Body size, colony size, abundance, and ecological impact of exotic ants in Florida's upland ecosystems

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ABSTRACT

Questions: Do naturalized exotic ant species have larger colonies and smaller workers relative to co-occurring native species? Do exotic ant species have a negative impact on the co-occurring ant and arthropod fauna in undisturbed native upland ecosystems?

Study system: Native and exotic ants sampled from four kinds of native upland ecosystems and one kind of disturbed ecosystem (fields) in north-central Florida. This fauna included a total of 94 species, 13 of which are exotic, from five different ecosystems.

Methods: Ants were intensively surveyed using a transect-based sampling design and four sampling methods (pitfalls, litter samples, baits, and hand collecting). We estimated average worker body weight and average colony size for all of the species, together with the relative abundance and species richness of native, exotic, and endemic species within ecosystems.

Results: The average body size of exotic ants was not obviously different from that of native species. The average colony size of exotic ants was smaller than that of native species, with the exception of *Solenopsis invicta*, which had the largest colony size of all species. Introduced ants (including *S. invicta*) were neither speciose nor abundant in any of the native woodland ecosystems. In contrast, in disturbed sites exotic ants accounted for about 40% of total ant abundance and 25% of species richness. Florida's intact, native upland ecosystems appear to be resistant to invasion of exotic ant species despite the fact that surrounding disturbed habitats host a large diversity and abundance of introduced species.

Keywords: biological invasion, body size, colony size, Formicidae, *Solenopsis invicta*.

INTRODUCTION

Why and where species become successful invaders and what impacts they have are poorly understood for most exotic species. At least five factors are likely to contribute to the most successful biological invasions: (1) attributes of the invader, (2) release from enemies, (3)

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community invasibility, (4) disturbance, and (5) propagule pressure (Mack *et al.*, 2000; Suarez *et al.*, 2005). An important challenge for ecology is to isolate and quantify each of these factors for a variety of exotic taxa. Examining the characteristics of established exotic species populations in the context of biogeography (habitat, historical factors, co-occurring fauna) as models for successful invasions is a starting point for isolating the factors responsible for the successful establishment of a given taxa and understanding what, if any, impacts they may have on native species (Simberloff, 1986; Sax *et al.*, 2005; Suarez *et al.*, 2005).

Introduced ants are important insect pests because they frequently negatively impact both economic interests and public health (Adams, 1986; Lofgren, 1986; Holway *et al.*, 2002). Some of the most conspicuous invasive species (e.g. *Linepithema humile* and *Solenopsis invicta*) have also been described as serious threats to native flora and fauna, particularly ecologically similar native ant species (Porter and Savignano, 1990; McGlynn, 1999a, 1999b; Holway *et al.*, 2002). Five ant species are listed among the 100 most important invasive exotic species in the world (Lowe *et al.*, 2004). Additionally, hundreds of other ant species have become established (McGlynn, 1999a, 1999b; Suarez *et al.*, 2005). Relative abundance, worker size, colony size, and foraging strategy are believed to be important in determining the competitive ability of ants (Hölldobler and Wilson, 1990; Holway *et al.*, 2002). Aggressive, mass-recruiting species with smaller workers (e.g. *L. humile* and *S. invicta*) are often successful at excluding competitors from food resources because they can employ higher numbers during conflicts over resources, which may convey a competitive advantage (Hölldobler and Wilson, 1990 and references therein; Franks and Partridge, 1993; Morrison, 2000). Some exotic ant species have been shown to have smaller workers relative to related non-invasive species from the same biogeographic region (Passera, 1994; McGlynn, 1999a). These observations led to the hypothesis that naturalized exotic ants tend to have larger colonies of smaller workers than native species.

The ant fauna of Florida is well-suited for examining the biogeography and species characteristics of exotic ants from local to regional scales. The entire fauna includes 218 species, 52 of which are established exotics (Deyrup, 2003). Here we use 'exotic' to describe any ant species that was transported to Florida by humans. This exotic ant fauna is the largest among any of the states in the USA and probably among the largest regional exotic faunas in the world. Furthermore, the ant fauna of Florida is representative of the entire southeastern coastal plain of the United States, but richer in endemics (Creighton, 1950; Deyrup, 2003). For the purposes of this paper, 'endemic' species are any species whose distributions are entirely confined to native upland ecosystems in Florida and adjacent Alabama and Georgia. The regional distribution of most species is well known and has been followed for decades (Deyrup *et al.*, 2000; Deyrup, 2003).

Species characteristics of social insects such as worker body size, colony size, and regional distribution are poorly known in most parts of the world (Hölldobler and Wilson, 1990; Holway *et al.*, 2002). Without these sociometric data, it is difficult to understand how and why some exotic social insects become established and abundant (Tschinkel, 1991). Here we build upon the knowledge of Florida's exotic and native ants (Deyrup *et al.*, 2000; Deyrup, 2003; King and Tschinkel, 2006; Tschinkel, 2006) by surveying the abundance and distribution of exotic species in representative undisturbed and disturbed ecosystems, and comparing the body size, colony size, and abundance of exotics relative to native species. We assessed the potential impact of exotic ants on co-occurring native ants and other arthropods by examining their frequency of occurrence in relation to exotic ants.

