reduced by over 90% [Porter & Savignano 1990 (but see Morrison 2002), Cammell et al. 1996, Human & Gordon 1997, Holway 1998a, Hoffmann et al. 1999]. Evidence of this

phenomenon comes from a variety of sources: (*a*) historical accounts (Newell & Barber 1913, Van Der Goot 1916, Haskins & Haskins 1965, Brandao & Paiva 1994), (*b*) longitudinal studies documenting the advance of invasive ants at the expense of natives (Greenslade 1971; Erickson 1971; Tremper 1976; Porter et al. 1988; Holway 1995, 1998b; Human & Gordon 1996; Hoffmann et al. 1999; Sanders et al. 2001), (*c*) studies documenting mutually exclusive distributions between native ants and invasive ants (Tremper 1976; Clark et al. 1982; Ward 1987; Porter & Savignano 1990; Morris & Steigman 1993; Cammell et al. 1996; Human & Gordon 1997; Heterick 1997; Way et al. 1997; Holway 1998a,b; Suarez et al. 1998; Kennedy 1998; Hoffmann et al. 1999; Vanderwoude et al. 2000), (*d*) large-scale studies illustrating the effects of invasive ants on latitudinal gradients in ant diversity (Gotelli & Arnett 2000), and (*e*) lab and field studies (only some experimental) demonstrating that invasive ants differ from native ants with respect to competitive ability, periods of activity, behavioral characteristics, or resource use (Clark et al. 1982; Jones & Phillips 1987, 1990; Porter & Savignano 1990; Morrison 1996; Human & Gordon 1996, 1999; Holway 1999; Morrison 1999, 2000; Holway & Case 2001).

Invasive ants may have the greatest effect on ecologically similar native ants. In the southeastern United States, for example, the fire ants *Solenopsis xyloni* and *S. geminata* appear highly sensitive to displacement by *S. invicta* (Wilson & Brown 1958; Porter et al. 1988; Morrison 2000, 2002). Likewise, in California, Argentine ants and ecologically similar native Dolichoderines (e.g., *Tapinoma sessile, Liometopum occidentale*) rarely, if ever, coexist (Ward 1987, Holway 1998a). Native ants that resemble invasive ants in their ecologies are by no means the only ants displaced. In California, for example, a variety of harvester ant species succumb to Argentine ants (Erickson 1971, Human & Gordon 1996, Suarez et al. 1998) despite little apparent overlap in food resources. *S. invicta* has also been reported to eradicate colonies of the harvester ant *Pogonomyrmex barbatus* in central Texas (Hook & Porter 1990).

Although invasive ants displace many species of native ants, some often persist. Hypogeic ants, for example, may persevere in areas occupied by invasive ants (Ward 1987) or persist longer than other taxa (Hoffmann et al. 1999). Tschinkel (1988) speculated that predation by the hypogeic *Solenopsis molesta* upon *S. invicta* brood may restrict monogyne colonies of *S. invicta* to disturbed habitats lacking *S. molesta*. Species resistant to displacement also include those adapted to physical conditions not tolerated by invaders. In California, the cold-tolerant *Prenolepis imparis* appears relatively immune to displacement by the Argentine ant (Tremper 1976, Ward 1987, Holway 1998a, Suarez et al. 1998), whereas the heat-tolerant *Dorymyrmex insanus* and *Forelius mccooki* coexist locally with Argentine ants along the periphery of hot, exposed areas not colonized by *L. humile* (Holway et al. 2002). Both *D. insanus* and *F. mccooki* co-occur with *S. invicta* as well (Summerlin et al. 1977, Camilo & Philips 1990, Morrison 2002). Heat tolerant native ants also appear to coexist with Argentine ants in South Africa (Witt & Giliomee 1999).

Other native ants may resist displacement by invasive ants primarily because of their strong competitive ability. In North America, for example, many authors have reported that species in the genus *Monomorium* can, to some extent, withstand interspecific competition by invasive ants. Several authors report *Monomorium minimum* co-occurring with red imported fire ants in the southeastern United States (Baroni-Urbani & Kannowski 1974, Howard & Oliver 1979, Stein & Thorvilosen 1989, Porter & Savignano 1990), and *M. ergatogyna* was the only native ant (of seven species tested) to resist displacement by Argentine ants at baits in northern California (Holway 1999). *Monomorium* species may persist both through their use of potent chemical defensive compounds (Adams & Traniello 1981, Andersen et al. 1991) and their tolerance of warm temperatures (Adams & Traniello 1981).

Mechanisms

Although the ability of invasive ants to displace native ants is well known, the mechanisms involved have, until recently, received relatively little attention. Even with a number of recent and informative studies, much remains to be learned. For example, native ants succumb to the combined effects of interference and exploitative competition, but an understanding of the relative importance of these two forms of competition is often unclear and undoubtedly varies depending on the invading species, characteristics of the native ant community, and other environmental variables. Furthermore, invasive ants are unusual in that introduced populations of most species typically maintain populous and expansive supercolonies. The abundance of invasive ants can exceed that of all native ant species combined in comparable uninvaded areas (Porter & Savignano 1990, Holway 1998a, Hoffmann et al. 1999). Although disparities in colony size are an important determinant of the competitive asymmetry between native and invasive ants, there exists only a rudimentary understanding of why invasive ants differ from native species in this important respect.

As with ants generally (Hölldobler & Wilson 1990), the interference repertoire of invasive ants includes both worker-level behaviors such as physical aggression and the use of chemical defensive compounds as well as colony-level behaviors such as recruitment of nestmates, interspecific territoriality, and nest raiding (Table 2). Despite the pervasiveness of physical aggression among competing ants as a whole, invasive ants are commonly described as exhibiting pronounced interspecific aggression (Hölldobler & Wilson 1977, 1990; Passera 1994; Human & Gordon 1999). Even though invasive ants may be more aggressive than the native ants they displace, differential aggression provides only a partial explanation for their interference prowess. In ants generally, interference competition, especially for valuable food finds or nest sites, is typically a colony-level activity. The outcome of such inter-colony contests depends primarily on asymmetries in recruitment response or local density (often reflective of differences in colony size) (Hölldobler & Lumsden 1980, Hölldobler & Wilson 1990, Adams 1990). Numerical advantages enjoyed by invasive ants contribute greatly to their interference ability (Greenslade 1971, Tremper 1976, Holway 1999, Morrison 2000, Holway & Case 2001).

TABLE 2   Competitive mechanisms and behaviors reported to be important in interactions between invasive ants and native ants

Species	Competitive mechanism or behavior	Study
Anoplolepis gracilipes	Use of chemical defensive compounds	Fluker & Beardsley 1970
	Use of physical aggression by workers	Haines & Haines 1978a
	Active both day and night	Haines & Haines 1978a
Linepithema humile	Use of chemical defensive compounds	Lieberburg et al. 1975, Holway 1999, Holway & Case 2001
	Use of physical aggression by workers	Newell 1908, Erickson 1971, De Kock 1990, Human & Gordon 1996, 1999, Holway 1999
	Initiates one-on-one interactions more often than do native ants	Human & Gordon 1999, Holway & Case 2001
	Raids nests of other species	Fluker & Beardsley 1970, De Kock 1990, D.A. Holway, unpublished observation, P.S. Ward, unpublished observation
	Workers prey upon winged queens of native ant species	Human & Gordon 1996
	Remains at baits longer than do native ants	Human & Gordon 1996
	Proficient at displacing native ants from baits	Human & Gordon 1996, Holway 1999
	Active both day and night	Human & Gordon 1996
	Active throughout the year	Holway 1998a
	Recruits to baits in higher numbers than do native ants	Human & Gordon 1996, Holway 1998b
	Recruits to more baits than do native ants	Holway 1998b
	Discovers and recruits to baits more quickly than do native ants	Holway 1998a, Holway 1999
	Adjusts foraging behavior to local worker density	Gordon 1995
Pheidole megacephala	Use of physical aggression by workers	Fluker & Beardsley 1970, Lieberburg et al. 1975
	Use of physical aggression by soldiers	Fluker & Beardsley 1970
	Recruitment of many workers	Lieberburg et al. 1975
	Active both day and night	Hoffmann 1998
Solenopsis invicta	Use of chemical defensive compounds (gaster flagging and stinging)	Bhatkar et al. 1972, Obin & Vander Meer 1985, King & Phillips 1992, Morrison 2000
	Use of physical aggression by workers	Bhatkar et al. 1972, Jones & Phillips 1987, Bhatkar 1988, King & Phillips 1992, Morrison 1999, Morrison 2000
	Raids nests of other species	Bhatkar et al. 1972, Hook & Porter 1990
	Retrieves baits in the lab more rapidly than do 2 species of native ants	Jones & Phillips 1990
	Discovers and recruits to baits more quickly than do native ants	Porter & Savignano 1990
	Recruits to baits in higher numbers than do native ants	Porter & Savignano 1990
	Recruits to baits in higher numbers than does native *S. geminata*	Morrison 1999

(Continued)

TABLE 2   (*Continued*)

Species	Competitive mechanism or behavior	Study
Solenopsis invicta (continued)	Retrieves more food than does native *S. geminata*	Morrison 1999
	Colony-level interference ability in the lab superior to that of native fire ants (*S. geminata* and *S. geminata* × *S. xyloni* hybrids)	Morrison 2000
	Active both day and night	Morrison 2000
Solenopsis geminata	Use of physical aggression by workers	Morrison 1996
	Recruits to baits in higher numbers than do native ants	Morrison 1996
	Reduces the access of *Monomorium monomorium* to baits	Morrison 1996
	Most dominant interference competitor (out of 19 species) at baits	Torres 1984
Wasmannia auropunctata	Remains at baits longer than do other ants	Clark et al. 1982
	Proficient at displacing other ants from baits	Clark et al. 1982
	Recruits to baits in higher numbers than do other ants	Clark et al. 1982; Tennant 1994
	Active both day and night	Clark et al. 1982
	Pirates food from other ants	Brandao & Paiva 1994

A poorly studied but potentially important component of the competitive displacement of native ants by invasive ants involves colony-level battles and nest raiding. Colonies of both *S. invicta* and *L. humile* engage in aggressive, episodic raids on nests of other species (Table 2). Although effects of colony-level battles remain difficult to quantify because individual events may occur only infrequently, such raids may eradicate native ant colonies. Hook & Porter (1990), for example, estimated that a colony of *P. barbatus* in central Texas lost over 1200 workers to *S. invicta* over a period of six to seven weeks; this colony was believed to die out eventually as a direct result of these incursions. Although the distinction between interference competition and intra-guild predation in such cases is not clear-cut, at present, there is little evidence that invasive ants consume native ants during these events. The role of nest raiding in this context should be investigated in greater detail.

