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Forest invader replaces predation but not dispersal services by a keystone species

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Abstract Invasive species generally occur and thrive in human-disturbed ecosystems, but *Brachyponera chinensis* (Asian needle ant, formerly '*Pachycondyla chinensis*') also invades intact forests. The invasion into native habitats potentially puts *B. chinensis* in direct competition with the keystone seed-dispersing ants in the genus *Aphaenogaster*. We observed *B. chinensis* colonizing artificial nests placed in deciduous forest of the north Georgia Piedmont (US). Their presence appeared to displace existing *Aphaenogaster rudis* and *Reticulitermes flavipes* (subterranean termite) colonies. We subsequently mapped the *B. chinensis* invasion as well as co-existing *A. rudis* and *R. flavipes* colonies by examining coarse woody material (CWM) for nesting colonies. We

tested whether the *B. chinensis* invasion changed with forest microclimates, covaried with *A. rudis* and/or *R. flavipes* occurrence, and whether it was associated with failed dispersal of a dominant understory herb. Our results and observations suggest that *B. chinensis* shares ecological niche requirements (temperature, moisture and CWM as nesting habitat) with *A. rudis*, severely diminishing the abundance of this native ant. In supplanting *A. rudis*, *B. chinensis* appears to play an equivalent role to *A. rudis* as a termite predator, but fails as a seed disperser. Essentially, the invader substitutes for the negative but not the positive species interactions, thereby apparently shifting ecological dynamics in the invaded system.

Keywords *Aphaenogaster rudis* · Asian needle ant · *Brachyponera chinensis* · Coarse woody material · *Pachycondyla chinensis* · *Reticulitermes flavipes* · Termite

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Introduction

Invasive species generally thrive in human-disturbed habitats (Elton 1958), and their predilection for altered environments may reduce their impact on native species that require intact habitats. Whereas few 'untouched' habitats remain (Zalasiewicz et al. 2008), second-growth deciduous forests can contain relatively intact tree canopies and generally host far fewer invasive species than altered, open habitats

(Guenard and Dunn 2010; Martin et al. 2009). Given that most invasive ant species prefer open, disturbed habitats (Guenard and Dunn 2010; King and Tschinkel 2008; Sanders and Saurez 2011), temperate forest communities generally have been spared from ant invasion (but see, Roura-Pascual et al. 2010). Unlike most invasive ants, *Brachyponera chinensis* Wheeler (Asian needle ant) thrives in undisturbed forest understories (Guenard and Dunn 2010)—though it also occurs in human-altered habitats (Guenard and Dunn 2010; Rice and Silverman 2013).

Brachyponera chinensis is known in its native and invaded ranges as a termite specialist, and exploiting subterranean termite prey may contribute to its success as an invader (Bednar et al. 2013; Bednar and Silverman 2011; Guenard and Dunn 2010). Occurrences of *B. chinensis* also are associated with depauperate native ant communities (Guenard and Dunn 2010), and particularly of note is its negative impact on the seed-dispersing *Aphaenogaster fulva-rudis-texana* complex (Bednar et al. 2013; Guenard and Dunn 2010; Rodriguez-Cabal et al. 2012; Umphrey 1996). Species in this complex are taxonomically cryptic (hereafter “*A. rudis*”) and are the most common and abundant group of ants throughout eastern deciduous forests (King et al. 2013). *Aphaenogaster rudis* ants actively prey on termites (Buczowski and Bennett 2007, 2008), and they are the keystone seed disperser for many understory herbs (Ness et al. 2009). Where *B. chinensis* invasion corresponds with *A. rudis* declines, seed dispersal services decline as well (Rodriguez-Cabal et al. 2012). Both *B. chinensis* and *A. rudis* appear to share several characteristics and habitat requirements, including possessing transient locations for their colonies, where they nest in rotting logs and, in particular, old termite tunnels (Bednar and Silverman 2011; Guenard and Dunn 2010; King et al. 2013; Yashiro et al. 2010). These data suggest, however, that *B. chinensis* may be a superior competitor than native woodland ants for nesting sites and termite prey.