METHODS

Upland ecosystems

Ants were intensively surveyed in four localities in north and central Florida between Columbia County in the north and Highlands County along the Lake Wales Ridge in the south. Using the ecosystem criteria of Myers and Ewel (1990a), we sampled in the four most common, widespread natural upland ecosystem types in Florida. The localities we sampled in were selected because they represent some of the least disturbed remaining native upland ecosystems in peninsular Florida. We sampled in temperate hardwood forests, or hardwood hammocks, in San Felasco Hammock State Park. Hardwood hammocks in Florida are associated with mesic, organically rich soils and have an extremely diverse overstory and understory relative to other temperate forests (Platt and Schwartz, 1990). Structurally, these forests have a closed canopy, a diverse understory, and a deep layer of leaf litter. We sampled in pine flatwoods in Osceola National Forest. Pine flatwoods are associated with flat topography and poorly drained, acidic, sandy soil (Abrahamson and Hartnett, 1990). They are characterized by an open overstory of pines (*Pinus palustris* Mill. and *P. elliottii* Engelm.) and a dense ground cover (Abrahamson and Hartnett, 1990). We sampled in high pine at the Katherine Ordway Biological Preserve. High pine is a savannah-like ecosystem that occurs on rolling topography and well-drained, sandy soil (Abrahamson *et al.*, 1984; Myers, 1990). These plant communities are characterized by an open canopy of pine and hardwoods and a sparse-to-dense herbaceous ground cover (Abrahamson *et al.*, 1984; Myers, 1990). We sampled in Florida scrub forests at the Archbold Biological Station. Florida scrub forests occur exclusively in the southeastern USA and are structurally characterized by a sparse overstory of pines, a dense understory of stunted hardwoods and shrubs, and very sparse herbaceous ground cover (Myers, 1990). These densely vegetated, stunted forest ecosystems are associated with xeric conditions and well-drained, sandy soil (Abrahamson *et al.*, 1984). Finally, we chose previously cleared (> 20 years ago), ungrazed fields as a contrast to the undisturbed ecosystems. These disturbed ecosystems can be found throughout the central inland ridges of north and central Florida and we sampled in fields near to our other plots in San Felasco Hammock State Park, Katherine Ordway Preserve, and Archbold Biological Station. Fields are characterized by an absence of trees and a moderate to dense herbaceous ground cover.

Sampling and measurements

We developed a sampling programme to produce a nearly complete species list with associated abundance data from a representative locality for each upland ecosystem and for the region as a whole. Four sampling methods (pitfall trapping, Berlese funnels, baiting, and hand collecting) were used in standardized replicate (3) transects in each ecosystem separated by large distances (1 km or more). Within each transect, a total of 36 pitfall traps and 36 litter samples were placed separately at 5-m intervals (180 m total) in two parallel lines separated by 10 m. A transect of 36 baits was placed between the pitfall and litter extraction lines with each bait corresponding to pitfall and litter extraction samples. Hand collecting consisted of systematically searching vegetation, tree trunks, logs, small twigs, and litter sifting for 2 h per site. This sampling programme was effective, sampling 70–90% of the known species in each ecosystem and the entire region (King and Porter, 2005) and

quantifying relative abundance of species. A full description of the sampling methods is given in King and Porter (2005).

We used both numerical abundance and sample-based incidence (frequency of species occurrences in samples) to assess relative abundance. Numerical abundance of ants in pitfalls and litter samples is probably the most accurate way of measuring differences in abundance within and among ecosystems (King and Porter, 2005). We used frequency of occurrence to measure spatial occupancy. Over large areas, sample-based incidence provides an effective, standardized estimate of spatial distribution that permits comparisons among sampling designs (Kaspari et al., 2000a, 2000b, 2004; Kaspari, 2001) and sampling methods (Longino and Colwell, 1997; King and Porter, 2005; King, 2007). These two complementary methods of assessing relative abundance are closely correlated over our large transects [$R^2 \geq 0.85$ (J.R. King, unpublished data)].

We used dry weight of workers of each species as our measure of size (Kaspari and Weiser, 1999; Weiser and Kaspari, 2006; King, 2007). Body mass is closely correlated with other variables, such as size of food particles workers can carry, the rate and distance at which workers forage, and desiccation resistance (Hood and Tschinkel, 1990; Kaspari and Weiser, 1999; Ness et al., 2004). Worker size is fundamentally connected to ecological niche, population dynamics, evolutionary rates, and community structure (Peters, 1983; Brown et al., 2004).

Our worker body mass values (Table 1) do not account for changes in seasonal fat content or worker polymorphism within species. Also, for *Pheidole* species we used only the weight of minor workers, as majors were uncommon in samples. There were 29 species, including four exotics, which were not weighed because they were mounted as vouchers. For these species, the body mass of a similar-sized species in the same genus was rounded to the nearest fraction (tenth, hundredth, and thousandth) of a milligram (Rogers et al., 1976; Kaspari and Weiser, 1999). Unweighed species were rare, appearing in less than 1% of samples.

We estimated mature colony size (rounded to the nearest 10, 100, or 1000) for each species (Table 1). For 40 species, estimates were based on collections of 3–24 entire colonies by the first author. Colony sizes for the remaining 54 species are from the literature (Van Pelt, 1958; Fowler, 1980; Hölldobler and Wilson, 1990; Heinze et al., 1993; Tschinkel, 1993, 1998, 2002, 2005; McInnes, 1994; Kaspari and Vargo, 1995; Wilson, 2003).

We assessed the relationship among introduced ant species, native ants, and non-ant arthropods across ecosystems. The species richness of native and introduced ant species was determined from all sampling methods, but analyses of non-ant arthropods used only data from pitfall and litter extraction samples because these were not collected at baits or by hand. Non-ant arthropods were identified by the first author to morphospecies within families – a highly conservative estimate of species richness per sample point. This was done to generate a relative sample-point estimate of non-ant arthropod species richness, which was averaged within sites to create a morphospecies occurrence value that could be compared across ecosystems (Porter and Savignano, 1990).

RESULTS

Overall, the ant fauna was diverse, with a total of 94 species from 31 genera. This included 13 exotic species and 9 endemics (Table 1). There were 12 arboreal species, one of which (*P. gracilis*) was exotic. The richest genera sampled were *Solenopsis* (10 species, 1 exotic), *Pheidole* (7 species, 1 exotic), *Camponotus* (6 species), *Paratrechina* (6 species), and

