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Article *in* Biological Invasions · November 2019

DOI: 10.1007/s10530-019-02133-3

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Biological Invasions

ISSN 1387-3547

Biol Invasions
DOI 10.1007/s10530-019-02133-3

Biol Invasions
https://doi.org/10.1007/s10530-019-02133-3

ORIGINAL PAPER

Regional-scale environmental resistance to non-native ant invasion

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Received: 3 February 2019 / Accepted: 9 November 2019

Abstract A successful invasion of novel habitat requires that non-native organisms overcome native abiotic and biotic resistance. Non-native species can overcome abiotic resistance if they arrive with traits well-suited for the invaded habitat or if they can rapidly acclimate or adapt. Non-native species may co-exist with native species if they require novel, underused resources or if they can out-compete similar native species. We investigated abiotic and biotic resistance to the progression of a *Brachyponera chinensis* invasion in the southeastern U.S. relative to the dominant native woodland ant (*Aphaenogaster*). We used observational data from long-term plots along the elevation gradient of the Southern Appalachian Mountain escarpment to investigate the patterns of *B. chinensis* invasion, and we used physiological thermal tolerance, aggression assays and stable isotope analysis to determine whether abiotic or biotic factors explained *B. chinensis* invasion. We found that *B. chinensis* exhibited an inflexible and relatively poor ability to tolerate cold temperatures, which corresponded with limited success at higher elevations in the Southern Appalachian Mountains. Though we found native ant resistance to *B. chinensis* invasion, it paled in comparison to the invasive ant's ability to form huge, cooperating supercolonies that eventually eliminated the native ant. Without biotic resistance, susceptible native species may only be protected if they can tolerate abiotic conditions that the invasive species cannot. For *Aphaenogaster* species, high elevations and northern latitudes beyond *B. chinensis*' cold tolerance may be their only refuge.

Keywords *Aphaenogaster picea* · *Aphaenogaster rudis* · *Brachyponera chinensis* · Friendly release · Southern Appalachian · Supercolony

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Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10530-019-02133-3) contains supplementary material, which is available to authorized users.

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Introduction

Non-native species must overcome native abiotic and biotic resistance to successfully invade novel territory. Non-native species can overcome abiotic resistance if they are equipped with traits well-suited for the invaded range habitat (Lee and Gelembiuk 2008; Schlaepfer et al. 2010; Warren II et al. 2018b) or if they can rapidly adjust ('niche shift') to the novel habitat (Hill et al. 2013; Moran and Alexander 2014). Once established, non-native species may co-exist with native species if the invader requires novel resources, essentially occupying an 'empty niche,' resulting in low interspecific competition (Stachowicz and Tilman 2005); for example, non-native species often thrive in anthropogenically altered habitat that is relatively inhospitable for native species (King and Tschinkel 2008; Moles et al. 2012). Where non-native species come in conflict with native species for shared resources, the non-native species often prevail because they bring superior competitive abilities and are released from the burden of negative species interactions, such as predation, herbivory, disease and territoriality (Callaway and Ridenour 2004; Liu and Stiling 2006; Warren II et al. 2018a).

Ants are cosmopolitan (*sans* Antarctica) and critical components of the world's biodiversity (Hölldobler and Wilson 1990). They are ecosystem engineers, predators, herbivores, scavengers, seed dispersers, pests and farmers (del Toro et al. 2012; Folgarait 1998; Warren II and Bradford 2012; Warren II and Giladi 2014) with distributions and behavior often delineated by large- and small-scale temperature gradients (Diamond et al. 2017; Dunn et al. 2007; Warren II and Chick 2013). Their distributions also are impacted by human economic activity as ants travel internationally via agricultural materials (McGlynn 1999; Suarez et al. 2005). As such, approximately 200 ant species reside in habitats where they were introduced outside their native range and, of those, approximately 20 have spread profusely—negatively impacting native biodiversity as they move across the landscape (Bertelsmeier et al. 2017; Holway et al. 2002; Suarez et al. 2010; Wetterer 2015).

Invasive ant populations typically share some general characteristics: most are omnivorous, unicolonial (multiple nests share workers) and polygynous (multiple queens in nests) (Holway et al. 2002). Ants from unicolonial, polygynous colonies support the formation of 'supercolonies' in which multiple, interconnected nests essentially act as one—in contrast with the more common monodomous (workers not shared between nests) and monogyne (single queen colonies) structure (Holway et al. 2002) in which workers enforce individual colony territories with intraspecific aggression. Supercolony formation has been observed in several aggressive non-native species including: *Linepithema humile* (Mayr, 1868), *Myrmica rubra* (Linnaeus, 1758), *Solenopsis invicta* (Buren, 1972), *Wasmannia auropunctata* (Roger, 1863) and *Brachyponera chinensis* [Emery, 1895] (Eyer et al. 2018; Holway 1998; Krushelnycky et al. 2010; Warren II et al. 2018a). A lack of intraspecific competition and low territoriality allows non-native ant supercolonies to reach abundances far greater than co-occurring native ants, and observational studies suggest that it gives the non-native ants an advantage against native ants (Holway et al. 1998; Suarez et al. 2001; Tsutsui et al. 2000). Warren II et al. (2018a) experimentally demonstrated that low intraspecific competition in non-native ants worked as a mechanism for invasive ant dominance given that intraspecific competition > interspecific competition, which violates the key assumption of coexistence theory (Chesson 2000; Clark et al. 2012). As such, low intraspecific competition may give the ants a "friendly release" that is as important for invasion success as greater competitive ability or lack of enemies (Warren II et al. (2018a) With that success, the dense, extensive ant invasions coincide with considerable decreases in native ants and other invertebrates, as well as disruptions of ecosystem services such as seed dispersal (Lach and Hooper-Bui 2009; Nelder et al. 2006; Rodriguez-Cabal et al. 2012).