We observed *B. chinensis* colonizing artificial nests placed in deciduous forest of the north Georgia Piedmont (US) in 2011 and 2012. Their presence appeared to displace existing *A. rudis* and *Reticulitermes flavipes* (subterranean termite) colonies from the nests. We returned in 2014 to map the *B. chinensis* invasion as well as co-existing *A. rudis* and *R. flavipes*

colonies by examining coarse woody material (CWM) for nesting colonies. Our overall objective was to examine whether the displacement patterns observed in the nest boxes occurred across the study site. Indeed, *B. chinensis*' impact on *A. rudis* is hypothesized to be through competition for nest sites and for termite prey (Bednar and Silverman 2011; Guenard and Dunn 2010). If *B. chinensis* outcompetes *A. rudis* for nest sites and termites, we expected little overlap in nest log occupancy by the two ant species. Given that both ant species prey on termites, but *B. chinensis* is considered a termite specialist, we expected a greater decline in termites with *B. chinensis* than *A. rudis* presence. Moreover, given that *A. rudis* is the keystone seed-dispersing ant in eastern deciduous forests, and *B. chinensis* delivers little or no seed-dispersing services (Rodriguez-Cabal et al. 2012), we expected that ant-dispersed plants in the vicinity of *B. chinensis* colonies would be more clumped than those near *A. rudis*. Our working hypothesis was that where *B. chinensis* replaced *A. rudis* it would exacerbate the negative predatory effects usually performed by the native ants on termites, and impair the positive effects on seed dispersal usually associated with *A. rudis*.

Methods

Study species

Brachyponera chinensis is native throughout Australasia, but the US populations appear to be from temperate Japan (Yashiro et al. 2010). It was first recorded in the southeastern US in the 1930s and occurs throughout eastern North America (Bednar and Silverman 2011; Guenard and Dunn 2010; Nelder et al. 2006; Rodriguez-Cabal et al. 2012; Smith 1934); however, *B. chinensis* populations recently have become noticeably more widespread and abundant within the invaded range. *B. chinensis* workers can deliver a venomous sting (Nelder et al. 2006), and they forage at least 30–60 cm from colony nests for live and dead invertebrates (Guenard and Silverman 2011). They are known as termite specialists both in their home and invaded ranges (Bednar and Silverman 2011; Matsuura 2002). *B. chinensis* forms colonies that range from a few dozen to thousands of workers, some without queens, some with multiple queens, and

workers may move between colonies (Creighton 1950; Gotoh and Ito 2008; Zungoli and Benson 2008).

Aphaenogaster ants occur worldwide and include at least 18 species in North America (N.A.) (Bolton 2010; Creighton 1950; Smith 1979; Umphrey 1996). In eastern N.A., *Aphaenogaster* species are the most abundant ants in mesic deciduous forests (King et al. 2013; Lubertazzi 2012). Many eastern N.A. *Aphaenogaster* species are hard to differentiate based on morphology and are genetically cryptic (Lubertazzi 2012; Ness et al. 2009; Umphrey 1996), but all engage in generalist, omnivorous foraging behavior, including retrieving woodland plant seeds, and they are the dominant seed dispersers in eastern deciduous forests (Ness et al. 2009). *A. rudis* ants generally forage approx. 60–120 cm from their nests (usually located under rocks or in CWM), and nests are moved every 30–60 days (Giladi 2004; Lubertazzi 2012; Ness et al. 2009; Pudlo et al. 1980; Smallwood 1982; Talbot 1951). *A. rudis* colonies generally are medium sized (200–400 workers) with single queens (King et al. 2013; Lubertazzi 2012).

Reticulitermes flavipes occurs throughout the eastern US, but occurs in far greater abundance moving southward (Emerson 1936; King et al. 2013). *R. flavipes* feed on dead wood in which they construct tunnels. Whereas the reproductive members of the colony may nest in wood or belowground (but see, Thorne et al. 1999), the majority of the colony resides in multiple pieces of aboveground dead wood connected by subterranean tunnels (Abe 1990; Korb 2007). Colonies in the region where we sampled generally have just one reproductive pair and numerous offspring that forage in $\sim 100 \text{ m}^2$ areas at densities up to 160 termites m^{-2} (King et al. 2013; Vargo et al. 2013).

Asarum arifolium Michx. (wild ginger, formerly *Hexastylis arifolia*) is a small understory evergreen with a distribution limited to the Southeastern United States. It is a long-lived perennial that maintains 1–2 leaves. *Asarum arifolium* forms nondescript flowers that lie on the forest floor and sets seed in mid-summer (Giladi 2004; Warren II et al. 2014). The seed has a relatively large appendage called an elaiosome that attracts foraging ants and induces them to retrieve the seed back to their nest (Warren II et al. 2014). It does not have clonal reproduction and is long-lived (Warren II 2007; Warren II and Bradford 2011).