Table 1. The 94 ant species arranged alphabetically under subfamilies

Species	Mass (mg)	Colony size	Hardwood hammock	Pine flatwoods	Florida scrub	High pine	Field
Amblyoponinae							
Amblyopone pallipes (Haldeman)	0.616	10	1P, 5L		1P		
Dolichoderinae							
Dorymyrmex bossutus[1] (Trager)	0.115	1000			3P	1P, 1L, 3B	49P, 12L, 37B, 3H
Dorymyrmex bureni (Trager)	0.189	1000				1B, 1H	
Dorymyrmex elegans[1] (Trager)	0.190	1000					
Dorymyrmex grandulus (Forel)	0.115	1000			1P	1P, 1B, 1H	
Dorymyrmex reginicula (Trager)	0.230	1000					4H
Forelius pruinosus (Roger)	0.061	10,000		20P, 11B, 2H	5P, 2L, 1B, 1H	31P, 10L, 25B, 2H	23P, 1L, 17B, 1H
Forelius sp. nov.[1]	0.062	10,000				6P, 1L, 1B, 1H	1B
Ecitoninae							
Neivamyrmex carolinensis (Emery)	0.153	30,000				2P	
Neivamyrmex opacithorax (Emery)	0.214	30,000				1P	
Neivamyrmex texanus Watkins	0.564	30,000				4P	1P
Formicinae							
Brachymyrmex depilis Emery	0.012	200	4L	17P, 16L, 5H	3P, 12L, 1H	2L	2P
Brachymyrmex sp. nov.	0.010	200	1L				
Brachymyrmex sp. nr. obscurior Forel	0.043	200					5P, 6L
Camponotus castaneus (Latreille)	5.860	350	1P, 1L, 3H	1P			
Camponotus discolor[2] (Buckley)	1.280	70				1H	
Camponotus floridanus (Buckley)	3.463	10,000	1P, 2L, 1B, 1H	20P, 7L, 7B, 2H	2P, 1L, 2H	5H	
Camponotus impressus[2] (Roger)	0.259	250				1H	
Camponotus nearcticus[2] Emery	5.800	70		1H			
Camponotus socius Roger	5.900	350		1B, 1H		4P, 1B, 2H	
Formica archboldi[1] M.R. Smith	1.700	500		18P, 2L, 9B, 2H			
Formica pallidefulva Latreille	1.717	400		5P, 4B	3P, 7L, 1B, 2H		
Formica schaufussi dolosa Wheeler	2.062	600		2P, 1B			
Paratrechina arenivaga (Wheeler)	0.090	100		6P, 2L, 1H	6P, 2L	7P, 2L, 3B	2P
Paratrechina concinna Trager	0.047	100	4P, 26L, 10B	5P, 4L, 1H	3P		2P, 1L
Paratrechina faisonensis (Forel)	0.084	100		20P, 13L, 1H	1B	5P, 1L, 2B	
Paratrechina parvula (Mayr)	0.052	100				1L, 1B	
Paratrechina phantasma[1] Trager	0.090	100				6P, 1B, 1H	11P, 2L
Paratrechina wojciki[1] Trager	0.035	100		6P, 6L, 2B	9P, 23L	3P, 7L	

Table 1.—(continued)

Species	Mass (mg)	Colony size	Hardwood hammock	Pine flatwoods	Florida scrub	High pine	Field
Myrmicinae							
Aphaenogaster ashmeadi (Emery)	0.640	300			3P, 2L, 4B	1P, 1B, 2H	
Aphaenogaster flemingi M.R. Smith	1.220	300		1P, 1B, 2H			
Aphaenogaster floridana M.R. Smith	0.640	50				4P, 1L, 1B, 1H	3P, 1L, 2B
Aphaenogaster lamellidens[2] Mayr	1.250	300	1L				
Aphaenogaster treatae Forel	0.759	300				1P, 1B	19P, 9L
Cardiocondyla emeryi[3] Forel	0.028	50					10P, 1B
Cardiocondyla nuda[3] (Mayr)	0.028	50					
Cardiocondyla wroughtonii[3] (Forel)	0.030	50		2P			
Crematogaster ashmeadi[2] Mayr	0.160	10,000		1P, 2H	2P, 5L, 1H	7P, 8L, 2B, 3H	
Crematogaster atkinsoni Wheeler	0.416	500		2L			
Crematogaster lineolata (Say)	0.200	200				1H	
Crematogaster minutissima Mayr	0.110	200		1P, 1L	2L		
Cyphomyrmex minutus Mayr	0.136	150			1P, 3L		1L
Cyphomyrmex rimosus[3] (Spinola)	0.256	150	3P, 4L, 2H	1P	3P, 1L	1P, 3L	14P, 1L
Eurhopalothrix floridanus Brown & Kempf	0.136	100	8L		2L	1L	
Monomorium viride Brown	0.037	10,000		19P, 15L, 13B, 2H	1H	3P, 3L, 1B, 1H	
Myrmecina americana Emery	0.268	50	2L				
Pheidole adrianoi[1] Naves	0.031	350				1P	
Pheidole dentata Mayr	0.077	800	33P, 45L, 74B, 13H	52P, 19L, 28B, 1H	70P, 52L, 71B, 3H	18P, 6L, 9B, 4H	23P, 5L, 7B, 1H
Pheidole dentigula M.R. Smith	0.030	300	31P, 87L, 4B, 2H	2L	22P, 62L		
Pheidole floridana Emery	0.027	1000		53P, 15L, 25B, 3H	38P, 39L, 35B, 1H	13P, 18L, 7B, 2H	7P, 4L, 2B
Pheidole metallescens Emery	0.036	1000			3P, 6L, 1B, 1H	21P, 15L, 21B	3P, 1L, 1H
Pheidole moerens[3] Wheeler	0.034	600	11P, 26L, 8B, 4H	1P, 2L	6P, 2L	19P, 2L, 9B, 2H	6P, 12L, 2B, 1H
Pheidole morrisi Forel	0.090	2500		5P	4P, 1L, 2B	19P, 1L, 3B, 1H	17P, 1L, 3B, 2H
Pogonomyrmex badius (Latreille)	2.778	4500			1L, 1H		2P, 4B, 1H
Pyramica bunki (Brown)	0.021	40		1P			
Pyramica clypeata (Roger)	0.021	50	1L				
Pyramica creightoni (M.R. Smith)	0.026	50		2P			1L
Pyramica deyrupi Bolton	0.021	50		2P, 4L			
Pyramica dietrichi (M.R. Smith)	0.021	50		1L			
Pyramica eggersi[3] (Emery)	0.021	50	3L		4P, 4L		L(1)
Solenopsis geminata (Fabricius)	0.325	28,000				8P, 14L, 17B, 1H	26P, 6L, 24B, 2H
Solenopsis globularia (F. Smith)	0.075	50			1P, 2L		
Solenopsis invicta[3] Buren	0.360	150,000					11P, 7L, 12B, 1H