Here, we examine abiotic and biotic influences on the progression of a *B. chinensis* invasion in the southeastern U.S. relative to the dominant forest ants of the *Aphaenogaster* genus. We used observational data from long-term plots along the elevation gradient of the Southern Appalachian Mountain escarpment (northern Georgia, northwestern South Carolina and southwestern North Carolina) and experimental data from physiological thermal tolerance analysis, aggression assays and isotopic diet analysis to elucidate the mechanisms behind the observed invasion. Given that co-occurring *Aphaenogaster* ants exhibit an increased ability to tolerate cold temperatures with increased elevation (Warren II and Chick 2013), we expected similar thermal plasticity in *B. chinensis* along the same gradients. Alternately, given that the invaded-range *B. chinensis* appears to originate from a small portion of its native range (Yashiro et al. 2010), it may have underwent a bottleneck or founder effect and lack the thermal plasticity to acclimate or adapt to colder high elevation temperatures. Given that Warren II et al. (2015) observed similar nesting (downed wood) and diet (*Reticulitermes flavipes* [Kollar, 1837]) preferences for *B. chinensis* and *Aphaenogaster* ants in a Southeastern U.S. forest, we expected that with increased *B. chinensis* invasion, we would see increased displacement of *Aphaenogaster* given their niche overlap. Alternately, across time, the *B. chinensis* and native ant populations may have stabilized through unique niches as *B. chinensis* appears more predatory (Suehiro et al. 2017) where *Aphaenogaster* ants are relatively omnivorous (Lubertazzi 2012).

Methods

Study sites

We used an aggregation of new and existing study sites (n = 30 sites) in the Southeastern U.S. (Georgia, South Carolina and North Carolina) to investigate abiotic and biotic influences on the progression of a *B. chinensis* invasion relative to the dominant forest ant, *Aphaenogaster* (Supplement 1). The first set of sites in Georgia originally were sampled in 1974 by Crozier (1977) and re-sampled in 2012 by Warren II and Chick (2013). Three sites (North and South Carolina) were sampled in 2017 during work on another ant project (Lafferty 2018). One site in Georgia was sampled in 2014 as part of another ant project (Warren II et al. 2015) and again in 2017. Finally, we added seven sites in 2018 to better sample the range of *B. chinensis* invasion and *A. rudis* occupation.

Study species

Brachyponera (formerly '*Pachychondyla*') *chinensis* is a venomous ponerine ant native to tropical and temperate regions in eastern Asia and Australasia. In its invaded range, it was first discovered near Decatur, GA (U.S.) in 1932, approximately 100 km from the most southwesterly study site used here, possibly dispersing through the shipment of nursery plants (Guenard and Dunn 2010; Ipser et al. 2004; Smith 1934). *Brachyponera chinensis* typically invades forest habitat, living in downed wood, but also has been found in suburban and urban settings (Guenard and Dunn 2010; Pecarevic et al. 2010; Rice and Silverman 2013). *Brachyponera chinensis* forms polydomous nests that can contain thousands of workers (Zungoli and Benson 2008, *Warren pers. obs.*). Unlike most invasive ants in North America, *B. chinensis* appears primarily predatory, mostly consuming termites and other arthropods (Bednar et al. 2013; Suehiro et al. 2017). The venomous sting of *B. chinensis* may be a public health threat (Nelder et al. 2006), and its invasion coincides with palpable decreases in native ant biodiversity (Bednar et al. 2013; Guenard and Dunn 2010).

Congeners in the *Aphaenogaster rudis* complex dominate eastern deciduous forests (King et al. 2013; Lubertazzi 2012). Our study included *A. rudis* [Enzmann, J., 1947] and *A. picea* [Wheeler, W.M., 1908] in the elevation and thermal tolerance experiments, but only *A. rudis* (which had the most range overlap with *B. chinensis*) in the aggression assay and isotope experiments. *Aphaenogaster rudis* generally occurs at lower elevations and latitudes relative to *A. picea* (Warren II and Chick 2013), but the *Aphaenogaster* congeners generally share the same ecological characteristics as they are seed dispersers, termite predators and generalist scavengers that nest in downed wood and under stones and occur in relatively high numbers and densities in forest understory habitats (Lubertazzi 2012; Ness et al. 2009; Warren II et al. 2015). *Aphaenogaster* ants are desiccation intolerant, and their monogyne and monodomous nests appear to get displaced from preferred moist nesting sites by co-occurring ants, including non-native species such as *B. chinensis* (Warren II et al. 2012, 2015).

Timed searches

We sampled each of the 30 study sites (Supplement 1) in June 2018 by turning and breaking downed wood until five *A. rudis* nests were discovered. At one site, elevation 402 m, the search was terminated after 45 min without an *A. rudis* nest being discovered. We calculated nest hour^{-1} from the number of minutes it took to find 5 nests.

Thermal tolerance

Thermal tolerance essentially delineates an organism's lower (critical thermal minimum, "CT_{min}") and/or upper (critical thermal maximum, "CT_{max}") physiological temperature limits, typically measured as the sub-lethal thermal limit at which motor function fails or "knock-down resistance" (Huey and Stevenson 1979). Thermal tolerances correspond with shifts in ant species along temperature gradients as ants sort between relatively tolerant or intolerant species (Warren II and Chick 2013; Penick et al. 2017). CT_{min} was the relevant thermal trait for this study given that our focus was on abiotic constraints with elevation and latitude gradients along which minimum temperatures are limiting for woodland ants (Bishop et al. 2016; Warren II and Chick 2013).