Invasive ants also compete with native ants indirectly via exploitative competition. As with interference ability, large colony size enhances exploitative ability because large colonies can simultaneously maintain large forces of scouts (i.e., workers actively searching for food) and recruits (i.e., workers in the nest available to help exploit rich food discoveries) (Johnson et al. 1987). Compared to the native ants they displace, invasive ants commonly excel at behaviors correlated with exploitative ability: rapid discovery of food, rapid recruitment, recruitment of large numbers of workers, extended duration of recruitment, and 24-hour activity (Table 2). Somewhat surprisingly, few field studies measure exploitative ability directly (e.g., food retrieval rates) (Morrison 1999). Despite putative differences in exploitative ability between native and invasive ants, the precise role of exploitative competition in the demise of native ants remains unclear. Exploitative competition

probably plays a minor role in situations where both invasive ants and native ants maintain separate and well-delineated territories (Morrison 2000) and where large or immobile food items (e.g., carrion, aggregations of Homoptera) need to be usurped from or defended against other colonies. In contrast, exploitative competition may be more important in situations where territories are actively being carved out (e.g., at the leading edge of an invasion front) and where small, particulate food items can be retrieved without recruitment of nestmates (e.g., small, dead insects).

Compared to the native species they supplant, invasive ants may excel at the two forms of competition simultaneously, allowing them both to exploit and to monopolize a majority of food resources. Coexistence among competing species of ants within a community can result from species-specific differences in competitive ability: An inverse relationship often exists between the ability of a species to discover food and its ability to dominate resources behaviorally or numerically (Wilson 1971, Fellers 1987, Banks & Williams 1989, Perfecto 1994, Morrison 1996; see Johnson 1981 and Nagamitsu & Inoue 1997 for a similar relationship among Meliponine bees). Relative to native ants, however, invasive ants may excel at both resource discovery and resource dominance, effectively breaking the trade-off (Davidson 1998, Holway 1999, Feener 2000). For example, compared to a northern California native ant community that was subject to the discovery-dominance trade-off, *L. humile* discovered food in less time than did all native species and also displaced a majority (six out of seven species) from baits (Holway 1999) suggesting that *L. humile* secures a majority of food resources in areas where it meets native ants. Although discovery-dominance trade-offs offer a simplistic view of community structure in that they ignore mechanisms known to affect coexistence (e.g., species-specific tolerances to the physical environment), they provide a conceptual framework for testing alternative hypotheses concerning the success of ant invasions (Davidson 1998, Adler 1999, Feener 2000). Moreover, given that competitive trade-offs are frequently invoked to explain species coexistence, their usefulness as a tool to explain cases where species fail to coexist (as in invasions) may well be general [see Tilman (1999) for a similar argument pertaining to plant invasions]. Numerical advantages probably allow invasive ants to achieve simultaneous proficiency at both resource dominance and resource discovery (Holway 1999, Morrison 2000), providing a proximate mechanism for why invasive ants break the dominance-discovery trade-off. A key unresolved question, however, is why invasive ants become so much more abundant than the native ants they displace.

Hypotheses to Explain the Abundance of Invasive Ants

Several hypotheses have been advanced to account for the disproportionate abundance of invasive ants. First, as with other introduced species, invasive ants have escaped competitors and natural enemies and may achieve larger colony sizes and increased colony densities as a consequence (Buren 1983, Porter et al. 1997). Second, because unicolonial ants do not defend territorial boundaries against

conspecifics, they can allocate workers to tasks other than colony defense and shunt resources to worker production that would otherwise be expended on fighting neighboring colonies of the same species (Hölldobler & Wilson 1977, Macom & Porter 1996, Holway et al. 1998). The loss of intraspecific territoriality and the formation of supercolonies may allow such species to monopolize resources and to displace competitors; this would lead to further increases in local density (Macom & Porter 1996). Third, invasive ants may consume resources, such as plant and homopteran exudates that native ants either fail to exploit or do so less efficiently compared to invasive ants. In this sense, invasive ants could function partly as herbivores, as has been suggested for tropical arboreal ants that maintain densities greatly in excess of what scavenging and predation alone could support (Tobin 1994, Davidson 1997). Access to carbohydrate-rich food resources such as plant and homopteran exudates may allow invasive ants to fuel workers at a high tempo, making possible the maintenance of high dynamic densities (ants/area/time), the defense of absolute territories, and further monopolization of resources (Davidson 1997, 1998). Because these processes in all likelihood operate simultaneously (Porter & Savignano 1990, Holway 1999, Morrison 2000), an outstanding challenge will be to uncover their relative importance. As a start, we review current evidence bearing on this issue for the two best-known invasive ants, *L. humile* and *S. invicta*.

LINEPITHEMA HUMILE   Early reports from the Argentine ant's introduced range described workers, queens, and brood moving freely among spatially separate nests (Newell & Barber 1913), and more recent studies have shown that a single large supercolony appears to occupy nearly the entire introduced range of *L. humile* in California (Tsutsui et al. 2000, Tsutsui & Case 2001). Argentine ants also appear unicolonial in every other part of their introduced range where this behavior has been studied (Passera 1994, Way et al. 1997, Tsutsui et al. 2000, Krieger & Keller 2000, Giraud et al. 2002). In contrast, although native populations of *L. humile* are also polygynous and maintain multiple nests, high levels of intraspecific aggression are commonly observed between nests over short (<100 m) spatial scales (Tsutsui et al. 2000, Tsutsui & Case 2001).

Despite gross differences in colony structure between the native and introduced ranges, workers in both areas tend to display intraspecific aggression toward workers from genetically different colonies (Tsutsui et al. 2000). This observation is of interest for at least two reasons. First, it suggests that nestmate recognition in Argentine ants has an underlying genetic basis, as in other ants (e.g., Stuart 1987; Carlin & Hölldobler 1986, 1987; Beye et al. 1998). Second, it provides an explanation for the widespread absence of intraspecific aggression in introduced populations of this species. Because introduced populations experienced a loss of genetic diversity during their introduction and establishment (Tsutsui et al. 2000, 2001), they do not appear to have sufficient genetic variation to elicit fighting between workers from different nests. Workers in the introduced range rarely encounter genetically different individuals; as a result, intraspecific aggression

seldom occurs, and almost all nests function in an apparently cooperative, uni-colonial fashion.

The shift in colony organization between native and introduced populations of Argentine ants helps explain their success as invaders. In lab experiments with pairs of colonies that either did or did not exhibit intraspecific aggression, aggressive pairs experienced higher mortality, lower foraging activity, and lower rates of colony growth after 70 days (Holway et al. 1998). Moreover, in 60% of nonaggressive nest pairs, colonies fused, even though some of these pairings were composed of colonies that were originally collected from locations up to 100 km apart (Holway et al. 1998). Although caution seems warranted in extrapolating the results of this lab study to the population level, these findings show in principle how the loss of intraspecific aggression could lead to increases in colony size and the formation of supercolonies—both of which would enhance interspecific competitive ability.

Other factors also contribute to the abundance of Argentine ants in their introduced range. In its native Argentina, *L. humile* coexists with many other species of ants (Suarez et al. 1999), including competitive dominants such as *S. invicta* and *S. richteri*. It seems likely that the absence of strong competitors such as *S. invicta* and *S. richteri* throughout most of the Argentine ant's introduced range contributes to its high abundance. *S. invicta*, for example, appears to have displaced *L. humile* where introduced populations of both species overlapped in the southeastern United States (Wilson 1951, Glancey et al. 1976). At present, there is no evidence concerning the role of escape from natural enemies in the success of introduced populations of Argentine ants. *L. humile* appears to lack phorid fly parasitoids (Orr et al. 2001) despite earlier reports to the contrary (Orr & Seike 1998, Feener 2000). Recent work suggests that previous studies of phorid fly parasitism involved different species of *Linepithema* (Orr et al. 2001, Tsutsui et al. 2001).

An additional factor that may promote high worker densities in introduced populations is the ability of *L. humile* to exploit resources that native ants either fail to consume or consume less efficiently than invasive ants. For example, Argentine ants have a strong predilection for homopteran honeydew. When Argentine ants tend Homoptera in agricultural systems (especially citrus orchards), protected Homoptera can attain locally high densities, possibly further increasing *L. humile* populations (Newell & Barber 1913, Way 1963). However, it remains unclear whether Argentine ants differ from native ants in their preference for honeydew. In riparian woodlands in northern California, for example, native ants such as *Liometopum occidentale* commonly tend Homoptera (Ward 1987).

SOLENOPSIS INVICTA   The monogyne form of *S. invicta* was first introduced to the United States around 1940 and spread quickly in the following decades throughout the southeast, where it now attains higher densities than it does in its South American native range (Porter et al. 1992). The success of this species has been attributed to a variety of causes including human modifications of the landscape, community simplifications resulting from prior invasions of other ants (e.g., *L.*

humile and *S. richteri*), and the use of pesticides (Morrison 2000). Escape from coevolved competitors, pathogens, and parasites probably also allowed increases in the density of its populations (Jouvenaz 1990; Porter et al. 1992, 1997). For example, the presence of host-specific parasitoids, such as phorid flies, can inhibit foraging in *S. invicta* colonies (Porter et al. 1995, Orr et al. 1995). Although the population-level effects of phorids on fire ants are unknown at present, the absence of phorids specialized on *S. invicta* throughout its introduced range may allow colonies there to grow faster and to attain larger sizes.