Species	Body mass (mg)	Colony size					
Solenopsis nickersoni Thompson	0.020	200	2P	27P, 16L, 1B	19P, 28L	6P, 9L	
Solenopsis pergandei Forel	0.025	10,000				6L, 2H	2P
Solenopsis picta[2] Emery	0.020	200	1P		3P	1L, 1H	
Solenopsis sp. nr. *abdita* Thompson	0.020	200	3L			2P, 5L	
Solenopsis sp. nr. *carolinensis* Forel	0.025	200	73P, 101L, 23B, 3H	63P, 59L, 7B, 3H	28P, 53L	19P, 34L	5P, 12L
Solenopsis tennesseensis M.R. Smith	0.008	200	3P, 44L, 1H	1P, 2L	1P, 50L	1P, 20L	5L
Solenopsis tonsa Thompson	0.008	200				1L	
Strumigenys emmae[3] (Emery)	0.053	100			1L		
Strumigenys louisianae (Roger)	0.053	90	9P, 31L	1L	1L	3L	3L
Strumigenys rogeri[3] (Emery)	0.027	100			1L		
Temnothorax bradleyi[2] Wheeler	0.160	50		1H			
Temnothorax palustris[1] Deyrup & Cover	0.140	50		1P, 5L			
Temnothorax pergandei Emery	0.168	50		65P, 37L, 6B	10P, 13L, 1H	8P, 13L, 1B, 3H	1L
Temnothorax texanus Wheeler	0.135	50				1P, 2L, 1B	
Tetramorium simillimum[3] (F. Smith)	0.058	300			1L		9P, 5L, 1B
Trachymyrmex septentrionalis[3] (McCook)	0.380	300	5P, 6L		7P, 3L, 1H	5P, 2L, 1H	5P, 1L, 1H
Wasmannia auropunctata[3] (Roger)	0.050	800					1B
Xenomyrmex floridanus[2] Emery	0.028	50			1L, 1H	1B	
Ponerinae							
Hypoponera inexorata (Wheeler)	0.070	50	1L	1L	1L	1L	
Hypoponera opaciceps (Mayr)	0.068	50	1L				
Hypoponera opacior (Forel)	0.068	50	12P, 88L, 4H	11L, 1B	15L	23L, 1B	1P, 2L
Odontomachus brunneus (Patton)	2.603	200	60P, 23L, 22B	42P, 12L, 4B	12P, 6L, 2H		
Odontomachus relictus[1] Deyrup & Cover	1.813	200			23P, 7L, 2B		11P, 1L, 1B
Odontomachus ruginodus[3] M.R. Smith	1.851	200					4P
Platythyrea punctata (F. Smith)	1.690	60					
Ponera exotica M.R. Smith	0.060	50	6L		1H		
Proceratiinae							
Proceratium pergandei (Emery)	0.210	25	1H				
Pseudomyrmecinae							
Pseudomyrmex ejectus[2] (F. Smith)	0.400	80	1P, 1L, 1H				
Pseudomyrmex elongatus[2] (Mayr)	0.400	80			1H		
Pseudomyrmex gracilis[2,3] (Fabricius)	1.350	80			1L, 1H		
Pseudomyrmex pallidus[2] (F. Smith)	0.400	30		1L, 1B		1L, 1H	1L, 1B

Note: Data columns are body mass (mg) of workers, colony size (number of workers), and frequency of occurrence in ecosystems listed by the type of samples in which workers occurred. P = pitfall trap, L = litter extraction, B = bait, and H = hand collected. A total of 108 (36 × 3 transects) pitfalls, litter samples, and baits were used in each ecosystem.

[1] Endemic species. [2] Arboreal species. [3] Exotic species (shown in **bold**).

Pyramica (6 species, 1 exotic). *Cardiocondyla*, an entirely exotic genus in Florida, was the genus richest in exotics with 3 species.

There was little evidence that exotic ant species had any impact on co-occurring ants in the undisturbed woodland ecosystems. On average, exotic ants were not abundant and did not occur frequently (Table 1, Fig. 1). Exotic species accounted for less than 1% of the average abundance and occurrence of ants in pine flatwoods and high pine, about 3% in Florida scrub, and approximately 8% in hardwood hammock. Similarly, when assessed by total mass of foragers (abundance × worker dry weight), exotic ants accounted for, on average, <1% of mass in pine flatwoods, Florida scrub, and high pine, and 2% in hardwood hammock. Exotic species did, however, occur in all ecosystems (Fig. 1), accounting for 16% of the total number of species in Florida scrub (7 of 43 species across all three transects), 10% in hardwood hammock (3 of 29), 8% in pine flatwoods (3 of 39), and 2% in high pine (1 of 48). In contrast, in fields, exotic ants accounted for about 40% of the total abundance and 25% of the total species occurrences and number of species (9 of 36 species; Table 1, Fig. 1), and 35% of the biomass of foragers.