Artificial nests

Thirty two artificial ant nests were placed in deciduous forest habitats in the Chattahoochee National forest (CNF, 412 m, 34.51322, -83.4787) in Georgia (US) as part of a larger study examining decomposition dynamics (Bradford et al. 2014). The artificial nests ($15 \times 12 \times 2 \text{ cm}$) were made of untreated pine with nest chambers created by routing 1.5-cm deep grooves into the wood with access via a $10 \times 4 \text{ mm}$ entrance between the wood and a transparent 1.5-mm thick acrylic plate. The artificial nests were placed with wood contacting soil on the forest floor and topped with a ceramic tile. The tile blocked light from passing through the acrylic plate but allowed easy access to view colonies inside occupied artificial nests without disturbing the nest. Eight nests were placed in each of four linear transects, 10 m apart, with transects following the slope aspect, two on south-facing slopes and two on north-facing slopes. We placed the nests in March 2011, and checked them June, August and November 2011, and March, May and June 2012. We also measured soil temperature at 5-cm depth and took three measures of volumetric soil moisture (Campbell HydrosenseTM) to 12-cm depth at each visit.

Colony surveys

In May 2014, we returned to the site to map the *B. chinensis* invasion and explore the potential consequences on native ants, termites and ant-dispersed plants. We surveyed four hectares through haphazard searching (a total of 1836 m linear distance) starting where *B. chinensis* was discovered in the artificial nests in 2012. Every downed log within a 2 m swath of linear distance was turned and opened to search for *B. chinensis*, *A. rudis* or *R. flavipes*. We also measured log temperature at 5-cm depth and volumetric log moisture at 12-cm depth into the wood or soil (depending on colony location).

Asarum arifolium is the most common ant-dispersed plant at the study site. Previous work in this study system, primarily focused on *A. arifolium*, showed that failed ant dispersal results in aggregation as seedlings cluster below parents. The clustering occurred in the absence of *A. rudis* due to spatial (saturated soil, Giladi 2004; Warren II et al. 2010), temporal (phenological asynchrony, Warren II and Bradford 2013) and experimental (Zelikova et al.

2011) ant exclusion. Moreover, Rodriguez-Cabal et al. (2012) showed that decreased seed retrieval at bait stations corresponded with reduced *A. arifolium* abundance. Essentially then, we expected increased plant aggregation where dispersal failed most. Upon finding a log occupied by *B. chinensis* or *A. rudis*, we located the nearest *A. arifolium* plant and then measured to its nearest neighbor to assess plant aggregation.

Data analysis

Artificial nests

Aphaenogaster rudis and *R. flavipes* colonized artificial nests in 2011, and *B. chinensis* colonized in 2012, sometimes displacing the other species. We used analysis of variance (ANOVA) models to examine the interaction between year and *B. chinensis* colonization on *R. flavipes* and *A. rudis* abundance in artificial nests.

Colony surveys

We examined the spatial distribution of *B. chinensis*, *A. rudis* and *R. flavipes* by creating a surface map based on GPS coordinates using the *ggmap* package (Kahle and Wickham 2013) in R. We investigated the effect of microclimate (soil moisture and temperature) and *B. chinensis* presence on *A. rudis* distributions using generalized linear models (GLMs) assuming a binomial error distribution. We evaluated soil moisture and temperature in independent models because the two variables typically covary in our study system. We used Akaike's Information Criterion (AIC, Akaike 1973) to select between models. GLM fit was evaluated using analysis of deviance (ANODEV) with a Chi square test. We included interactions terms in each model to evaluate potential microclimate effects in the absence of *B. chinensis*. We also used GLM ANODEV models to examine the impact of *A. rudis* and *B. chinensis* on *R. flavipes* presence assuming a binomial error distribution. We tested for multicollinearity (variance inflation <2.5) and overdispersion ($\Phi < 1$) in all GLM ANODEV models. We considered coefficients with p value ≤ 0.05 significant. We discuss coefficients with p value ≤ 0.10 as having "marginal significance" (sensu Hurlbert and Lombardi 2009). We tested for differences in nearest neighbor distance

of *A. arifolium* herbs where we found *B. chinensis* and where we found *A. rudis* using Student's t test.