In the 1970s, polygyne colonies of *S. invicta* were first reported from the United States (Glancey et al. 1973), and the polygyne form is now widespread (but discontinuously distributed) in the southeast, particularly in Texas and Florida (Porter et al. 1991, 1992). As in the United States, the distribution of polygynous colonies of *S. invicta* varies in South America; polygyny is present in Argentina (Jouvenaz et al. 1989, Ross et al. 1996) but apparently absent in Brazil (Jouvenaz et al. 1989, Porter et al. 1992). Although the monogyne form of *S. invicta* is considered highly invasive (Wilson & Brown 1958, Apperson & Powell 1984, Tschinkel 1993), the polygyne form may be a bigger problem (Porter & Savignano 1990). In Florida, population densities (estimated using biomass) of polygyne *S. invicta* are two times higher than those of the monogyne form (Macom & Porter 1996). Likewise, in Texas, colonies of the polygyne form can recruit up to twice as many workers to baits compared to colonies of the monogyne form (MacKay et al. 1994). The higher densities of the polygyne form, compared to the monogyne form, may result from diminished intraspecific aggression and a concomitant reduction in intraspecific territoriality, an increased ability to monopolize resources from interspecific competitors, or differences in patterns of sex allocation (Macom & Porter 1996). Because polygyne and monogyne populations presently occur together in parts of the southeastern United States, an interesting opportunity exists to test in more detail how colony structure variation alone influences the ecological effects of these invasions.

The transition from monogyny to polygyny described above has been a topic of much interest. Ross & Keller (1995) and Ross et al. (1996) have hypothesized that polygyny became prevalent in introduced populations in response to ecological constraints, as proposed for the evolution of cooperative breeding in other taxa (Emlen 1982). Following introduction to the United States, population densities of monogyne *S. invicta* increased. With increasing colony densities, suitable nest sites became saturated, reducing the fitness of queens that attempted to found colonies independently and favoring queens seeking adoption into established colonies (Nonacs 1993, Ross & Keller 1995). Frequent queen adoption may have then led to an erosion of nestmate recognition abilities as levels of genetic diversity increased within polygyne colonies (Hölldobler & Michener 1980). This loss of nestmate recognition could then have further increased polygyny as colonies accepted more foreign queens (Hölldobler & Wilson 1977, Ross et al. 1996), leading to a runaway process of ever-increasing polygyny (Pamilo 1991, Ross et al. 1996).

In light of recent studies that illuminate the genetic machinery underlying monogyny and polygyny in *S. invicta* (Keller & Ross 1999, Krieger & Ross 2002),

it appears unlikely that polygyny arose in introduced populations as a result of ecological constraints alone. These studies implicate genetic differences between the social forms at the *Gp-9* locus as the primary, and perhaps exclusive, determinant of colony queen number in *S. invicta*. Queens from the two social forms can be distinguished by their genotype at the *Gp-9* allozyme locus. Virtually all egg-laying queens in introduced polygyne colonies are *Bb* heterozygotes at *Gp-9* (Ross 1997) and possess a distinctive polygyne queen phenotype: physically small queens with fewer fat reserves and more gradual oogenesis than monogyne queens (Keller & Ross 1993). Workers in polygyne colonies accept additional queens based on their genotype at *Gp-9* (Keller & Ross 1998). Monogyne queens, on the other hand, are heavy, possess the large fat reserves necessary for independent colony founding, exhibit rapid oogenesis (Keller & Ross 1993), and possess the *BB* genotype at *Gp-9* in both the native and introduced ranges (Ross 1997). Workers in monogyne colonies do not permit additional queens to join (Keller & Ross 1998). The *bb* genotype is thought to be lethal, and is almost completely absent in adult workers and queens in both ranges (Ross 1997).

Thus, the reproductive strategies of monogyne and polygyne queens appear to be fixed by genetics, regardless of the ecological context. Previous work on the infiltration of mature colonies by dispersing monogyne queens further supports the idea that genetic factors limit queen number in *S. invicta* colonies. In populations of monogyne *S. invicta*, for example, ecological constraints on independent colony founding are so strong that some overwintered, monogyne queens attempt to infiltrate previously established colonies (Tschinkel 1996, DeHeer & Tschinkel 1998). When these monogyne queens, which presumably possess the BB genotype at *Gp-9*, attempt to enter colonies that contain queens, they are likely killed by workers, (Tschinkel 1996, DeHeer & Tschinkel 1998, VanderMeer & Alonso 2002) as described above. Thus, it appears that these dispersing queens are only able to successfully enter colonies that have lost their queen (DeHeer & Tschinkel 1998, VanderMeer & Alonso 2002). These studies illustrate that newly produced queens appear to be caught, on one hand, between ecological constraints that reduce opportunities for independent colony founding and, on the other hand, strong genetic constraints that prevent monogyne queens from successfully entering established colonies.

EFFECTS OF ANT INVASIONS ON OTHER TAXA

Although the displacement of native ants by invasive ants is the most obvious effect of ant invasions, many additional effects occur following invasion. Given the variety of ecological roles filled by native ants, it seems likely that reductions in native ant diversity and abundance would indirectly affect many different taxa. Moreover, because invasive ants are widespread, abundant, aggressive, and omnivorous, one would predict that they would disrupt invaded communities (Diamond & Case 1986, Pimm 1991, Parker et al. 1999). These effects might be most noticeable on island ecosystems that lack native ants. Numerous lines of empirical

evidence support these predictions and illustrate the diversity of ecological effects that result. Nonetheless, the effects of ant invasions remain incompletely studied, reflecting the inadequate state of knowledge concerning the consequences of species introductions generally (Parker et al. 1999, Pimentel et al. 2000). Much evidence bearing on the effects of ant invasions, for example, is either anecdotal or correlative, and few studies determine if effects of invasive ants differ from those of native ants that are displaced. Experimental, long-term and large-scale studies are therefore needed to develop a more quantitative understanding of the impacts caused by invasive ants. Below we discuss the known ecological effects of ant invasions but recognize that current information on this topic is incomplete.

Competition and Predation

A clear understanding of the ecological role of invasive ants as predators and competitors is hampered by a poor understanding of their diets, studies that confuse predation and scavenging, and those that fail to distinguish between predation and competition. Although many lines of evidence illustrate the role of invasive ants as predators of at least certain taxa, the same cannot be said of competition. Some evidence exists for ants generally competing with both vertebrates (Brown & Davidson 1977, Aho et al. 1999) and non-ant invertebrates (Halaj et al. 1997), but there is, at present, little unequivocal evidence demonstrating the existence of competition (especially exploitative competition) between invasive ants and non-ant taxa. For these reasons, we discuss predation and competition together.

IMPACTS OF INVASIVE ANTS ON INVERTEBRATES   Every species of invasive ant listed in Table 1 has been implicated in the decline of non-ant invertebrates, but the effects of *L. humile* and *S. invicta* have been examined in the most detail (Table 3). Some of the best evidence illustrating the role of invasive ants as predators of invertebrates comes from studies conducted in agricultural settings that document invasive ants preying on insect herbivores (Table 3). As in agro-ecosystems, invasive ants occupying less manipulated environments also prey opportunistically on invertebrate eggs, larvae, and certain adult forms (Table 3). Such predation may jeopardize populations of some invertebrates, especially those on oceanic islands, such as Hawaii, which evolved in the absence of predaceous ants (Zimmerman 1970, Gillespie & Reimer 1993, Cole et al. 1992). Zimmerman (1970), for example, recounts the disappearance (and apparent extinction) of a once abundant wingless and ground-dwelling fly from forests on Oahu shortly after introduction of *P. megacephala*. In addition to affecting other invertebrates through predation, invasive ants may also compete with non-ant invertebrates.

Reported impacts of invasive ants on invertebrates range from qualitative observations, such as the absence of a species from an invaded area, to studies that estimate changes in diversity, abundance, or biomass between invaded and uninvaded areas (Table 3). *Solenopsis invicta* appears to cause declines in a variety of invertebrate groups including ground-dwelling arthropods (Nichols & Sites 1989,