In June 2018, we collected *B. chinensis* and *A. rudis* workers ($n = 10$ each) from 12 *B. chinensis* nests and 18 *A. rudis* nests at 22 of the study sites (Supplement 1) and transported them to the Highlands Biological Station (Highlands, NC) for thermal tolerance testing. We minimized spatiotemporal confounding by sampling sites randomly during a short period (3 days), and the sampling sequence did not follow elevation gradients. Each ant worker was placed in 16 mm glass test tubes plugged with moistened cotton (to maintain humidity and reduce stress). The cotton plugs also reduced movement during subsequent thermal testing. The field-collected test tubes were placed in racks and in a cooler with ice to prevent overheating during transport to the laboratory (with an insulator between the test tube racks and ice). Thermal testing was done on the same day as collection. From each 10-ant sample, ants were randomly assigned, five each, to CT_{min} or control (same test tube conditions as the thermal tolerance samples without placement in the water bath). None of the control specimens lost their righting response during the testing.

For CT_{min} (cold tolerance), we pre-cooled an Ac-150-A40 refrigerated water bath (NesLab, ThermoScientific, Portsmouth, NY, USA) to 20 °C. We placed five test tubes with ants into the bath and allowed them to equilibrate for 10 min, at which point the temperature was decreased by -1.0 °C min^{-1}. The ants were checked 60 s after the unit reached the next temperature interval. At every interval, the ants righting responses were observed by lifting each test tube out of the bath very briefly. If the individual was immobile the test tube would be turned and tapped to verify the ability to stay upright. Once an individual lost their ability to right it was removed, and the corresponding interval temperature recorded. Testing concluded after all individuals in a sample lost the ability to right themselves.

Aggression bioassays

In June and July 2017 and 2018, we collected *B. chinensis* ($n = 57$) and *A. rudis* ($n = 56$) workers from 16 nests (8 *B. chinensis* and 8 *A. rudis*) at 8 sites in Georgia and South Carolina (distance between sites ranged from 0.038 to 60 km apart) for pairwise aggression bioassays (Supplement 1). Workers from each nest were placed together in plastic containers in a cooler with ice to prevent overheating during transport to the laboratory at the Highlands Biological Station. We then paired individuals from separate nests for arena trials; the assay pairings were balanced between *A. rudis* × *A. rudis*, *A. rudis* × *B. chinensis* and *B. chinensis* × *B. chinensis* with 10 replicates each ($n = 120$ total pairwise trials). The workers were placed in 100 mm diameter petri dishes initially segregated by a 40 mm petri dish lid placed over one ant. The ants were allowed to acclimatize for 120 s to recover from handling and then both coaxed under the 40 mm lid for closer proximity. The paired ants were observed for 300 s after acclimatization with behaviors recorded as (0) passive reactions (running away, indifference), (1) antennation (ant touches other ant with antenna), (2) mandible opening, (3) physical aggression (biting or stinging), (4) death of one ant. The paired ants came in close enough proximity for interaction in all trials. These behaviors were recorded throughout the trials and mean and maximum aggression calculated. Workers only were used once, and petri dishes were cleaned with alcohol between trials.

Isotope analysis

We used isotope fractionation to assess the trophic position and niche requirements of *B. chinensis* and *A. rudis.* We randomly selected 5–10 workers from 12 nests each of *B. chinensis* and *A. rudis* at six sites (2 nests at each site) [Supplement 1]. The ants were live collected, transported on ice back to the Highlands Biological Station and freeze killed at 3 °C overnight. The ants were then dried for 48 h at 50 °C. As ants change their diets throughout the year, we removed the gaster (abdomen) before submitting ant samples for isotope analysis to get an integrated diet analysis not influenced by recent consumption (Smith and Tillberg 2009). The gaster was removed from each ant using forceps cleaned with 95% alcohol between each removal. Approximately 2.5 mg of ants from each nest ($n = 24$; 12 *B. chinensis* and 12 *A. rudis*) were placed in folded tin capsules for δ13C and δ15N ratio analysis using continuous-flow isotope-ratio mass spectrometry at the Yale Analytical and Stable Isotope Center (New Haven, CT U.S.).

Data analysis

We used analysis of variance (ANOVA) and Tukey HSD test to determine whether there was a difference in elevation between where we found *B. chinensis*, *A. picea* and *A. rudis* nests. We also used ANOVA to determine whether there was a difference in *A. picea* or *A. rudis* density, as indicated by search time (*A. rudis* nests discovered·hour^{-1}), with and without *B. chinensis* presence. We used analysis of covariance (ANCOVA) to evaluate $\mathrm{CT}_{\mathrm{min}}$ as a function of elevation, species (*B. chinensis*, *A. rudis*) and an elevation × species interaction term. Given that we found an elevation × species interaction, we also examined each species $\mathrm{CT}_{\mathrm{min}}$ as a function of elevation using linear models. We evaluated differences in the mean and maximum levels of inter- and intra-species aggression (*B. chinensis* × *B. chinensis*, *A. rudis* × *A. rudis* and *B. chinensis* × *A. rudis*) and distance between paired nests using ANOVA and Tukey HSD test. We included a pairing × distance interaction term to account for species-specific distance effects. All statistical analyses were performed using the R statistical program (R Development Core Team Version 3.5.1 2019).