Results

Artificial nests

Ants or termites colonized some of the same nest boxes (but in different years), and on one nest transect that appeared to be a transition zone, *A. rudis* and *B. chinensis* colonized the same nest boxes in different years (Fig. 1). In all cases, *B. chinensis* appeared to displace the termites or native ants. We did not find significant impacts of *B. chinensis* colonization on *R. flavipes* abundance from 2011 to 2012 (Table 1a; Fig. 2a), but no termites occurred in artificial nests colonized by *B. chinensis*. However, *B. chinensis* colonization had a statistically significant negative impact on *A. rudis* abundance (Table 1b). The significant year \times *B. chinensis* interaction term indicated that *A. rudis* abundance increased in all artificial nests from 2011 to 2012 in the absence of *B. chinensis* colonization, but went to zero in nest boxes that *B. chinensis* colonized (Fig. 2b).

Colony surveys

We returned to the site in 2014 to map the invasion and to examine whether the observations from the artificial nests appeared to hold in the natural patterning of CWM colonization (Fig. 1). We surveyed an area of 3.674 km² and found 193 *B. chinensis*, 120 *A. rudis* and 113 *R. flavipes* colonies. We also found 2 *Prenolepsis imparis*, 2 *Camponotus* spp., 6 *Crematogaster ashmeadi* and 1 *Nylanderia* sp. colonies.

The separation between *A. rudis* and *B. chinensis* did not appear a consequence of species-specific microhabitat preferences. The best-fit model predicting *A. rudis* colony presence included temperature rather than soil moisture (Δ AIC = 39), but only *B. chinensis* had a significant negative effect on *A. rudis* presence (Table 2a). *R. flavipes* presence in CWM decreased significantly with the presence of *B. chinensis* and *A. rudis* (Table 2b; Fig. 3).

Lastly, we collected data on the aggregation of the most common, ant-dispersed understory herb at the study site, *A. arifolium*, to gain insight into the possibility that the invasion might disrupt the dispersal

Fig. 1 Digital map of *B. chinensis* (“B”), *A. rudis* (“A”) and *R. flavipes* (“R”) 2011 occurrences in CWM in Chattahoochee National Forest, US. The larger letters indicate where the species were found in artificial nest boxes, and letter overlap indicates nests first colonized by *A. rudis* or *R. flavipes* in 2011 and subsequently *B. chinensis* in 2012

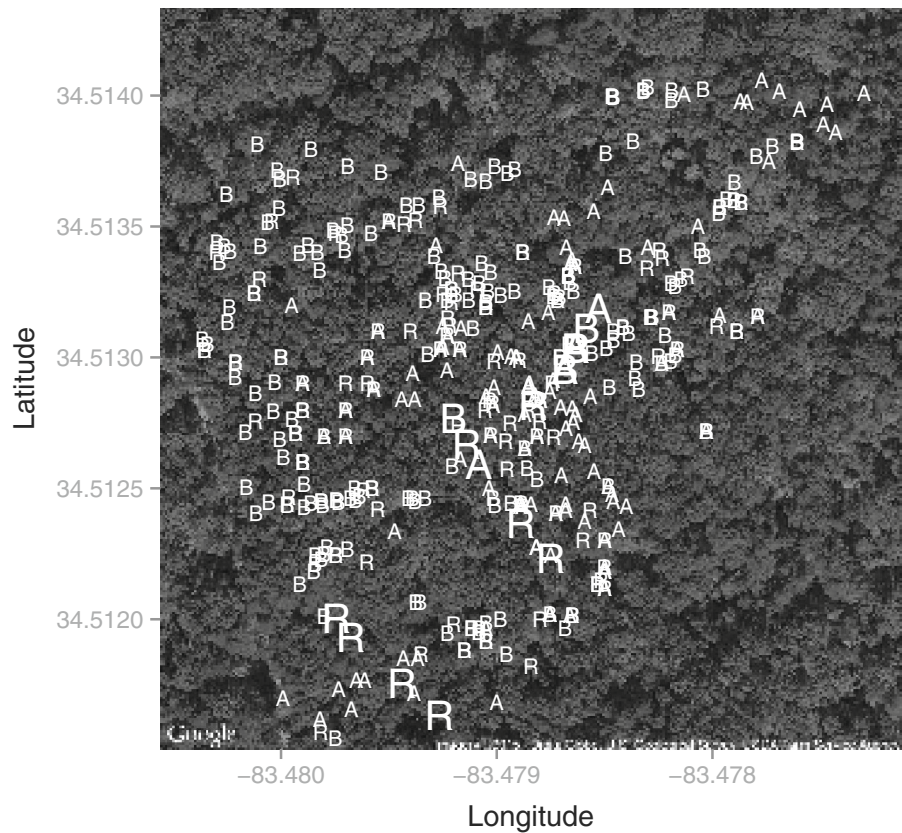


Table 1 Analysis of variance of (a) *R. flavipes*, (b) *A. rudis* abundance in artificial nests as a function of year (2011–2012) and *B. chinensis* colonization