The average number of species was significantly different among ecosystems ($F_{4,10} = 4.93$, $P = 0.02$) with high pine having the most species ($n = 35$) followed by Florida scrub ($n = 29$),
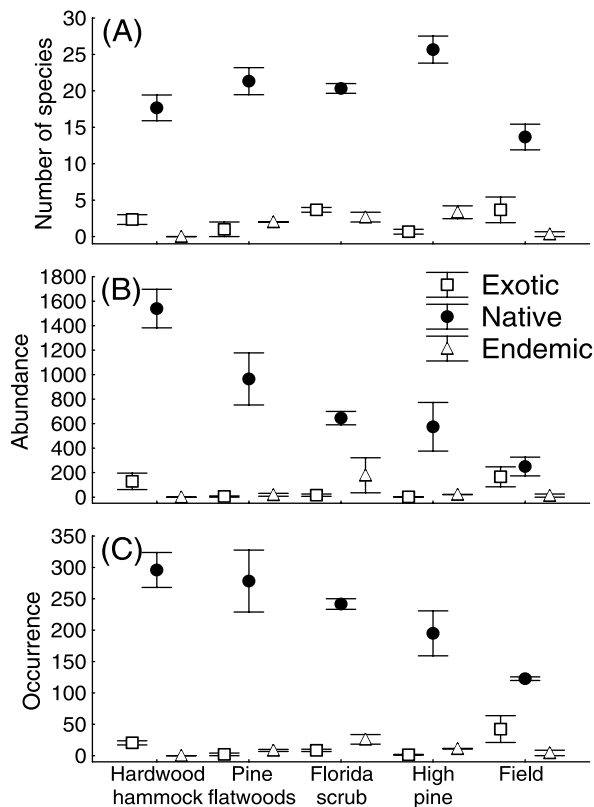

Fig. 1. The mean (A) number of species, (B) numerical abundance, and (C) occurrence of native, exotic, and endemic species in samples in upland ecosystems. Symbols represent mean values for native, exotic, and endemic species and error bars represent 1 standard error of the mean.

pine flatwoods ($n = 27$), hammock ($n = 21$), and fields ($n = 20$). The average number of exotic species was not significantly different among ecosystems ($F_{4,10} = 2.48$, $P = 0.11$), although there were more exotic species in fields (2% in high pine, 4% in pine flatwoods, 11% in hardwood hammock, 14% in Florida scrub, and 23% in fields). Similarly, the average number of exotic species occurrences was not significantly different among ecosystems ($F_{4,10} = 3.09$, $P = 0.07$) but exotic species were more common in fields (23% of total occurrences compared with <1% in high pine, <1% in pine flatwoods, 3% in Florida scrub, and 6% in hardwood hammock). In summary, these results indicate that while exotic species did occur in all ecosystems, they were not abundant in undisturbed ecosystems but were abundant in more disturbed field ecosystems.

There was a difference among average worker body sizes in all of the ecosystems (Fig. 2). The range of body sizes in undisturbed ecosystems was greater than in fields with larger species in all cases (Fig. 2). The mean body size of workers was similar among undisturbed ecosystems but smaller, on average, in fields ($F_{4,10} = 2.62$, $P = 0.10$). Average worker size per species was between 0.42 and 0.56 mg in undisturbed ecosystem sites but 0.23 mg in field sites. This represents approximately a 50% difference between average worker body size in
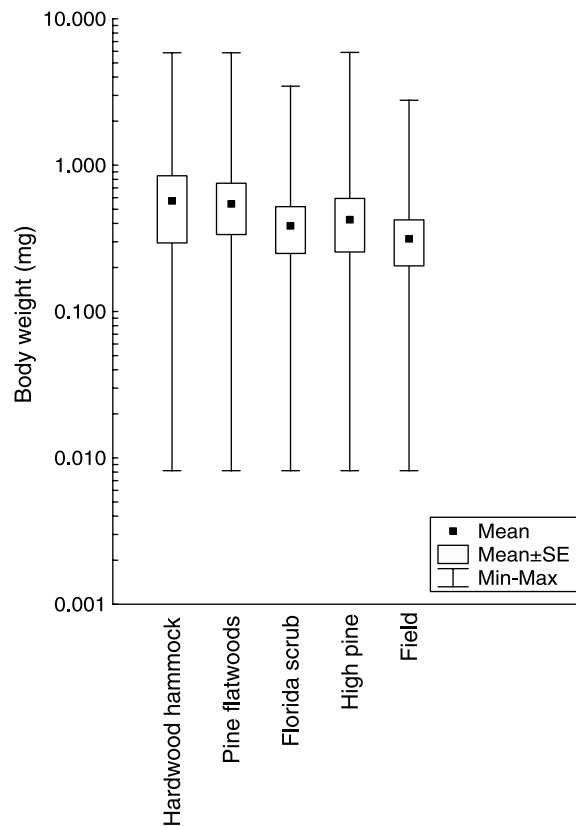

Fig. 2. The mean, standard error, and range of dry body weight (mg) of ant workers in upland ecosystems. There was no significant difference in mean weight (ecosystems, $F_{4,10} = 2.62$, $P = 0.098$) but mean body weight in fields was approximately 50% lower than all other ecosystems. The ordinate (y-axis) is scaled logarithmically.

undisturbed habitats versus fields when all species are considered (native and exotic). The smallest species included *Brachymyrmex* sp. nov., *B. depilis*, and the two smallest *Solenopsis* (Diplorhoptrum) species, *S. tennesseensis* and *S. tonsa* (Table 1). The largest species were *Camponotus castaneus* and *C. socius*. Neither exotic species nor endemic species were ever among the very largest or very smallest workers in any ecosystem.

Generally, the body size of workers from closely related species within a genus was similar, including exotic/native and native/endemic comparisons (Table 1). For example, the exotic, *Pheidole moerens*, was little different in size from three similar native *Pheidole*, *P. dentigula*, *P. floridana*, and *P. metallescens* (Table 1). When there was a difference between the body size of native and exotic species in the same genus, the exotic species were often larger (e.g. exotic and native species in the genera *Cyphomyrmex*, *Pseudomyrmex*, and *Odontomachus*), but there was one example of an exotic species that was smaller than the native species in the genus *Strumigenys* (Table 1). There was also no clear pattern among native/endemic comparisons. For example, there were both larger and smaller native species than endemics in the genera *Dorymyrmex*, *Paratrechina*, and *Temnothorax*.