TABLE 3 Reported effects of invasive ants on non-ant taxa

Species	Ant	Location	Reported effect/mechanism	Study
BIRDS				
Sooty tern (*Sterna fuscata*)	*A. gracilipes*	Bird Island, Seychelles	Failure to nest in invaded areas	Feare 1999
White tern (*Gygis alba*)	*A. gracilipes*	Bird Island, Seychelles	Death of chicks	Feare 1999
California gnatcatcher (*Polioptila melanura*)	*L. humile*	CA, USA	Nest failure	Sockman 1997
Northern bobwhite (*Colinus virginianus*)	*S. richteri*	TX, USA	Mortality of pipping chicks	Johnson 1961
Least tern (*Sterna antillarum*)	*S. invicta*	MS, USA	Dead chicks covered with ants, ant suppression increased chick survival	Lockley 1995
Colonial waterbirds (7 spp.)	*S. invicta*	TX, USA	Ant suppression increased nesting success	Drees 1994
Crested caracara (*Caracara plancus*)	*S. invicta*	TX, USA	Dead chicks covered in ants	Dickinson 1995
Northern bobwhite (*Colinus virginianus*)	*S. invicta*	TX, USA	Bobwhite densities decline after invasion, and increase after ant suppression	Allen et al. 1995
Northern bobwhite (*Colinus virginianus*)	*S. invicta*	GA/FL/SC, USA	Bobwhite densities decline after invasion	Allen et al. 2000
Northern bobwhite (*Colinus virginianus*)	*S. invicta*	TX, USA	Ant suppression increased chick survival	Mueller et al. 1999
Northern bobwhite (*Colinus virginianus*)	*S. invicta*	Laboratory study	Ant exposure reduced chick survival	Giuliano et al. 1996
Cliff swallow (*Hirundo pyrrhonota*)	*S. invicta*	TX, USA	Mortality of pipping chicks, nesting success reduced in invaded areas	Sikes & Arnold 1986
Barn swallow (*Hirundo rustica*)	*S. invicta*	TX, USA	Nest predation	Kopachena et al. 2000
Black rail (*Laterallus jamaicensis*)	*S. invicta*	FL, USA	Mortality of pipping chick	Legare & Eddleman 2001
Wood duck (*Aix sponsa*)	*S. invicta*	TX, USA	Predation on nestlings and pipped eggs	Ridlehuber 1982
Loggerhead shrike (*Lanius ludovicianus*)	*S. invicta*	FL, USA	Reduced food supply	Yosef & Lohrer 1995
REPTILES & AMPHIBIANS				
Skink (*Mabuya seychellensis*)	*A. gracilipes*	Bird Island, Seychelles	Disappearance of skinks in invaded areas	Feare 1999
Coast horned lizard (*Phrynosoma coronatum*)	*L. humile*	CA, USA	Displacement of ant prey	Suarez et al. 2000
Coast horned lizard (*Phrynosoma coronatum*)	*L. humile*	Laboratory study	Lower growth rate on *L. humile* diet	Suarez & Case 2002
Coast horned lizard (*Phrynosoma coronatum*)	*L. humile*	CA, USA	Lack of overlap between lizards and ants	Fisher et al. 2002

(Continued)

TABLE 3 (*Continued*)

Species	Ant	Location	Reported effect/mechanism	Study
Texas horned lizard (*Phrynosoma cornutum*)	*S. invicta*	TX, USA	Displacement of ant prey	Donaldson et al. 1994
Six-lined racerunner (*Cnemidophorus sexlineatus*)	*S. invicta*	AL, USA	Predation of eggs	Mount et al. 1981
Alligator (*Alligator mississippiensis*)	*S. invicta*	FL, USA	Killed hatchlings, lower hatchling mass	Allen et al. 1997a
Alligator (*Alligator mississippiensis*)	*S. invicta*	LA, USA	Predation of nestlings, pipped eggs	Reagan et al. 2000
Gopher tortoise (*Gopherus polyphemus*)	*S. invicta*	GA, USA	Predation of hatchlings	Landers et al. 1980
Loggerhead sea turtle (*Caretta caretta*)	*S. invicta*	GA/FL, USA	Predation of eggs and hatchlings	Moulis 1997, Wilmers et al. 1996
Green turtle (*Chelonia mydas*)	*S. invicta*	FL, USA	Predation of pipping hatchlings	Wilmers et al. 1996
Florida red-bellied turtle (*Pseudemys nelsoni*)	*S. invicta*	FL, USA	Predation of pipping hatchlings in lab	Allen et al. 2001
Slider turtle (*Trachemys scripta*)	*S. invicta*	SC, USA	Predation of eggs and hatchlings	Buhlmann & Coffman 2001
Snapping turtle (*Chelydra serpentina*)	*S. invicta*	AL, USA	Ants on dead hatchlings	Conners 1998a
Box turtle (*Terrapene carolina*)	*S. invicta*		Mortality from stings	Montgomery 1996
Rough green snake (*Opheodrys aestivus*)	*S. invicta*	AL, USA	Ants puctured eggs	Conners 1998b
Hognose snake (*Heterodon simus*)	*S. invicta*	SE, USA	"Responsible for decline"	Tuberville et al. 2000
Houston toad (*Bufo houstonensis*)	*S. invicta*	TX, USA	Mortality from stings	Freed & Neitman 1988
Reptile populations	*W. auropunctata*	New Caledonia	Decrease in populations in invaded areas	Jourdan et al. 2001
FISH				
Redear sunfish (*Leponis microlophus*)	*S. invicta*	Laboratory study	Ingestion of fire ants	Green & Hutchins 1960
Rainbow trout (*Oncorhynchus mykiss*)	*S. invicta*	TX, USA	Ingestion of fire ants	Contreras & Labay 1999
MAMMALS				
Christmas Island shrew (*Crocidura attenuata*)	*A. gracilipes*	Indian Ocean	Shrew disappeared from island	Meek 2000
Gray shrew (*Notiosorex crawfordi*)	*L. humile*	CA, USA	Negative relationship between number of shrew captures and ant density	Laakkonen et al. 2001
White-tailed deer (*Odocoileus virginianus*)	*S. invicta*	TX, USA	Fawn recruitment higher in treated areas	Allen et al. 1997b
White-tailed deer (*Odocoileus virginianus*)	*S. invicta*	TX, USA	Ants increase deer movement	Mueller et al. 2001
Northern pygmy mice (*Baiomys taylori*)	*S. invicta*	TX, USA	Ants influence seasonal microhabitat use	Smith et al. 1990
Northern pygmy mice (*Baiomys taylori*)	*S. invicta*	TX, USA	Capture rate higher in treated areas	Killion et al. 1995
Deer mice (*Peromyscus maniculatus*)	*S. invicta*	Laboratory study	Mice change foraging in presence of ants	Holtcamp et al. 1997

Organism	Ant species	Location	Effect	Reference
Cotton rats (*Sigmodon hispidus*)	*S. invicta*	TX, USA	Trapped rats killed by ants	Flickinger 1989
Small mammals (4 spp.)	*S. invicta*	TX, USA	Negative relationship between number of mammal captures and ant mound density	Ferris et al. 1998, Killion & Grant 1993
Small mammals (3 spp.)	*S. invicta*	TX, USA	Trapped mammals killed by ants	Masser & Grant 1986
INVERTEBRATES (GENERAL)				
Land crab (*Cardisoma* sp.)	*A. gracilipes*	Bird Island, Seychelles	Dead crabs in invaded areas	Feare 1999
Insects (especially large beetles)	*A. gracilipes*	Bird Island, Seychelles	Ants seen killing insects	Feare 1999
Invertebrates	*A. gracilipes*	Seychelles	"Responsible for decline"	Haines & Haines 1978b
Araneae (Tetragnatha)	*A. gracilipes*	HI, USA	Spiders absent from invaded areas	Gillespie & Reimer 1993
Collembola, flies, spiders	*L. humile*	CA, USA	Reduced or absent in invaded areas	Human & Gordon 1997
Flies and beetles	*L. humile*	CA, USA	Reduced abundance in invaded areas	Bolger et al. 2000
Longhorn beetle (*Desmocerus californicus*)	*L. humile*	CA, USA	Negative association between beetle and ant	Huxel 2000
Arthropods (8 orders)	*L. humile*	HI, USA	Reduced abundance in invaded areas	Cole et al. 1992
Yellowjackets (4 spp.)	*L. humile*	CA, USA	Ants attack colonies	Gambino 1990
Honeybees (*Apis mellifera*)	*L. humile*	W. Cape, S. Africa	Ants collect 42% of nectar before bees forage	Buys 1987
Invertebrates	*P. megacephala*	N. Territory, Austrailia	42–85% decrease in abundance	Hoffman et al. 1999
Araneae (Tetragnatha)	*P. megacephala*	HI, USA	Spiders absent from invaded areas	Gillespie & Reimer 1993
Araneae (Tetragnatha)	*S. papuana*	HI, USA	Spider abundance reduced in invaded areas	Gillespie & Reimer 1993
Lone star tick (*Amblyomma americanum*)	*S. richteri*	LA, USA	Predation of ticks in non-treated areas	Harris & Burns 1972
Mosquito (*Psorophora columbiae*)	*S. invicta*	Laboratory study	Ants prey upon mosquito eggs	Lee et al. 1994
Tree snail (*Orthalicus reses reses*)	*S. invicta*	FL, USA	Predation of snails	Forys et al. 2001a
Apple snails (*Pomacea paludosa*)	*S. invicta*	FL, USA	Ants attack and kill snails in dry tanks	Stevens et al. 1999
Swallowtail butterfly (*Papilio cresphontes*)	*S. invicta*	FL, USA	Eggs, pupae, and most larvae consumed	Forys et al. 2001b
Ceratoma catalpae (Lepidoptera)	*S. invicta*	GA, USA	Predation on prepupae & pupae greater	Ness 2001
Cotesia congregata (Hymenoptera)	*S. invicta*	GA USA	Pupal survival lower relative to native ants	Ness 2001
Monarch butterfly (*Danaus plexippus*)	*S. invicta*	TX, USA	Larvae and eggs absent in invaded areas	Calvert 1996
Mites (Erythraeidae), Scarab (*Canthon*)	*S. invicta*	TX, USA	Absent from invaded areas	Porter & Savignano 1990

(Continued)

TABLE 3 (*Continued*)