	df	SS	F value	p value
(a) <i>Reticulitermes flavipes</i>				
Year	1	0.580	0.183	0.671
<i>Brachyponera chinensis</i>	1	1.726	0.542	0.465
Year × <i>B. chinensis</i>	1	3.710	1.164	0.285
(b) <i>Aphaenogaster rudis</i>				
Year	1	2.355	0.857	0.358
<i>Brachyponera chinensis</i>	1	0.776	0.857	0.596
Year × <i>B. chinensis</i>	1	13.969	5.086	0.028

mutualism between these herbs and their keystone disperser, *A. rudis*. We found significantly more plant aggregation ($t = 2.279$, $df = 58$, p value = 0.026), as indicated by decreased nearest neighbor distance, where we found *B. chinensis* (77 cm) than where we found *A. rudis* (128 cm) [Fig. 4].

Discussion

We hypothesized that where the exotic ant *B. chinensis* replaced the native ant *A. rudis* it would exacerbate the negative predatory effects usually performed by the native ants on termites, and impair their positive effects on seed dispersal. As expected (Guenard and Dunn 2010; Rodriguez-Cabal et al. 2012), *B. chinensis* appeared to displace the common forest ant *A. rudis*. However, although *B. chinensis* is considered a termite specialist, it appeared to replace—as opposed to exacerbate—*A. rudis* as a termite predator in the forest habitat. In contrast, it apparently did not replace the role of *A. rudis* as a seed disperser, causing a common forest understory herb to be more aggregated within the invasion. Our results suggest that *B. chinensis* invasions may disrupt some, but not all, keystone species ecological roles in forest habitats.

Invading ants generally correlate with decreases in native ant abundance and diversity (Guenard and Dunn 2010; Lessard et al. 2009; Sanders and Saurez 2011), but negative correlations between invasive and

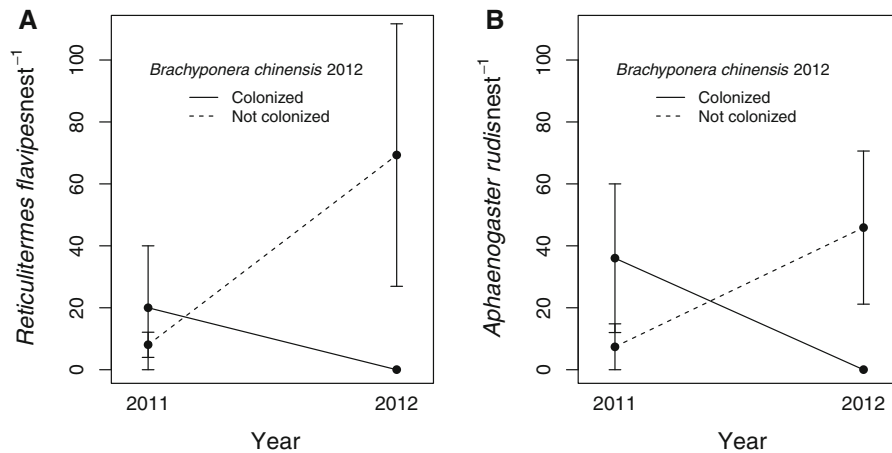


Fig. 2 Interaction plots showing mean (\pm SE) changes in *R. flavipes* termite (a) and *A. rudis* ant (b) abundance with the colonization of artificial nests ($n = 32$) by the invasive ant *B. chinensis* 2011–2012. In both cases, the native species increased

in artificial nest colony abundances where *B. chinensis* did not colonize, but dropped to zero where *B. chinensis* colonized [although only the effect on *A. rudis* (b) was statistically significant]