Results

In the mid-2010s, *Brachyponera chinensis* appeared at several research sites in northern Georgia (U.S.). For example, *B. chinensis* was observed displacing *A. rudis* from artificial ant nests at a 402-m site in north Georgia in 2012, and by 2014 approximately 50% of the ant nests at the site were *B. chinensis* (Warren II et al. 2015). When we returned to the site in 2018 for this study, we did not find a single *A. rudis* nest. Similarly, we could not find *A. rudis* at a 252-m site in South Carolina (U.S.) heavily invaded by *B. chinensis*, but how long the site has been invaded is unknown. *Brachyponera chinensis* also appeared at three sites (out of 18) searched in 2018 in north Georgia where it did not occur in 2012 (Warren II and Chick 2013), and it was clearly segregated from the remaining *A. rudis* populations. At the five sites where *B. chinensis* and *A. rudis* co-occurred, we found *B. chinensis* nests nearest the roadway and *A. rudis* nests 50–200 m into the forest. At one site where a *B. chinensis* population (> 5 nests) was found in 2012 (685 m), and two sites where populations were found in 2017 (686 and 1001 m), *B. chinensis* disappeared by 2018 (Fig. 1a).

In 2018, *Brachyponera chinensis* and *Aphaenogaster* ants mainly occupied different elevations in the Southern Appalachian Mountain region (*Df* = 2, *SS* = 763,597, *MS* = 381,798, *f-value* = 12.755, *p value* < 0.001) [Fig. 1a]. *Aphaenogaster picea* ants occurred most (mean ± SE) at 805 ± 66 m, *A. rudis* occurred at mid-elevation (618 ± 37 m), and *B. chinensis* mostly occurred at 421 ± 39 m. *Brachyponera chinensis* mostly overlapped with *Aphaenogaster* ants at elevations between 480 and 580 m. Where *Aphaenogaster* ants and *B. chinensis* overlapped, *Aphaenogaster* ants were less common (based on timed searches) than where *B. chinensis* was absent (*Df* = 1, *SS* = 402.8, *MS* = 402.8, *f-value* = 3.722, *p value* < 0.066) [Fig. 1b]. The lack of a *B. chinensis* × *Aphaenogaster* species interaction term indicated that *B. chinensis* impacted *A. picea* and *A. rudis* similarly. With *B. chinensis* present, we found 10.4 ± 0.4 (mean ± SE) *A. rudis* nests hour^{-1} whereas where *B. chinensis* was absent, we found 20.3 ± 2.4 *A. rudis* nests hour^{-1}.

$\mathrm{CT}_{\mathrm{min}}$ decreased with elevation (*Df* = 1, *SS* = 18.257, *MS* = 18.257, *f-value* = 61.040, *p value* < 0.001) and between ant species (*Df* = 2, *SS* = 17.060, *MS* = 8.529, *f-value* = 28.510, *p value* < 0.001) [Fig. 2]. *Brachyponera chinensis* (mean ± SE) minimum thermal tolerance (6.3 ± 0.2 °C) was higher than *A. rudis* minimum thermal tolerance (5.0 ± 0.2 °C) which was higher than *A. picea* minimum thermal tolerance (3.9 ± 0.1 °C). $\mathrm{CT}_{\mathrm{min}}$ decreased with elevation for *A. picea* (*Coef.* = − 0.002, *SE* = 0.001, *t-value* = − 3.489, *p value* = 0.008) and *A. rudis* (*Coef.* = − 0.002, *SE* = 0.001, *t-value* = − 3.444, *p value* = 0.005) whereas it did