With the exception of *Solenopsis invicta*, the colony size of exotic species was, on average, smaller than that of native and endemic species (Fig. 3a, b), although the difference was not
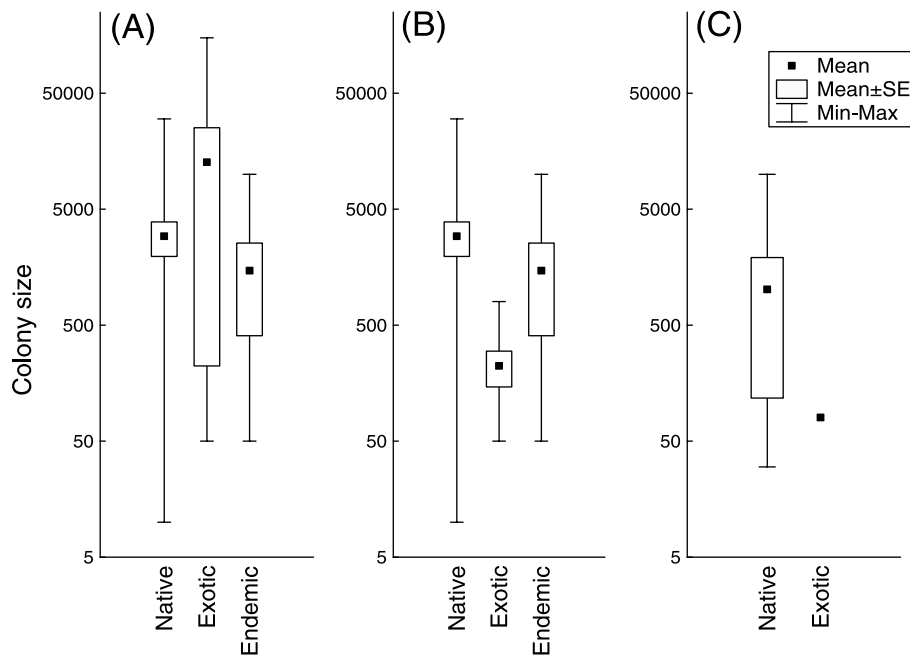

Fig. 3. The mean, standard error, and range of body weight (mg) of (A) ground-nesting ants with *S. invicta*, (B) ground-nesting ants without *S. invicta*, and (C) arboreal species. There was no significant difference between native, endemic, and exotic colony size for either (A) ground-nesting species including *S. invicta* (colony size, $F_{2,79} = 1.70$, $P = 0.19$) or (B) ground-nesting species excluding *S. invicta* (colony size, $F_{2,78} = 0.80$, $P = 0.45$), although native species were, on average, more than 10 times larger in the latter case. There was no significant difference between native and exotic colony size for (C) arboreal species (colony size, $F_{1,10} = 0.09$, $P = 0.80$), although there was only one exotic arboreal species (*Pseudomyrmex gracilis*) to compare with native species. The ordinate (y-axis) is scaled logarithmically.

statistically significant. The colony size of *S. invicta* was by far the largest among all species (Table 1), accounting for a large change in the average colony size of exotic species when they were factored in (Fig. 3c). When *S. invicta* was excluded from the analysis (Fig. 3b), the average colony size of exotic species was more than ten times smaller than that of native species and nearly ten times smaller than that of endemic species ($F_{2,78} = 0.80$, $P = 0.45$). Although there was only one exotic arboreal species for comparison (*P. gracilis*), the pattern was similar for arboreal species (Fig. 3a), with the average colony size of exotic species more than ten times smaller than that of native species ($F_{1,10} = 0.10$, $P = 0.77$). The range of both exotic and endemic species colony sizes was narrower than that of native species and exotic and endemic species, with the exception of *S. invicta* (Fig. 3, Table 1).

The relationships between exotic species, native ants, and non-ant arthropods also revealed that exotic species appear to have a minimal impact on the native fauna. There was no significant relationship between the average number of species occurrences of native species and exotic species across ecosystems (Fig. 4a). Similarly, the frequency of occurrence of exotic ants was not significantly related to the frequency of occurrence of non-ant morphospecies, although the trend was weakly negative (Fig. 4b). In contrast, there was a significant positive relationship between the occurrence of native ants and the occurrence of non-ant morphospecies (Fig. 4c), suggesting that the factors affecting native ant species abundance, such as ecosystem productivity or spatial heterogeneity, also affect the species richness of co-occurring arthropods. The patterns we report here were unchanged when abundance or biomass of ants was used in place of occurrence data.

The overall composition of the fauna revealed that relatively undisturbed (anthropo-genically), open canopy ecosystems supported the highest number of ant species, while closed canopy hardwood forest and previously disturbed field sites supported the fewest (Fig. 1). Closed canopy hardwood hammocks are cooler than the more open, pyrophytic ecosystems and the ant fauna is largely limited to species associated with (adapted to) shady mesic forest in the southeastern and eastern temperate USA. In contrast, the warmer, open pine flatwoods, scrub, and high pine ecosystems support a mixture of xeric- and mesic-adapted species. The specific habitat associations of endemic species also contributed to increases in species richness in pine flatwoods, scrub forest, and high pine ecosystems. For example, *Temnothorax palustris* is restricted to pine flatwoods in northern Florida and *Pheidole adrianoi* and *Dorymyrmex elegans* are restricted to high pine and scrub in northern and central Florida (Table 1). Most of the endemic species in the regional fauna are adapted to the more xeric high pine and Florida scrub ecosystems. Fields supported a mixture of native and introduced species that are generally associated with disturbed habitats and include a number of species, including *S. invicta*, that are considered competitively dominant.