Species	Ant	Location	Reported effect/mechanism	Study
Gryllus sp., Trombidiidae, Linyphiidae	*S. invicta*	TX, USA	Reduced abundance in invaded areas	Nichols & Sites 1989
Canopy arthopods	*S. invicta*	TX, USA	Fewer in ant-infested trees	Kaspari 2000
Carrion decomposers (6 families)	*S. invicta*	TX, USA	Ant presence reduces arthropod abundance	Stoker et al. 1995
Dung-breeding Diptera (5 spp.)	*S. invicta*	TX, USA	Fly production increases when ants excluded	Schmidt 1984
Coprophagous Scarab beetles	*S. invicta*	TX, USA	2 of 8 spp. lower abundance with ant	Summerlin et al. 1984a
Horn fly (*Haematobia irritans*) and *Orthellia caesarion*	*S. invicta*	TX, USA	Ants prey upon eggs and larvae	Summerlin et al. 1984b
Plant-decomposers	*S. invicta*	TX, USA	Reduced abundance and diversity, eat fruit	Vinson 1991
Dung-inhabiting spp. (Diptera, Coleoptera)	*S. invicta*	FL, USA	Abundance increases after ants excluded; ants prey on larvae, pupae and adult flies	Hu & Frank 1996
Scorpions, some spiders, invert abund.	*W. auropunctata*	Galapagos, Ecuador	Eliminated or reduced	Lubin 1984
Pseudoscorpions	*W. auropunctata*	New Caledonia	Excluded from invaded areas	Jourdan 1997
Terrestrial invertebrates	*W. auropunctata*	New Caledonia	Partial exclusion from invaded areas	Jourdan 1997
Crickets	Many species	HI, USA	Crickets reduced or absent when ants present	La Polla et al. 2000
INVERTEBRATES (HERBIVORES IN AGRICULTURAL SYSTEMS)				
Cacao weevil (*Pantorhytes szentivanyi*)	*A. gracilipes*	Papua New Guinea (cacao)	Harasses adults, causes dispersion	Baker 1972, Room & Smith 1975
Mirid bugs (2 spp.)	*A. gracilipes*	Papua New Guinea (cacao)	Disturbance of feeding and egg laying	Entwistle 1972
Araucaria looper (*Millionia isodoxa*)	*A. gracilipes*	Papua New Guinea (hoop pine)	Late instar larvae attacked	Wylie 1974
Beetle pests (3 spp.)	*A. gracilipes*	Seychelles (coconut)	Thought to attack and control pests	Lewis et al. 1976
Coconut bug (*Amblypelta cocophaga*)	*A. gracilipes*	Solomon Islands (palms)	Observations of nutfall changes	Greenslade 1971
Eucalyptus borer (*Phoracantha aemipunctata*)	*L. humile*	Central/south Portugal	Predation on eggs	Way et al. 1992
Chyrsoperla carnea	*L. humile*	CA, USA (tulip trees)	98% of eggs removed on infested trees	Dreistadt et al. 1986
Citrus red mite (*Panonychus citri*)	*L. humile*	CA, USA (citrus)	Interferes with spider mite destroyer	Haney et al. 1987
Liothrips urichi	*P. megacephala*	HI, USA (*Clidemia hirta*)	Higher predation in ants exposed areas	Reimer 1988
Hemipteran and lepidopteran pests	*S. geminata*	Philippines (rice)	Ant-collected larvae, nymphs and eggs	Way et al. 1998

Golden apple snail (Pomacea canaliculata)	S. geminata	Philippines (rice)	Ants observed collecting eggs and young	Way et al. 1998
Cabbage webworm	S. geminata	Malaysia (cabbage)	Ants prey on prepupal and pupal stages	Sivapragasam & Chua 1997
Fall armyworm (Spodoptera frugiperda)	S. geminata	Honduras (maize)	Negative association with ant density	Cañas & O'Neil 1998
Diaprepes abbreviatus	S. geminata	Caribbean (citrus)	Able to prey on all life stages	Jaffe et al. 1990
Soybean looper (Pseudoplusia includens)	S. geminata	FL, USA (soybeans)	Egg predation higher when ants present	Nickerson et al. 1977
Boll weevils (Anthonomus grandis)	S. invicta	TX, USA (cotton)	Ant removal increased emergence, survival	Jones & Sterling 1979
Cotton leafworm (Alabama argillacea)	S. invicta	TX, USA (cotton)	Egg removal	Gravena & Sterling 1983
Helicoverpa zea	S. invicta	TX, USA (cotton)	Egg removal	Nuessly & Sterling 1994
Southern green stinkbug eggs	S. invicta	LA, USA (soybean)	Dominant egg predator in young soybean	Stam et al. 1987
Sugarcane borer (Diatrea saccharalis)	S. invicta	LA, USA	Predation of larvae	Negm & Hensley 1969
Fall armyworm (Spodoptera frugiperda)	S. invicta	LA, USA (sugarcane)	Higher infestations in ant-suppressed plots	Fuller et al. 1997
Weevil (Hypera postica)	S. invicta	GA, USA (greenhouse)	Larvae removal	Morrill 1978
Lacewing (Chrysoperla rufilabris)	S. invicta	GA, USA (pecans)	Eggs, larvae, and pupae decline	Tedders et al. 1990
Syrphid (Allograpta oblique)	S. invicta	GA, USA (pecans)	Ants preyed on puparia	Tedders et al. 1990
Lepidopteran larvae	S. invicta	OK, USA (peanuts)	Ants carried Lepidoptera larvae	Vogt et al. 2001
Herbivores (16 of 16 taxa)	S. invicta	AL, USA (cotton)	Negative association with ant density	Eubanks 2001
Herbivores (13 of 16 taxa)	S. invicta	AL, USA (cotton)	Negative association with ant density	Eubanks 2001
Fleahopper (Pseudatomoscelis seriatus)	S. invicta	Laboratory study	100% mortality when exposed to ants	Breene et al. 1990
Capsid bug (Sahlbergella singularis)	W. auropunctata	W. Africa	Reduces mirids and other insects	Entwistle 1972
INVERTEBRATES (HOMOPTERA)				
Scale (Coccus viridis)	A. gracilipes	Indonesia (coffee)	Reduced parasitism, increased growth	Van Der Goot 1916
Ceroplastes rubens, Coccus viridis	A. gracilipes	Seychelles (cinnamon)	5–160× more abundant when ants present	Haines & Haines 1978b
Black scale, Saissetia oleae	L. humile	Laboratory study	Decreased parasitism	Barzman & Daane 2001
Scale (Coccus hesperidium)	L. humile	Laboratory study	Decreased parasitization by 27–98%	Bartlett 1961
Red scale (Aonidiella aurantii)	L. humile	South Africa (citrus)	Associated with outbreaks	Samways et al. 1982
Mealybug (Planococcus ficus)	L. humile	South Africa (grapes)	Associated with outbreaks	Addison & Samways 2000

(Continued)

TABLE 3 (Continued)

Species	Ant	Location	Reported effect/mechanism	Study
Mealybug, (*Pseudococcus adonidum*)	*L. humile*	CA, USA (Cherimoyas)	Infestation correlated with ant trail intensity	Phillips et al. 1987
Walnut aphid (*Chromaphis juglandicola*)	*L. humile*	CA, USA (walnuts)	Removes parasitized aphids	Frazer & Van den Bosch 1973
Scale (*Coccus viridis*)	*P. megacephala*	HI, USA (*Pluchea indica*)	Removes predators, increases reproduction	Bach 1991
Mealybug (*Dysmicoccus neobrevipes*)	*P. megacephala*	HI, USA (pineapple)	Infestation increases with ant abundance	Beardsley et al. 1982
Mealybug (*Dysmicoccus brevipes*)	*P. megacephala*	HI, USA (pineapple)	Interferes with natural enemy behavior	Gonzalez-Hernandez et al. 1999
Scale (*Coccus viridis*)	*P. megacephala*	HI, USA (coffee)	Interferes with or preys on natural enemies	Reimer et al. 1993
Soft scale, mealybug	*P. megacephala*	South Africa (citrus)	Associated with outbreaks	Samways et al. 1982
Cassava mealybug (*Phenacoccus manihoti*)	*P. megacephala*	Ghana (cassava)	Creates tent shelter, deters natural enemies	Cudjoe et al. 1993
Mealybugs (*Planococcus njalensis*, *P. Citri*)	*P. megacephala*	Ghana (cocoa)	2–4× more abundant when ants tending	Campbell 1994
Brown citrus aphid (*Toxoptera citricida*)	*S. invicta*	Puerto Rico (citrus)	Decreases natural enemy larvae	Michaud & Browning 1999
Corn leaf aphid (*Rhopalosiphum maidis*)	*S. invicta*	Laboratory study	Increases parasitoid search time, destroys mummies	Vinson & Scarborough 1991
Cotton aphid (*Aphis gossypii*)	*S. invicta*	Laboratory study	Aphid predators ineffective when ants present	Vinson & Scarborough 1989
Cowpea aphid (*Aphis craccivora*)	*S. invicta*	Laboratory study	Deters coccinellid aphid predators	Dutcher et al. 1999
Mealybug (*Planococcus citri*)	*W. auropunctata*	Bahia, Brazil (cocoa)	4× more abundant when ants present	De Souza et al. 1998

Porter & Savignano 1990 [but see Morrison 2002]), canopy arthropods (Kaspari 2000), and decomposers (Vinson 1991, Summerlin et al. 1984a, Stoker et al. 1995, Hu & Frank 1996). Argentine ants also affect other invertebrates negatively, but studies report mixed results (Table 3), ranging from little apparent impact (Holway 1998a) to declines in the abundance of two orders (Human & Gordon 1997), three orders (Bolger et al. 2000), and eight orders (Cole et al. 1992).

Much of the evidence from which we draw conclusions about community-level effects on invertebrates comes from studies that compare faunas of invaded areas with those of comparable, uninvaded areas. If carefully designed and replicated, such comparisons can yield insights into a wide variety of impacts associated with ant invasions. This approach, however, has a number of important limitations. First, invaded and uninvaded sites may differ inherently with respect to environmental variables such as soil moisture, soil type, elevation, disturbance history, distance to edge, or the presence of other invaders. In such cases, the effects of invasive ants can be difficult to tease apart from the effects of covarying environmental variation (but see Bolger et al. 2000). Second, in community-level comparisons, the effects of invasive ants on a single species may be hard to detect or to test for statistically; this is especially true for rare species. Moreover, it is often difficult to generalize about effects on a given taxon from one community to another. For example, whereas some studies report negative effects of invasive ants on spiders (Lubin 1978, Haines & Haines 1978b, Cole et al. 1992, Gillespie & Reimer 1993), others either failed to detect significant effects (Porter & Savignano 1990, Human & Gordon 1997, Holway 1998a) or found positive associations (Bolger et al. 2000). Taken together, these results permit little insight into the kinds of interactions that take place between spiders and invasive ants. It seems likely that certain spiders (e.g., ground-dwelling species, Hawaiian endemics) are more affected by invasive ants than others (e.g., web-building species, species that evolved with ants), but even these generalizations are not well supported by data.