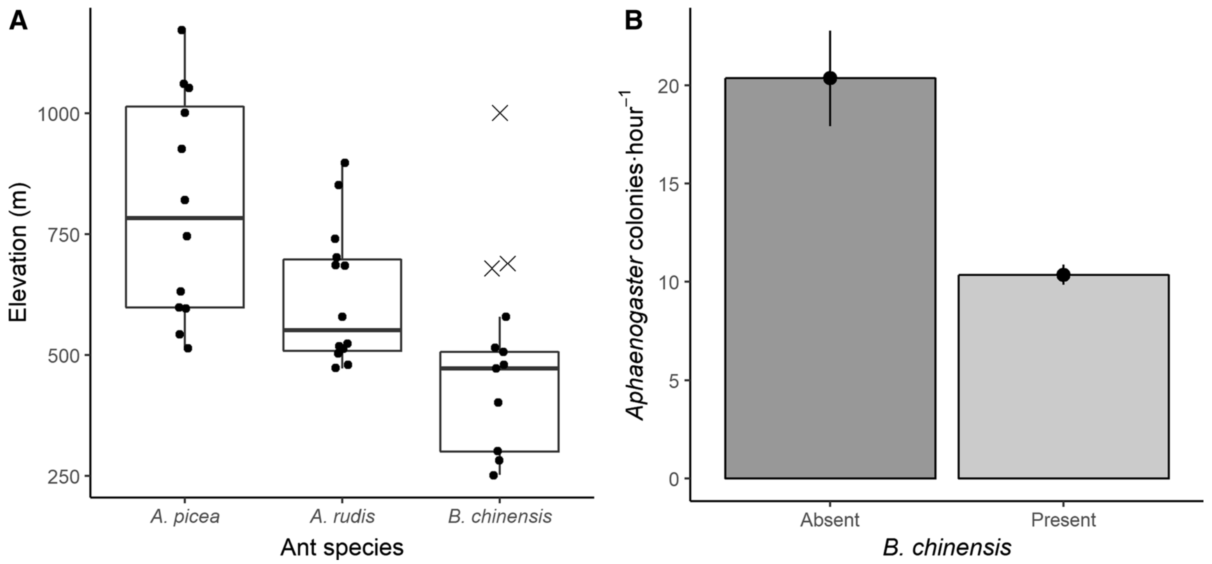
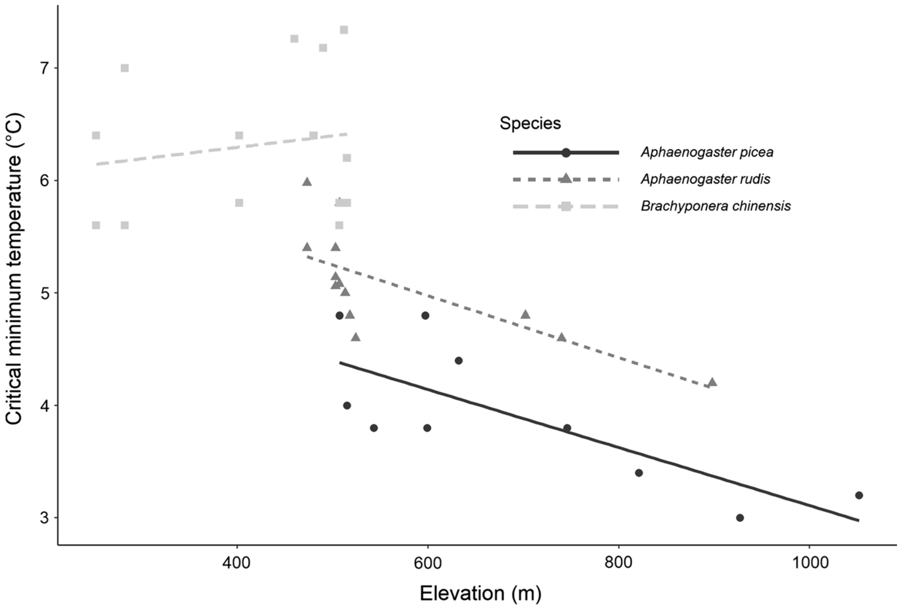


Fig. 1 **a** Box and whiskers plot showing elevations in Georgia, South Carolina and North Carolina (U.S.) where populations of the native *Aphaenogaster rudis* and *A. picea* ants and the non-native ant *Brachyponera chinensis* were found in 2018. Locations where *B. chinensis* were found in previous years but had disappeared in 2018 are marked with an "x". *Aphaenogaster* populations were found at higher elevations than *B. chinensis*. (**b**) Barplot showing *Aphaenogaster* nests discovered in timed searches in Georgia, South Carolina and North Carolina (U.S.) at locations with *B. chinensis* present and absent. *Aphaenogaster* populations were less dense (based on timed searches) with *B. chinensis* than were it was absent

Fig. 2 Critical thermal minimum temperatures ($\mathrm{CT}_{\mathrm{min}}$) across elevation gradients in Georgia, South Carolina and North Carolina (U.S.) for *Aphaenogaster picea* (solid line, points), *A. rudis* (dashed line, triangles) and *Brachyponera chinensis* (dashed line, squares). *Brachyponera chinensis* $\mathrm{CT}_{\mathrm{min}}$ did not change with elevation whereas *A. picea* and *A. rudis* $\mathrm{CT}_{\mathrm{min}}$ decreased with increased elevation



not change with elevation for *B. chinensis* (*Coef.* = 0.001, *SE* = 0.001, *t-value* = 0.616, *p value* = 0.549).

Mean aggression differed by species pairing (*DF* = 2, *SS* = 12.760, *MS* = 6.382, *f-value* = 23.210, *p value* < 0.001), and a Tukey HSD post hoc test indicated that the *A. rudis* × *A. rudis* aggression index was higher than *B. chinensis* × *B. chinensis* aggression, with *A. rudis* × *B. chinensis* aggression in between (Fig. 3a). Mean aggression did not change