The most common and abundant species across all ecosystems, *Pheidole dentata* and *Solenopsis carolinensis* (Table 1), are widespread throughout the southeastern coastal plain (Creighton, 1950; Thompson, 1989; Wilson, 2003). *Pheidole dentata* is a conspicuous, ground-dwelling species frequently associated with woodland ecosystems across the southern USA, including Florida (Creighton, 1950; Wilson, 2003). Among Florida's native *Pheidole* species, *P. dentata* has relatively large individual worker size (Table 1). In contrast, *S. carolinensis* is a subterranean species of the Diplorhoptrum subgenus, commonly referred to as thief ants for their habit of consuming the brood of other species of ants (Thompson, 1989). In general, Diplorhoptrum workers are among the smallest temperate ant species and are among the smallest ants (Table 1) (Kaspari and Weiser, 1999).
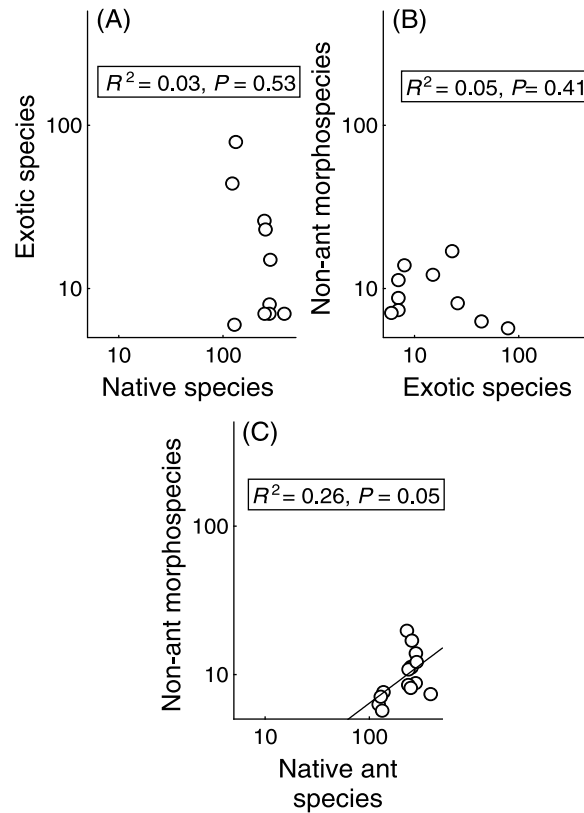
Fig. 4. The relationship between (A) the occurrence of native ants and exotic ants, (B) the mean occurrence of non-ant arthropod morphospecies and exotic ants, and (C) the mean occurrence of morphospecies and native ants. None of the variables were strongly correlated and only the occurrence of native ants and non-ant morphospecies was linear. All values were $\log_{10}(x+1)$ transformed to allow transformation of zero values. For simplicity in these graphs, 'native' ants includes endemic species.

The exotic ant fauna sampled in this study represents a diversity of natural histories, ranging from specialized predators associated with more mesic sites (e.g. *Strumigenys rogeri* and *Pyramica eggersi*) to species distributed primarily in disturbed habitats such as pastures and roadsides (e.g. *Cardiocondyla nuda* and *S. invicta*). Among the exotic species captured, *Pheidole moerens* was the most abundant and widespread (Table 1). Probably a relatively recent addition to the ant fauna [ca. 1970s (Deyrup *et al.*, 2000)], *P. moerens* is most similar in size and habits to *P. dentigula* and *P. floridana* among native species. Our results suggest that neither native species has been displaced in the habitats where they co-occur with *P. moerens*. The next most abundant and widespread introduced species, *Cyphomyrmex rimosus*, is a fungus-growing species that is most similar in size and habits to the native species *Trachymyrmex septentrionalis*, and *C. minutus* [a 'dubious' native (see Deyrup *et al.*, 2000)]. Again, there is no evidence that these native species are adversely affected by the presence of *C. rimosus*; *T. septentrionalis* is among the most, if not *the* most, abundant ant in high pine ecosystems in the region (Seal and Tschinkel, 2006). Differences in food preferences

(*T. septentrionalis*) or body size (*C. minutus*) may account for the apparent lack of impact. The imported fire ant, *S. invicta*, was absent from the native upland ecosystems, but occurred in the disturbed fields. The remainder of the introduced species occurred at very low abundances and did not obviously impact native species to a measurable degree in undisturbed ecosystems.

DISCUSSION

The results of this study do not support generalized scientific conclusions and public perceptions about exotic ant species: that they are dominant and have displaced native ants and other arthropods in native habitats, and are characterized by larger colonies of smaller workers. Our perceptions of exotic ants, like many exotic taxa, have been unduly influenced by case studies of the major invasive pest species (e.g. Porter and Savignano, 1990; Sanders *et al.*, 2003) and the tendency to view any exotic species as inherently threatening (Brown and Sax, 2004). Accordingly, our general understanding of the ecology of the large – and growing – pool of exotic ants, most of which are quite different from these major pest species, is mis- or uninformed.

Although many factors probably determine the success of many invasive species, there is continued interest in whether the attributes of exotics may convey a competitive advantage over native species (Bruno *et al.*, 2005). In this study, the abundance and species characteristics of exotic species suggest that although some species (e.g. *S. invicta*) possess characteristics such as large colonies and small workers that might predispose them to competitive superiority, the overall pattern is that established exotic species tend to have smaller colonies and workers of larger size relative to native species. Furthermore, the distribution of most exotic ant species in this region (Deyrup *et al.*, 2000; King and Tschinkel, 2006; Tschinkel, 2006) and elsewhere (e.g. Suarez *et al.*, 1998; Bolger, 2007) is confined to ecosystems impacted by disturbance; in the most disturbed sites, such as improved pasture, exotic species account for up to 90% of the total number of ants (King and Tschinkel, 2006). Disturbance may also be the primary threat to many native species because of their habitat specificity or inability to readily recruit into disturbed habitats (King and Tschinkel, 2006). Some endemic species did persist in fields (Table 1, Fig. 1), but they were rare and less diverse than in undisturbed ecosystems. It does not appear that exotic species are the reason for their decline (Fig. 4) (King and Tschinkel, 2006).

In addition to our data on relative abundance, we base our conclusion that exotic species are having little impact on native species in native habitats on the existing historical record of the ant fauna in this region. Van Pelt (1947, 1956, 1958) studied the ant fauna of north and central Florida 60 years ago. This period predates the invasion of a number of the exotic ant species in the fauna, particularly the most abundant and widespread species such as *S. invicta*, *P. moerens*, and *C. rimosus* (Deyrup *et al.*, 2000). While Van Pelt's (1947, 1956, 1958) collection methods were different (he used hand collecting), he did estimate the relative abundance of species in several kinds of disturbed and undisturbed habitats similar to those in the present study. He found an ant fauna very similar to that we report, both in its composition and species richness but without most of the exotic species [*Cardiocondyla* species were, however, present (Van Pelt, 1947, 1956, 1958)]. This suggests that the relative abundance and faunal composition of native ant species is unrelated to the presence of the exotic species [King and Tschinkel (2006) and Tschinkel (2006) showed a similar pattern in disturbed habitats in the absence of *S. invicta*].