IMPACTS OF INVASIVE ANTS ON VERTEBRATES   Considerable correlative and limited experimental evidence suggests that vertebrate populations may also decline as a result of ant invasions. Putatively affected taxa (Table 3) include mammals (Killion & Grant 1993, Ferris et al. 1998, Meek 2000, Laakkonen et al. 2001), lizards (Donaldson et al. 1994, Feare 1999, Jourdan et al. 2001, Fisher et al. 2002), and birds (Allen et al. 1995, Feare 1999). Decreases in vertebrate populations have been attributed to most invasive ant species, including *L. humile* (Laakkonen et al. 2001, Fisher et al. 2002), *W. auropunctata* (Jourdan et al. 2001), and *A. gracilipes* (Feare 1999, Meek 2000), although most reports involve *S. invicta* (Wojcik et al. 2001).

Whereas a causal relationship between ant invasion and vertebrate population decline is commonly suggested, the specific mechanisms responsible are often obscure. Predation is frequently argued to be important; this is especially true for studies on *S. invicta*. But accounts are often limited to situations in which animals cannot escape attack (Table 3). Small mammals in cages or traps, for example,

are vulnerable to predation by *S. invicta* (Masser & Grant 1986, Flickinger 1989) (Table 3). Vertebrates also suffer nest predation by invasive ants. *Solenopsis invicta* has been implicated in nest failure for at least seven species of birds and nine species of reptiles (Table 3). The impacts of other invasive ants on the nesting success of vertebrates remain understudied, but both *A. gracilipes* and *L. humile* may cause nest failure in some bird species (Table 3). In some cases, it is unclear if ants caused nest failure or simply recruited to dead or dying nestlings. Moreover, it is often uncertain whether invasive ants reduce nesting success more than native ants do (Travis 1938, Chalcraft & Andrews 1999).

In addition to predation, invasive ants may affect vertebrates through other means. High densities of invasive ants may reduce the suitability of nest sites (Ridlehuber 1982) and alter behavioral patterns (Pedersen et al. 1996, Holtcamp et al. 1997), possibly increasing susceptibility to predation (Mueller et al. 2001). Changes in arthropod communities associated with ant invasions may also contribute to declines of insectivorous vertebrates including loggerhead shrikes [Lymn & Temple 1991 (but see Yosef & Lohrer 1995)], northern bobwhites (Allen et al. 1995), and horned lizards (Donaldson et al. 1994, Suarez et al. 2000).

The link between ant invasions and vertebrate declines is also supported by limited experimental evidence. Research on least terns *Sterna antillarum* (Lockley 1995), northern bobwhites *Colinus virginianus* (Mueller et al. 1999), and colonial waterbirds (Drees 1994) demonstrates that suppression of *S. invicta* can enhance nesting success between 27% (Lockley 1995) and 92% (Drees 1994). Similarly, captures of northern pygmy mice *Baiomys taylori* increased by over 50% after six months of fire ant suppression (Killion et al. 1995). It should be noted, however, that large-scale ant suppression using pesticides probably results in changes beyond the reduction of invasive ants (Yosef & Lohrer 1995, Hill & Dent 1985). Pesticides can negatively affect species directly through poisoning (Collins et al. 1974, Hill & Dent 1985, Williams et al. 2001) and indirectly through the reduction of arthropod prey (Lymn & Temple 1991).

To illustrate better the diversity of mechanisms by which invasive ants may affect vertebrate populations, we describe in more detail two relatively well-studied examples: the northern bobwhite (*C. virginianus*) and the coastal horned lizard (*Phrynosoma coronatum*).

Northern bobwhites and red imported fire ants   Several lines of evidence link declining northern bobwhite populations in the southeastern United States to invasion by *S. invicta*. First, significant correlations exist between the timing of fire ant infestation and drops in bobwhite density estimated from Christmas bird counts in Texas (Allen et al. 1995) and in Florida and South Carolina (Allen et al. 2000). Second, exposure to red imported fire ants decreases the growth rates and survival of chicks (Giuliano et al. 1996) and alters their time budgets, reducing time available for sleeping and foraging (Pedersen et al. 1996). Lastly, suppression of *S. invicta* leads to increases in both chick survival (Mueller et al. 1999) and adult density (Allen et al. 1995). It should be noted, however, that native fire ants

(*S. geminata*) also decrease nesting success in northern bobwhites (Travis 1938). The role of *S. invicta* in the decline of bobwhites has been debated in part for this reason (Brennan 1993).

Coastal horned lizards and Argentine ants   The invasion of *L. humile* into southern California is also correlated with the decline of a vertebrate species, the coastal horned lizard. This reptile has disappeared from up to 50% of its former range as a result of habitat destruction and collection for the pet trade (Fisher et al. 2002). However, portions of its remaining range, particularly in coastal California, may be unsuitable owing to invasion by Argentine ants. Like other *Phrynosoma* (Pianka & Parker 1975), the diet of *P. coronatum* consists primarily of ants, particularly large harvester species (e.g., *Messor* and *Pogonomyrmex*) that can constitute over 50% of their prey (and $\gg$50% of prey mass) (Suarez et al. 2000). Like many aboveground foraging ants, harvester ants are vulnerable to ant invasions (Hook & Porter 1990; Human & Gordon 1996; Suarez et al. 1998, 2000). Moreover, Argentine ants are unsuitable nutritional surrogates for native ants (Suarez & Case 2002). Hatchling horned lizards lose weight when raised on either Argentine ants or arthropods typical of invaded communities, whereas hatchlings raised on *Crematogster californica*, a common native ant, were able to maintain growth rates comparable to those of wild lizards (Suarez & Case 2002). Horned lizards avoid eating Argentine ants in the field, possibly because of their small size, noxious chemical defenses, or aggressive mobbing behavior (Suarez et al. 2000). It is also possible that Argentine ants can cause nest failure in horned lizards, although this remains to be tested. As a consequence of these factors, horned lizards are either absent from or occur at low densities in areas occupied by Argentine ants in coastal southern California (Fisher et al. 2002). The effects of invasive ants may extend to other horned lizard species as well. In Texas, the red imported fire ant has been implicated in the decline of the Texas horned lizard (*Phrynosoma cornutum*) (Donaldson et al. 1994).

Effects on Mutualistic Interactions

Ants enter into a variety of mutualistic interactions with plants and other insects. These interactions may be obligate or facultative, loose associations or species-specific, and may not always be mutually positive. How these interactions change in the context of ant invasions is a largely unexplored line of research teeming with questions of evolutionary, behavioral, and ecological significance. Much of what is known comes from agricultural settings. The extent to which patterns observed in agro-ecosystems occur in less manipulated settings remains to be documented in detail.

HOMOPTERA   The relationship between ants and honeydew-excreting Homoptera including scale insects, mealybugs, aphids, and treehoppers, is well known (Way 1963, Buckley 1987, Hölldobler & Wilson 1990). Among the benefits Homoptera

derive are protection from natural enemies, removal of exudates that may otherwise foul the immediate environment, increased feeding potential, and relocation to more favorable parts of the host plant (Way 1963). In exchange, ants acquire a reliable, defendable source of carbohydrate-rich food (Sudd 1987, Hölldobler & Wilson 1990). Whereas partnerships are often facultative and non-species specific (Way 1963), certain pairings may yield mutually higher benefits than others (Greenslade 1972, Bristow 1984, Gaume et al. 1998).

Although there have been few direct comparisons among invasive and other ants, the presence of invasive ants is frequently associated with local increases in homopteran abundance, both in the introduced and native ranges (Table 3). It should be noted, however, that *Solenopsis* may be an exception to this general pattern (Adams 1986, Tedders et al. 1990, Clarke & DeBarr 1996, Dutcher et al. 1999; but see Vinson & Scarborough 1989, Michaud & Browning 1999). In spite of these numerous reports, it is often unclear why invasive ants are exceptional tenders relative to native ants, and research examining the dynamics of these interactions in nonagricultural settings is almost completely lacking. Ants with modified crops, such as *L. humile* and *A. gracilipes*, can ingest relatively large quantities of liquid food, allowing them to excel at collecting honeydew (Eisner 1957, Davidson 1998). In addition, because tending ants can be a limiting resource for Homoptera (Sudd 1987, Cushman & Whitham 1991, Breton & Addicott 1992), the high abundance achieved by invasive ants may remove this limitation and allow Homoptera to thrive. Invasive ants may be especially effective at deterring natural enemies of Homoptera (Table 3).

Why is sustaining high densities of Homoptera beneficial for ants? As discussed above, access to carbohydrate-rich resources may be related to ecological dominance in ant communities (Davidson 1997, 1998). Empirical evidence on this point is scarce, correlative, and limited to agricultural settings but generally supports the hypothesis. The presence of Homoptera appears necessary for the maintenance of *A. gracilipes* in cocoa plantations in Papua New Guinea (Baker 1972). Likewise, in cocoa in Ghana, *P. megacephala* achieves dominance only when the Homoptera with which it is most closely associated are present (Campbell 1994). Similarly, *L. humile* does not appear to become dominant in South African vineyards with low levels of Homoptera (Addison & Samways 2000).