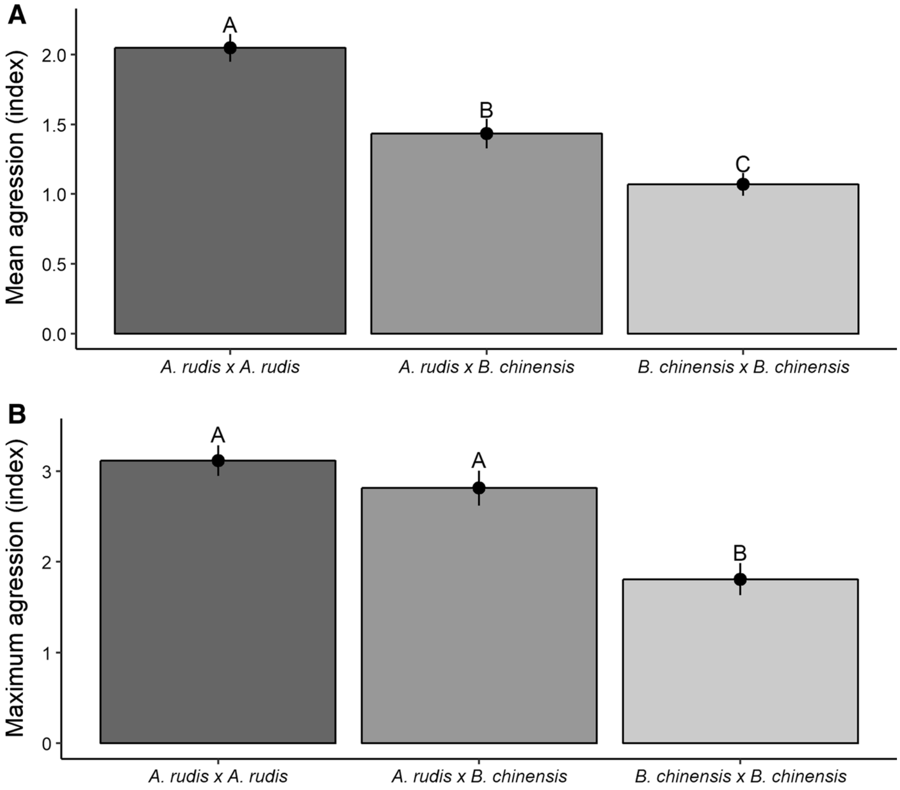


Fig. 3 **a** Mean and **b** maximum aggression indices for *Aphaenogaster rudis* intraspecific aggression assays, *A. rudis* × *Brachyponera chinensis* interspecific aggression assays and *B. chinensis* aggression assays. Mean aggression was highest in *A. rudis* × *A. rudis* assays, lower in *A. rudis* × *B. chinensis* assays and lowest in *B. chinensis* × *B. chinensis* assays ($p < 0.001$). Maximum aggression was the same in *A. rudis* × *A. rudis* and *A. rudis* × *B. chinensis* assays, and lowest in *B. chinensis* × *B. chinensis* assays ($p < 0.001$)

with nest distance ($DF = 1$, $SS = 0.696$, $MS = 0.696$, $f\text{-}value = 2.573$, p *value* < 0.113) or the pairing × distance interaction term ($DF = 2$, $SS = 0.480$, $MS = 0.240$, f-*value* $= 0.887$, p *value* < 0.416). Maximum aggression differed by species pairing type ($DF = 2$, $SS = 24.670$, $MS = 12.355$, $f\text{-}value = 13.220$, p *value* < 0.001) as *A. rudis* × *A. rudis* and *A. rudis* × *B. chinensis* maximum aggression were higher than *B. chinensis* × *B. chinensis* aggression (Fig. 3b). Maximum aggression did not change with nest distance ($DF = 1$, $SS = 1.613$, $MS = 1.613$, f-*value* $= 1.795$, p *value* < 0.184) or the pairing × distance interaction term ($DF = 2$, $SS = 3.840$, $MS = 1.922$, $f\text{-}value = 2.138$, p *value* < 0.125). *Aphaenogaster rudis* ants were the initiators in all aggressive interactions.

The mean (± SE) *A. rudis* stable nitrogen isotope value (δ15N) was (3.76 ± 0.4 ‰) and *B. chinensis* was (3.87 ± 0.3 ‰), and the *A. rudis* carbon isotope (δ13C) was (− 26.07 ± 0.2 ‰) and *B. chinensis* (− 25.45 ± 0.1 ‰) [Fig. 4].

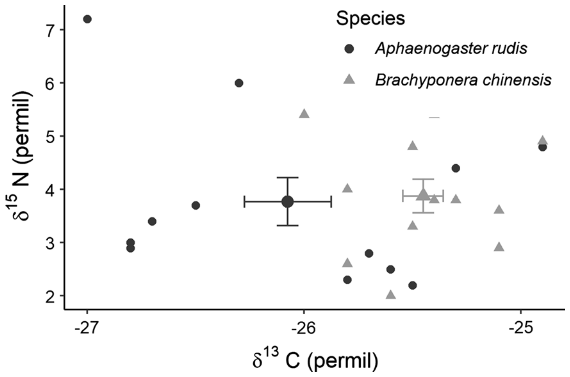


Fig. 4 Mean (± SE) stable carbon (δ13C) and nitrogen (δ15N) isotopes for *Aphaenogaster rudis* (circles) and *Brachyponera chinensis* (triangles) ants collected in Georgia and South Carolina (U.S.)

Discussion

We found increasing limitation to the Asian needle ant's (*B. chinensis*) invasion upward and northward along elevation gradients in the Southern Appalachian Mountains, apparently explained by its inflexible physiological tolerance for cold. Unlike co-occurring native and non-native ants, *B. chinensis* exhibited no physiological plasticity in thermal tolerance, and populations at higher elevations appeared unable to persist. In contrast, we found little evidence of native biotic resistance hindering *B. chinensis* invasion. *Brachyponera chinensis*, unlike the native *A. rudis*, did not appear to limit itself through typical intraspecific interactions. *Brachyponera chinensis* nests across three states (northern Georgia, northwestern South Carolina and southwestern North Carolina) instead acted as one massive nest, exhibiting almost no intraspecific aggression. In the process, *B. chinensis* appears to be displacing the dominant native ant, *A. rudis*, with which it shares very similar niche requirements.

Biotic resistance

Aphaenogaster rudis typically dominates Eastern U.S. deciduous forests (King et al. 2013; Lubertazzi 2012), but not where *B. chinensis* invades (Guenard and Dunn 2010; Rodriguez-Cabal et al. 2012; Warren II et al. 2015). The study of species invasions often captures 'snapshots' so that it is difficult to differentiate whether non-native species displace native species or prefer unique, often anthropogenically altered, habitats that the native species do not (King and Tschinkel 2008). *Brachyponera chinensis* is unique as an invasive ant in invading relatively undisturbed forest habitats (Guenard and Dunn 2010; Rodriguez-Cabal et al. 2012, *pers. obs.*). Within those forests, *B. chinensis* and *A. rudis* share nesting microhabitats, moist downed wood, and they appear to compete for those habitats, particularly somewhat decayed wood with *Reticulitermes flavipes* (Kollar, 1837) tunnels (Rodriguez-Cabal et al. 2012; Warren II et al. 2015).