Table 2 Analysis of (a) deviance of *A. rudis* abundance in downed logs as a function temperature and *B. chinensis* presence, (b) variance of *R. flavipes* abundance in downed logs as a function of *A. rudis* and *B. chinensis* presence

	df	Deviance	Res. dev.	p value
(a) Deviance of <i>Aphaenogaster rudis</i>				
Temperature	1	0.231	72.888	0.631
<i>Brachyponera chinensis</i>	1	95.436	73.118	<0.001
Temperature \times <i>B. chinensis</i>	1	0.415	72.472	0.519
(b) Variance of <i>Reticulitermes flavipes</i>				
<i>Aphaenogaster rudis</i>	1	14.979	448.980	<0.001
<i>Brachyponera chinensis</i>	1	108.697	340.280	<0.001

native species do not rule out the possibility that they have unique habitat requirements rather than compete for the same microenvironment (King and Tschinkel 2008, 2013; Menke and Holway 2006). We had the opportunity to observe artificial nest colonization so we could measure the before and after effects of exotic ant nest colonization on native species. We found that *B. chinensis* colonization appeared to knock *A. rudis* colonies out of artificial nests. At a larger spatial scale, we rarely found the two species occupying the same downed logs (and when they did, never closer than 1 m in the log). Both sets of observations suggest that the invasive and native ant share microhabitat requirements, providing a mechanism for the apparent displacement of the native ant. Notably, *A. rudis* is not only the most abundant ant in eastern US deciduous forest logs, but potentially the most

abundant forest-floor macroarthropod in southeastern US mixed temperate forests (King et al. 2013). Given *A. rudis*'s prevalence in forests, its systematic absence with *B. chinensis* presence is unlikely by chance. Moreover, a considerable decline in *A. rudis* occurrence (up to 96 %) has been documented with *B. chinensis* invasion at other locations (Guenard and Dunn 2010; Rodriguez-Cabal et al. 2012). The most common ant species we found other than *A. rudis* was *C. ashmeadi*, an arboreal species that seems little impacted by *B. chinensis* (Guenard and Dunn 2010), possibly because *B. chinensis* cannot climb and hence does not forage above the forest floor.

We focused on plant aggregation because the end result of failed seed dispersal by ants is increased seedling clumping around parents. Results from previous studies have linked failed dispersal with

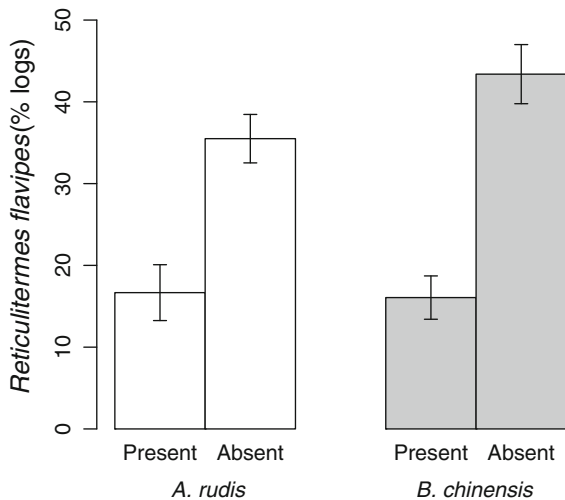


Fig. 3 There were similar reductions in *R. flavipes* presence in CWM where *A. rudis* or *B. chinensis* ants were present

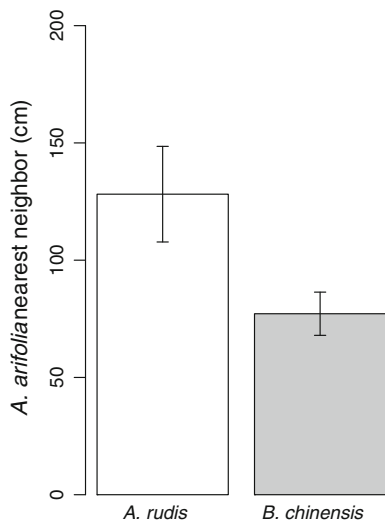


Fig. 4 *Asarum arifolium* plants cluster more closely together in the presence of the exotic *B. chinensis* ant than in the presence of the native seed-dispersing *A. rudis* ant. Greater plant clustering indicates failed seed dispersal

unsuitable abiotic habitat for *A. rudis* (Giladi 2004; Warren II and Bradford 2013; Warren II et al. 2010; Zelikova et al. 2011). We did not find microclimate associated with plant aggregation, suggesting that “unsuitable habitat” in this instance was a biotic consequence of *B. chinensis* presence. Moreover, seed removal is not, in itself, an indication of an effective seed disperser. Many ant species remove seeds from bait stations, but they may damage the seeds, place

them in unsuitable conditions or drop them along the way (Warren II and Giladi 2014). Hence, plant aggregation may be a better hallmark of failed ant dispersal services than removal from a bait card. Further investigation is needed to determine *B. chinensis*’ effectiveness as a seed disperser, but our results, and those of others (Rodriguez-Cabal et al. 2012), suggest that it is much less effective than *A. rudis*.