High densities of Homoptera associated with invasive ants may have repercussions for the host plant. Since Homoptera feed on plant phloem, large aggregations can lead to direct damage, fouling from mold, and higher susceptibility and exposure to phytopathogens (Way 1963, Buckley 1987). Evidence is plentiful. The ants listed in Table 1 have all variously been classified as pests because of their tending ability (Table 3). Alternatively, the ant-Homoptera mutualism may be beneficial to the host plant in cases where ants attack other herbivores (Messina 1981, Compton & Robertson 1988). For example, in Portugal, aphids attract *L. humile* to pines where the ants in turn prey upon larvae of the pine processionary moth, a major defoliator (Way et al. 1999). Three-cornered alfalfa nymphs attract *S. geminata* to soybean plants where they remove 77% of soybean looper eggs; only 37% of eggs

are removed from plants lacking nymphs (Nickerson et al. 1977). In addition, ants benefit plants when they remove enough honeydew to prevent sooty mold (Bach 1991).

PLANTS   Ant-plant mutualisms range from obligate interactions involving specialized domatia or food structures characteristic of true myrmecophytes to more facultative, nonspecific interactions (Buckley 1982, Keeler 1989, Hölldobler & Wilson 1990, Huxley & Cutler 1991). Not surprisingly, invasive ant-plant relationships fall in the facultative, nonspecific end of the spectrum and include tending, seed dispersal, and interactions in flowers. When native ants are displaced, invaders may usurp their roles and alter the dynamics of the interaction, or they may fail to replace natives functionally, in some cases disrupting relationships beneficial to the plant (Lach 2002). Invasive ants may also interact with plants in ways that native ants do not, to the potential detriment of the plant. Moreover, positive and negative effects of the same ant on the same plant may counteract or combine; such variability makes it difficult to generalize about the effects of invasive ants on plants (Lach 2002).

Flowers and pollination   If the ability to capitalize on carbohydrate-rich resources is important to becoming invasive, we might expect invasive ants to be attracted to floral nectar. However, few studies have examined associations among invasive ants and flowers. The acceptability of floral nectar to ants generally has been debated (Janzen 1977, Baker & Baker 1978, Feinsinger & Swarm 1978), and while it is clear that ants are repelled by the chemical or mechanical defenses of the flowers of some species (Willmer & Stone 1997, Ghazoul 2000), they readily consume nectar from the flowers of others (Haber et al. 1981, Koptur & Truong 1998).

Since ants are notoriously poor pollinators (Beattie et al. 1984, Hölldobler & Wilson 1990, Peakall et al. 1991), ants that are able to use floral nectar may be doing so at a cost to both the plant and legitimate pollinators. Data supporting these hypotheses are scant, but Buys (1987) found that Argentine ants exploited 42% of black ironbark nectar before honeybees began foraging, and Visser et al. (1996) documented a decline in arthropod visitors to *Protea nitida* flowers when *L. humile* was present in high numbers. Argentine-ant associated declines in seed set have been suspected (Potgieter 1937, Durr 1952), but unequivocal evidence is so far lacking (Buys 1990). Alternatively, the presence of invasive ants in flowers may enhance pollination, if it results in increased repositioning frequency of pollinators (Lach 2002). Other invasive ants are also known to visit flowers, sometimes to the observed detriment of the plant (Knight 1944, Adams 1986, Lofgren 1986, Hara & Hata 1992, Hata et al. 1995). Detrimental effects on pollinators may also occur through interactions away from the plant (e.g., Cole et al. 1992) (Table 3).

Extrafloral nectaries   As with flowers and honeydew-excreting Homoptera, we would expect that invasive ants exploit extrafloral nectaries (EFNs) as a carbohydrate-rich resource. EFNs are generally attractive to ants (Carroll & Janzen 1973),

and a number of hypotheses exist to account for the association. Plants with EFNs may attract ants in order to deter herbivores (Bentley 1977, Buckley 1982) or to distract ants from potentially detrimental activities such as tending Homoptera (Becerra & Venable 1989) or visiting flowers (Zachariades & Midgley 1999).

The paucity of research on invasive ant-EFN interactions precludes concluding whether invasive ants are more or less likely than native ants to be attracted to EFNs and to fulfill any of the roles played by native ants. There are scattered reports of invasive ants, both in their native and introduced ranges, visiting EFNs (Meier 1994), and a few of these studies measure the effects of the ants on the plant (Koptur 1979, Agnew et al. 1982, de la Fuente & Marquis 1999, Fleet & Young 2000) compared to other ants (Horvitz & Schemske 1984, Freitas et al. 2000, Hoffmann et al. 1999, Ness 2001). Although EFNs attract ants generally, the invasive ant-plant interaction may differ from the native ant-plant interaction if the invaders and native ants diverge in their nutritional preferences, periods of activity, foraging behavior, interactions with herbivores, or abundance (Lach 2002). For example, *S. invicta* visits *Catalpa bignonioides* EFNs less frequently than native ants because of differences in seasonal diet preferences; however, it is exceptionally intolerant of herbivores, so plant protection is not diminished (Ness 2001).

Seed dispersal   Seed dispersal by ants, or myrmecochory, is another type of mutualism between ants and plants. Ants transport seeds away from a parent plant, often in exchange for an elaiosome, a lipid-rich attachment to the seed (Buckley 1982, Beattie 1985). The few studies to date suggest that invasive ants may be poor seed dispersers relative to at least some ants they displace. In South Africa, Argentine ants displace most native ants that are effective seed dispersers, but they fail to disperse or to bury seeds, instead eating the elaiosome and leaving the seed aboveground where it is susceptible to rodent predation and fire (Bond & Slingsby 1984). Some of the smaller native ants are able to coexist with *L. humile* and continue dispersing small seeds, but displacement of the larger native ants may lead to declines in large-seeded plant species (Christian 2001). Similarly, in Corsica, *L. humile* appears less effective than *Aphaenogaster spinosa*, a dominant native ant, at dispersing the seeds of a rare endemic plant, but the consequences for the plant's population dynamics are unclear (Quilichini & Debussche 2000). Other invasive ants also may affect seed dispersal. Red imported fire ants, for example, collect the seeds of eliaosome-bearing herbaceous plants in South Carolina and leave them scarified and exposed on their trash piles (Zettler et al. 2001). In Australia, *P. megacephala* outcompetes native ants on some rehabilitated sand mines where it takes seeds of the elaiosome bearing *Acacia concurrens* (Majer 1985). Whereas both *S. geminata* and *W. auropunctata* interfere with seed dispersal of a myrmecochorous herb within their presumed native range in Mexico (Horvitz & Schemske 1986), any effect on seed dispersal in their introduced ranges is undocumented. Additional experimental studies will clarify the extent to which invasive ants affect plant communities through the disruption of ant-mediated seed dispersal. Experiments

that control for the effects of invasive ants on plant vigor and reproduction (e.g., pollination) and other confounding variables will be particularly valuable.

OTHER MUTUALISMS   Hölldobler & Wilson (1990) review symbiotic relationships between ants and other arthropods, a small subset of which can be considered mutualistic. Clearly, those species involved in obligate and species-specific relationships with native ant species that are vulnerable to displacement by invasive ants may themselves succumb to local extinction following invasion. Despite this concern, little research has been published on how ant invasions affect the ecology of myrmecophilic arthropods. Argentine ants, for example, may imperil lycaenid butterflies in South Africa because they displace the native ants that tend them, but probably do not fulfill their tending roles (A. Heath, unpublished observation). Whereas *A. gracilipes* participates in mutualistic relationships with a coprophagous reduviid bug in India (Ambrose & Livingstone 1979) and two species of coreid bugs on Malaysian bamboo (Maschwitz et al. 1987), and tends larvae of a lycaenid butterfly in Sulawesi (Kitching 1987), the origins of this ant are disputed, and it is unclear whether these constitute new associations or coevolved relationships.

Other Ant-Plant Interactions

DIRECT IMPACTS ON PLANTS   Direct effects of ants on plants include soil excavation around root systems, herbivory, and seed predation. Fire ants, for example, damage plants (Taber 2000) and frequently incorporate plant materials in their diet (Risch & Carroll 1986, Trabanino et al. 1989, Tennant & Porter 1991). In India, *S. geminata* attacks cucumber, tomato, cotton, and potato crops (Lakshmikantha et al. 1996). *Solenopsis invicta* also damages seeds, seedlings, and root systems of a variety of agricultural crops (Adams 1986, Banks et al. 1991, Drees et al. 1991, Vinson 1997, Shatters & Vander Meer 2000). Effects are likely not limited to agricultural systems; only 18 of 96 crop and noncrop seed species tested with *S. invicta* colonies in a laboratory experiment were resistant to damage (Ready & Vinson 1995). It is important to note, however, that in the southeastern United States, *S. invicta* commonly displaces *S. geminata*, a species that exhibits an even greater preference for seeds (Tennant & Porter 1991). Therefore, the impacts of *S. invicta* as a seed predator (e.g., Zettler et al. 2001) must be considered in the context of declining populations of *S. geminata*. Although most reports of invasive ants damaging plants focus on fire ants, *A. gracilipes* undermines the roots of several agricultural plants (Haines & Haines 1978b, Veeresh 1990), and *L. humile* damages figs and orange blossoms (Newell & Barber 1913) and spreads avocado stem canker (El Hamalawi & Menge 1996). Because of their high abundance, invasive ants may damage plants to a greater extent than do native ant species, but few direct comparisons exist.

EFFECTS ON HERBIVORES AND HERBIVORE ENEMIES   As discussed above, invasive ants prey upon a wide variety of invertebrates including herbivores that are

important plant pests. Supportive evidence includes direct observations, correlations in abundance between ants and herbivores, and controlled cage experiments (Table 3). As yet, there is no evidence for a hierarchy of prey desirable or acceptable to predaceous ants (Way & Khoo 1992). As for studies examining the predatory habits of invasive ants generally, the majority of studies on herbivore predation focus on *S. invicta*, which preys upon or drives off numerous species of insect herbivores, sometimes to the benefit of the plant, in a diversity of agricultural systems (Table 3; reviewed in Taber 2000). Similarly, populations of *A. gracilipes* in cacao (Baker 1972, Room & Smith 1975) and planted hoop pine (Wylie 1974), and *W. auropunctata* in cacao in West Africa (Entwistle 1972) are encouraged for their detrimental effects on economically important herbivores.