We note that in previous samplings at one site near Cornelia, GA in the Chattahoochee National Forest (402 m elevation), no *B. chinensis* ants were observed (Giladi 2004; Warren II 2007), but the non-native ant arrived and noticeably displaced *A. rudis* from artificial nests by the early 2010s (Warren II et al. 2015). In the mid-2010s, *B. chinensis* and *A. rudis* appeared to split natural nesting locations, downed wood, about 50/50 at the site, though they never shared the same log (Warren II et al. 2015). In 2018, however, we did not find a single *A. rudis* nest at the site. The rapidity of displacement we observed in Georgia resembles that observed by Guenard and Dunn (2010) in North Carolina.

Experimental and observational data suggest little ecological difference between *B. chinensis* and *A. rudis*. Whereas *B. chinensis* has been proffered as a termite specialist in its invaded range, Warren II et al. (2015) found no difference in termite impacts between *B. chinensis* and *A. rudis* (which also prey upon termites, Buczkowski and Bennett 2007, 2008). Moreover, Suehiro et al. (2017) suggests that *B. chinensis* is less dependent on termites in its invaded than home range. We found very similar isotopic diet signatures for *B. chinensis* as did Suehiro et al. (2017) for invaded-range *B. chinensis*, and these were not dissimilar from *A. rudis*. Indeed, relatively higher stable nitrogen isotopes indicates a more carnivorous diet, but *B. chinensis* and *A. rudis* exhibited nearly identical stable nitrogen isotopes ($\Delta 0.11$ ‰). The stable carbon isotopes for *B. chinensis* and *A. rudis* were less similar ($\Delta 0.62$ ‰), with *B. chinensis* exhibiting a higher carbon isotope ratio, indicating that the ants may differ in trophic levels as a higher carbon also indicates a more carnivorous diet than herbivores (Suehiro et al. 2017). Invasive non-native ants typically are omnivorous (Holway et al. 2002) and have a greater focus on carbohydrate-based diets in their invaded compared to home ranges (Tillberg et al. 2007; Wilder et al. 2011), but *B. chinensis* may follow an opposite pattern, appearing to consume a more carnivorous diet in the invaded range (Suehiro et al. 2017) where it has been observed as a voracious forest predator (Bednar et al. 2013; Bednar and Silverman 2011). We found that the *B. chinensis* food niche requirements were similar to the omnivorous native *A. rudis*, which is a forest scavenger with a diet fueled by small invertebrates (Buczkowski and Bennett 2007, 2008; Lubertazzi 2012), with possibly more focus on prey than plants.

Brachyponera chinensis and *A. rudis* both are very good 'discoverers' in that they quickly find and retrieve food (Bednar et al. 2013; Fellers 1987; Warren II and Giladi 2014). Their success is based on the number of active foragers, and *B. chinensis* foraging success certainly is somewhat enhanced by their relatively high numbers as invaded-range *B. chinensis* form interconnected nests with 100–5000 workers (Zungoli and Benson 2008, *pers. obs.*); *A. rudis* is the dominant native woodland ant with numerous nests of 100–500 workers that forage constantly and quite effectively (King et al. 2013; Lubertazzi 2012). Ant competition long has been conceptualized as a trade-off between discovery (indirect competition through higher rates of food retrieval) and dominance (direct suppression through aggressive encounters), though some species, particularly non-native ants, are good at both (Holway et al. 2002; Parr and Gibb 2011). Hence, if both *B. chinensis* and *A. rudis* are good discoverers, it might be expected that *B. chinensis* ants are better aggressive competitors given its ability to displace *A. rudis*. Bednar et al. (2013) observed *B. chinensis* attack and kill *A. rudis* in laboratory experiments, and we observed considerable interspecific aggression between *B. chinensis* and *A. rudis*; however, we found that *A. rudis* ants were the initiators in all aggressive interactions. We also found that *B. chinensis* intraspecific aggression was considerably lower than interspecific aggression with *A. rudis* or intraspecific aggression between *A. rudis* nests. Menzel (2012) also found *B. chinensis* no more aggressive than sympatric native ants, including an *A. rudis* congener, *A. carolinensis* (Wheeler, W.M., 1915). Aggression bioassays are used to assess ant worker interactions between nests, though isolated interactions may not predict whole colony interactions (Roulston et al. 2003). Still, Warren II et al. (2018a) found pairwise aggression bioassays like those used here reasonably predictive of *M. rubra* and *A. rudis* whole colony behavior.

A key assumption in ecological theory is that multiple species coexist because intraspecific competition is higher than interspecific competition (Chesson 2000). That is, a species competes with itself more than it does with other species, and therefore a species reduces its own specific resources than it reduces the resources of competing species. Without intraspecific competition, i.e., self-limitation, a population can grow unchecked and monopolize, or even deplete, local resources (Berryman and Turchin 2001). Non-native species may gain advantage by escaping enemies in novel habitats ("enemy release," Keane and Crawley 2002), and they also may gain advantage by escaping intraspecific competition (and associated territoriality) in novel habitats ("friendly release," Warren II et al. 2018a). For ants, relatively low (to absent) intraspecific competition occurs in supercolonies (polydomy) whereby workers, and sometimes queens, move freely through otherwise independent ant nests. Polydomy is common in highly invasive ant species (Eyer et al. 2018; Holway 1998; Krushelnycky et al. 2010), including *B. chinensis* (Allen 2017; Paysen 2007), consistent with our findings of relatively low intraspecific aggression displayed between separate *B. chinensis* nests. Some invasive ants also form supercolonies in their native ranges, including *B. chinensis* (Murata et al. 2017), but supercolony formation in native ranges is less common and less populous than those occurring in invaded ranges (Errard et al. 2005; Huszár et al. 2014; Suarez et al. 2008).