We observed both *B. chinensis* and *A. rudis* workers quickly grab *R. flavipes* workers after we disturbed CWM, indicating a very rapid predator response. We also found the presence of either ant species negatively correlated with termite presence in artificial nests and CWM. Both species are known termite predators (Bednar et al. 2013; Bednar and Silverman 2011; Buczkowski and Bennett 2007, 2008), and we found no difference in their putative impacts on *R. flavipes*. *B. chinensis* is known as a termite specialist in its home and invaded ranges, and its invasion success has been attributed to its prowess at termite hunting (Bednar et al. 2013; Bednar and Silverman 2011). However, *A. rudis* is also a known termite predator in eastern US deciduous forests (Buczkowski and Bennett 2007, 2008; Warren II and Bradford 2012). Both species are very successful in attacking termite colonies in open and sand nests, and *B. chinensis* out-performs *A. rudis* as a predator in such conditions (Bednar et al. 2013; Buczkowski and Bennett 2008). Termites can fend off ant attack in hard structures (such as CWM), however, by creating physical barriers (foraging tunnels) and placing large-headed soldiers in tunnels so that colonies remain protected (Buczkowski and Bennett 2008). In the lab, *B. chinensis* and *A. rudis* are roughly equivalent as predators of termite colonies in hard structures (Bednar et al. 2013) and our results suggest that this also may be true in CWM under field conditions.

Our results and observations suggest that *B. chinensis* shares ecological niche requirements with *A. rudis*, the dominant, keystone ant in eastern US deciduous forests, severely diminishing the native ant where they co-occur. In supplanting *A. rudis*’ ecological niche, *B. chinensis* adeptly fills the role of termite predator, but fails as a seed disperser. The appearance and apparent recent expansion of *B. chinensis* in intact southeastern deciduous forest ecosystems, and its impact on the most abundant native species, *A. rudis*, has potential broad implications for the role of

Aphaenogaster ants in eastern temperate forest ecosystems. Given that *B. chinensis* forms larger colonies and shares at least some food preferences with *A. rudis*, it would seem that it better exploits woodland food resources than the native ant. However, *A. rudis* has very wide food choices, and future work may focus on competition for all food resources. Another explanation for the dramatic drop in *A. rudis* abundance could be that *B. chinensis* is preferentially preying upon *A. rudis* as *B. chinensis* will kill *A. rudis* workers in direct interactions in laboratory experiments (Bednar 2010). They also may prey upon newly mated queens or newly founded colonies. However, previous results (Guenard and Dunn 2010), and those presented here, suggest that competition for nest sites is the best-supported explanation for *A. rudis* displacement by *B. chinensis*.

Darwin (1859) suggested that successful invaders arrive where resources are not fully used by existing species. Hence, invasive species fill the “empty niche.” Our results suggest the opposite, *B. chinensis* invades where *A. rudis* already occupies niche space, including microclimate, termite predation and the use of woody debris for nesting. Furthermore, Chase and Leibold (2003) put forward a species niche that not only includes its requirements, but also its ecological impacts. *B. chinensis* appears then to not only have similar niche requirements to *A. rudis*, but to also fail to replace *A. rudis* as a keystone seed disperser in deciduous forests. These are considerable invasion impacts without even considering the direct impact of *B. chinensis* on *A. rudis* abundance and distribution. Invasive species generally are assumed to be superior competitors, and invasions often correspond with negative impacts on native species (Gurevitch and Padilla 2004; Vila et al. 2011), but research has yet to consistently establish competition as the mechanism of species invasion (Felker-Quinn et al. 2013; Liu and Stiling 2006; Ordonez et al. 2010). We find a clear inverse pattern between *B. chinensis* and *A. rudis* occurrence but experimental research is needed to establish whether competition is the primary mechanism. What we can infer, nonetheless, is that *B. chinensis* invasion alters an ecological system by assuming only the negative and not positive biotic interactions of the native species it replaces.

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