The predatory habits of invasive ants may also harm beneficial insects, resulting in negative impacts for the plants on which the interactions occur. In Zanzibar, for example, neither *A. gracilipes* nor *P. megacephala* affects the coconut bug, *Pseudotheraptus wayi*, but both species displace the native weaver ant, *Oecophylla longinoda*, an effective predator of this pest (Way 1953, Zerhusen & Rashid 1992). *Pheidole megacephala* also displaces beneficial ants from coconut palms in the Solomon Islands but fails to fulfill their roles as predators of the coconut bug, *Amblypelta cocophaga* (Greenslade 1971). In Malaysia and Indonesia, *A. gracilipes* eliminates the native ants (*Oecophylla smaragdina* and *Dolichoderus* spp.) that protect cacao against mirid *Helopeltis* spp., but it in turn fails to prey on these pests (Way & Khoo 1989). Invasive ants may also prey on or otherwise displace non-ant enemies of herbivores (Table 3).

Other Effects

OBLIGATE ASSOCIATES AND VISUAL MIMICS   Ants generally support a rich fauna of associates, many of which are other insects (Hölldobler & Wilson 1990). Some of these taxa form obligate, species-specific associations with ants; examples include mymecophilic beetles as well as dipteran and hymenopteran parasitoids. Although little studied from the perspective of ant invasions, such taxa would seem highly vulnerable, especially because many obligate associates of ants are rare and local to begin with (Hölldobler & Wilson 1990). For example, *S. geminata* supports species-specific phorid fly parasitoids (Morrison et al. 1999) that almost certainly decline in abundance as their host is displaced by *S. invicta* throughout the southeastern United States. Arthropods (mostly insects and spiders) are also visual mimics of ants. Through their superficial resemblance to ants, some of these mimics must enjoy safety from predators uninterested in ants as prey. To the extent that native ants serve as models to support the existence of such mimicry, visual mimics also seem in jeopardy from ant invasions.

SOIL CHEMISTRY, TURNOVER AND EROSION   Because the nesting activities of ants turn over large quantities of soil and alter its chemistry and physical structure (Hölldobler & Wilson 1990, Jolivet 1996, Folgarait 1998), the replacement of

native ants by invasive ants might generate ecosystem-level effects. Such changes might be especially important in situations where the nesting behaviors of native and invasive ants differ greatly. For example, in coastal California, Argentine ants displace *Messor* and *Pogonomyrmex* harvester ants (Erickson 1971, Human & Gordon 1996, Suarez et al. 1998). These harvester ants construct deep, long-lived nests in which seeds are cached and refuse (rich in organic matter and often including uneaten seeds) is discarded in a midden surrounding the nest entrance (MacMahon et al. 2000). Argentine ants, in contrast, typically occupy short-lived nest sites and usually fail to penetrate very deeply underground. It thus seems likely that the replacement of harvester ants by Argentine ants alters soil characteristics. The importance of such effects is unknown but deserves further scrutiny.

SYNERGISTIC EFFECTS   In some circumstances, the success of invasive ants may be facilitated by other invaders. Such mutually positive interactions may be a common feature of invasions (Simberloff & Von Holle 1999), but their frequency and importance with respect to ant invasions are not well known. Such interactions probably do occur in this context and deserve closer scrutiny. In Australia, for example, *P. megacephala* tends an EFN-bearing weed and may encourage its spread by deterring herbivores; the ant presumably benefits as well through the acquisition of food resources (Hoffmann et al. 1999). See Koptur (1979) for a similar example involing *L. humile* and a weedy vetch in California. The evidence linking ant dominance to availability of carbohydrate-rich resources suggests that honeydew-producing Homoptera too might facilitate the spread of invasive ants and vice versa. Bach (1991) describes such an interaction between *P. megacephala*, a non-native homopteran, and an introduced plant in Hawaii. Although not interpreted in terms of the spread of these non-native organisms, Bach's study illustrates that complexes of non-native species could invade in concert.

DIRECTIONS FOR FUTURE RESEARCH

In this review, we have attempted to synthesize a wealth of published information concerning the causes and consequences of ant invasions. Whereas many recent studies have enhanced a general understanding of these invasions, at the same time, they point to large gaps in knowledge. Given the focus on *L. humile* and *S. invicta*, there is an obvious need for research on additional species of currently or potentially invasive ants, especially those invading tropical environments. Below, we outline what we consider to be other key research needs.

Comparisons of Native and Introduced Populations

It is remarkable that almost all of what is known about the biology of invasive ants comes from studies of introduced populations. Although the same could be said of other invasive species (Steneck & Carlton 2001), this bias seems especially prominent for invasive ants. For example, accurate information about the location and boundaries of native ranges for most of the species listed in Table 1

either remains incomplete or is lacking all together. Two recent studies (Ross et al. 1996, Tsutsui et al. 2000) demonstrate the extent to which introduced populations can differ from native populations and in doing so make it clear that native populations should serve as an essential benchmark for any evolutionary inference. Given the likelihood of differences between native and introduced populations, between-range comparisons have great potential to add to what is known about ant invasions. Such comparisons will aid in the identification of geographic origins (Ross & Trager 1990, Tsutsui et al. 2001), clarify poorly resolved taxonomic and phylogenetic relationships, and elucidate the forces responsible for transitions in social organization (Ross et al. 1996, Tsutsui et al. 2000). Comparisons of native and introduced populations of invasive ants may also shed light on the relative importance of competitive release from native ants (Buren 1983), escape from natural enemies (Porter et al. 1997), and shifts in colony organization (Holway et al. 1998, Tsutsui et al. 2000) as factors influencing invasion success.

More Experimental, Large-Scale and Long-Term Studies

As is true for invasion biology generally, ecological research on invasive ants has largely been correlative or observational. A more comprehensive understanding of the causes and consequences of ant invasions will be achieved only through the implementation of manipulative experiments and studies conducted at larger spatial or temporal scales.

The value of manipulative field experiments in invasion biology is constrained somewhat by ethical concerns associated with introducing known invaders into new areas as an experimental treatment, but experiments nonetheless hold promise as a means to clarify both the causes and the consequences of ant invasions. Both short-term removals (Morrison 1996, Holway 1999) and short-term introductions (Bhatkar et al. 1972; Roubik 1978, 1980; Schaffer et al. 1983; Torres 1984; Human & Gordon 1996, 1999; Holway 1999) allow the study of behavioral interactions between native and introduced species of social insects. Although longer-term introduction experiments are often ethically untenable, a greater number of long-term removals (or partial removals), especially ones conducted at the leading edge of invasion fronts, should be attempted. Examples include studies that use pesticides to lower the density of red imported fire ants (Howard & Oliver 1978, Sterling et al. 1979, Allen et al. 1995, Adams & Tschinkel 2001). Although the confounding effects of pesticide treatment need to be carefully considered, experiments that lower the density of invasive ants can be highly informative.

Increasing the spatio-temporal scale of invasive ant research is also important. Some of the most dramatic examples of the impacts associated with ant invasions come from long-term (Erickson 1971, Greenslade 1971) or large-scale (Gotelli & Arnett 2000) studies. Long-term studies are an especially powerful means by which to study the ecological effects of ant invasions, as they allow explicit before-and-after comparisons of the same physical areas. A recent study by Morrison (2002) exemplifies this approach and illustrates how the ecological effects of ant invasions can vary greatly through time. Although few examples exist, studies conducted

across large spatial scales can clarify the determinants of geographic variation in invasion success, the factors governing range limits, and the extent to which the effects of ant invasions exhibit scale dependency.

Better Estimates of Density and Biomass

A comprehensive understanding of the ecological effects of ant invasions is also hindered by a lack of quantitative comparisons of the density and biomass of invasive and native ants. Such comparisons are needed to gauge the impacts associated with ant invasions but are also of more general interest in that they provide information on how the density and biomass of an important group of consumers are related to diversity.

The red imported fire ant is perhaps unique among invasive ants in that colony density and biomass can be estimated from mound number and mound volume, respectively (Tschinkel 1992, Porter et al. 1992). Interesting and informative comparisons of density and biomass thus exist for native and introduced populations (Porter et al. 1992, 1997) and areas occupied by the two social forms in the introduced range (Macom & Porter 1996). It is also possible to relate measures of colony size and biomass in *S. invicta* to territory area (Tschinkel et al. 1995).

Less progress has been made in trying to measure the density or biomass of other invasive ants or to compare such measures with those of native ants. Such comparisons are difficult to make in part because, unlike *S. invicta*, other invasive ants maintain diffuse supercolonies composed of ephemeral and poorly defined nests that may differ greatly from one another in size.

Prevention and Control

As information accumulates concerning the ecology of invasive ants, a framework for identifying potential invaders will hopefully be constructed from common features and knowledge of mechanisms. In the interim, a "guilty until proven innocent" policy (Ruesink et al. 1995) seems warranted given the great difficulty involved in eradicating established populations and the numerous problems that can result from successful invasion. Although ants have been advocated as agents of biological control in agricultural settings and may in fact be useful in such circumstances (Way & Khoo 1992), introducing any ant species into a new location seems unwise.

As with invasions of other organisms, identifying new infestations of invasive ants as rapidly as possible must greatly increase opportunities for eradication. Established populations present difficult challenges in that eradication over large areas is unfeasible and even local management, at present, remains difficult (Davidson & Stone 1989, Williams et al. 2001). Nonetheless, the development of integrated pest management strategies that incorporate both time-honored approaches and innovative ideas should remain an important goal. For example, if unicolonial-like colony structures are an important determinant of the high densities of some invasive ants, then tactics that lead to the dissolution of

supercolonies through increased intraspecific aggression could be profitable lines of attack (Suarez et al. 1999). Such strategies, while not resulting in eradication, could be used in concert with more traditional approaches to decrease both the magnitude and variety of negative ecological effects associated with these invasions.

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