We have specifically avoided any attempt to 'test' popular hypotheses about how native species richness affects exotic species success (e.g. Elton, 1958) or null models of species invasion patterns (e.g. Fridley *et al.*, 2004). Generally, there is not yet sufficient information about these exotic ant species to determine whether a fit into such a predictive model can be translated into a biological reality. For example, recent experimental work has revealed that the long-standing assumption (Tschinkel, 2006) that one of the primary mechanisms for the success of *S. invicta* is superior competitive ability relative to native species is probably not true for many monogyne populations (King and Tschinkel, 2006). For all of the communities included in this study, there is also evidence that assembly rules (species co-occurrence and body size overlap) do not fit the expected patterns if they were dictated by interspecific competitive interactions (King, 2007). Long-term study of ant invasions (e.g. Morrison, 2002) has also shown that the stability of exotic populations and their long-term impact is not readily predictable. Thus, our results help to begin to address the lack of basic species-level information for non-pest exotic ants and to better understand the sum-total of their impact on native ant assemblages. Most importantly and surprisingly, our data suggest that even in what is arguably the most successfully invaded regional (non-island) ant fauna in the world, the impact of exotic species is negligible in undisturbed ecosystems with an intact native ant fauna.

Exotic species characteristics

We hypothesized that exotic ants might have two primary adaptive advantages over related native species in successfully invaded areas: (1) smaller body size and (2) larger colony size, which supposes an advantage during interference competition (Franks and Partridge, 1993; Passera, 1994; McGlynn, 1999a; Morrison, 2000; Holway *et al.*, 2002). Despite the wide diversity of exotic species we sampled (or perhaps because of it?), there was no evidence that exotic species had either smaller workers (Table 1) or larger colonies (Fig. 3). Indeed, our results suggest that the opposite is true: among related species, exotic species tended to have larger workers and, with the exception of *S. invicta*, smaller colonies.

These patterns still need to be tested elsewhere in a similar manner, but our results suggest an alternative mechanism may be important in shaping worker body size. Average worker body size (for all species) was smallest in the most disturbed field ecosystems (Fig. 2). Indeed, average worker body size (mass) in fields was approximately 50% less than that of all other ecosystems, whether species were native or exotic. Generally, such disturbed habitats are where exotic ant species first become established and dominant. Paralleling Hölldobler and Wilson's (1990) dominance–impoverishment rule (impoverished faunas promote dominant species), this pattern suggests that conditions in disturbed habitats favour smaller worker body size. This constraint is then reflected in the smaller size of many successful exotic species that are most successful in these habitats. In sum, small body size is probably an adaptive advantage for existence in highly disturbed ecosystems that may or may not be related to interspecific competitive advantage (King and Tschinkel, 2006). Similarly, colony size, while very large for one exotic species (*S. invicta*), tends to be smaller than for most native species.

Biogeography of ant invasions in Florida

The biogeography of Florida's ant fauna has been well-described by Mark Deyrup (examples include Deyrup and Trager, 1986; Deyrup *et al.*, 2000; Deyrup, 2003). Briefly summarized, the ant fauna of

Florida includes geographically diverse faunal groupings. These include widespread eastern or Nearctic species, southeastern North American species, West Indian and southern Florida species, widespread western species, and a large number of introduced species ($n = 52$) originating from both the Old and New World tropics. The overlap of species from these different regions in the genera *Aphaenogaster*, *Crematogaster*, *Camponotus*, *Temnothorax*, *Pheidole*, *Pyramica*, and *Solenopsis* is particularly conspicuous.

The northern peninsula and panhandle of Florida are essentially contiguous with the eastern and Appalachian North American regions and represent the southernmost reaches of the flora and fauna of these regions. Moving south through the peninsula, older ecosystems (e.g. mixed hardwood forests, pine flatwoods, and high pine), contiguous with eastern, southeastern, and Appalachian ecosystems of the continental southeastern USA give way to less diverse, younger south Florida ecosystems (e.g. sawgrass prairie) near the tip of the peninsula. The patterns of spread of a number of exotic species across the entire southern end of the state and into Alabama and Georgia suggests that habitat factors (particularly disturbance), but probably not regional climate differences (i.e. the shift from subtropical southern Florida to warm temperate northern Florida), are the limiting factor for many of the established exotic ant species (Deyrup *et al.*, 2000; King and Tschinkel, 2006, in press; Tschinkel, 2006).

Thus, the current, limited success of introduced ant species in relatively undisturbed ecosystems of northern Florida, while promising from a conservation standpoint, must be placed in the context of historic and ongoing anthropogenic disturbance in the form of habitat alteration throughout Florida and the southeastern coastal plain. Relatively undisturbed woodland ecosystems are scattered across the region and limited in size and proximity to other natural areas (Myers and Ewel, 1990b; Jue *et al.*, 2001). In contrast, disturbed ecosystems, particularly urban environments, pasture, and roadsides, are widespread, contiguous, and abundant. These areas comprise the surrounding matrix in which natural areas occur. A growing number of exotic species currently confined only to disturbed habitats may potentially become established and increasingly abundant in most upland ecosystems if their large, persistent populations are adjacent to upland habitats [as propagule pressure increases (Suarez *et al.*, 2005)]. Furthermore, without climatic limitations and with the aid of human transport, it is reasonable to expect that there will be continued spread of a number of these exotic species throughout the disturbed habitats of the southeastern coastal plain (King and Tschinkel, in press). Thus, the apparently negligible impact of introduced species we observed under current conditions provides an impetus for protecting these upland areas from factors that clearly increase the relative abundance and impact of introduced species. In particular, road-building, habitat modification (e.g. clearing), and soil-disturbance are all events that will likely contribute to the invasion process (Deyrup *et al.*, 2000; Holway *et al.*, 2002; King and Tschinkel, 2006; Bolger, 2007) while significantly reducing or eliminating entire populations of endemic species.

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