One explanation for exaggerated supercolony formation with invasion is that genetic paucity in the founder populations limits cuticular hydrocarbon variation, (through which ants recognize nestmates) so that individual nest members are indistinguishable among ants (Fournier et al. 2016; Furst et al. 2011). This explanation is consistent with the *B. chinensis* invasion in the Southeastern U.S. as the Georgia, South Carolina and North Carolina populations are genetically identical (Yashiro et al. 2010), and inbreeding is not a negative consequence of *B. chinensis* founder effects (Eyer et al. 2018), which means that the advantage of supercolony formation stemming from genetic paucity may not bear the expected negative burden of low genetic diversity.

Abiotic resistance

We found that *B. chinensis* populations in the southeastern U.S. exhibited minimum thermal tolerances ranging from 5.6 to 7.3 °C with a mean minimum thermal tolerance approximately 1.8 °C higher than the native woodland *A. rudis* ants, with which it shared mid-elevation habitats (480–600 m). *Aphaenogaster rudis* populations range from the Southeastern to Northeastern U.S. as well as from low to high elevations; we only found persistent *B. chinensis* populations at low elevations—consistent with the higher, less plastic minimum temperature tolerance of *B. chinensis*. Additionally, we found three *B. chinensis* populations at elevations $>$ 650–1000 m in previous years sampling, but did not successfully collect these nests in 2018, as these populations apparently did not persist. Similarly, MacGown and Hill (2010) searched for a previously reported *B. chinensis* population in the Great Smoky Mountains National Park at approximately 620 m, but did not find that it persisted.

Brachyponera chinensis has been projected as a potential invader in the Northeastern U.S. (Bertelsmeier et al. 2016), but our findings suggest the ant is quite limited by colder climates, such as those further north and higher in elevation. Whereas *B. chinensis* has been reported in the Northern U.S., the stability of those populations, as with those discovered at higher elevations in the Southern U.S., is not verified (Guenard et al. 2018; Lucky et al. 2014; Pecarevic et al. 2010). Genetic analysis indicated that the Southeastern U.S. populations all come from the temperate region of Japan (Yashiro et al. 2010)—which may preclude them from moving upward and northward if their thermal tolerances are fixed due to low genetic diversity. By contrast, *S. invicta* (red imported fire ant), an invasive ant from South America, was projected to be limited from spreading northward of the Southeastern U.S. (Korzukhin et al. 2001), yet it shows considerable thermal plasticity and has been able to colonize and persist at high elevations in the Southern Appalachian Mountains (Lafferty 2018). These differences may reflect the time since *B. chinensis* and *S. invicta* invasions, the number of introductions and genetic complexity or simply species-specific differences.

We measured thermal tolerance as a mechanism underlying *B. chinensis*'s ability to colonize upward (elevation) and northward (latitude), but thermal acclimation may also occur through behavioral changes. For example, moving upward and northward, we generally found *B. chinensis* populations closer to roadways. The forest edges likely were warmer than the forest interior (though these distributions may also reflect the recency of colonization if the ants disperse along roadways.) Non-native species may compensate behaviorally for their lesser physiological cold tolerance by delaying spring foraging phenology until warmer temperatures arrive, as observed with *B. chinensis* (Warren II et al. 2015). *Aphaenogaster rudis* begins foraging when temperatures reach approximately 3–10 °C in our study area (Warren II et al. 2011), whereas *B. chinensis* does not seem to forage until temperatures reach at least 15 °C (Zungoli and Benson 2008). Moreover, Warren II et al. (2015) observed *A rudis* colonizing artificial nests at the 402-m site in north Georgia in April whereas *B. chinensis* did not appear until May (at which time it displaced several *A. rudis* nests). In an urban areas, *B. chinensis* began foraging earlier (and survived at lower temperatures) than *L. humile* (Argentine ant), and the early start was suggested to give it a competitive advantage in resource acquisition (Rice and Silverman 2013). Our data suggest that *B. chinensis* gains no such phenological advantage against *A. rudis*, but it was still able to increase in population size and eventually eliminate the native ant.

We found no evidence of biotic resistance to *B. chinensis* invasion, its success likely based (at least in part) on its own intraspecific lack of biotic resistance in the Southeastern U.S. With invasion, *B. chinensis* appears to eliminate the dominant native ants (*Aphaenogaster*; with which it shares considerable resource overlap) in approximately 10 years. At the same time, *B. chinensis*' inability to persist at higher elevations in the Southern Appalachian Mountains and its inflexible and relatively poor ability to tolerate cold temperatures, suggests its primary invasion may be limited to the Southeastern U.S. Without biotic resistance, vulnerable native species may only remain viable if they can tolerate abiotic conditions beyond the invasive species' tolerance (King and Tschinkel 2008; Moles et al. 2012). For *B. chinensis* invasion, *Aphaenogaster* species may only remain unaffected in eastern U.S. deciduous forests at high elevations and latitudes beyond the invasive ant's cold tolerance.

Acknowledgements We would like to thank Ellie Sanders, Audrey Egler, Bethany Sharkey and David Reese from the Highlands Biological Station Climate Change Ecology course for field assistance. We also would like to thank Highlands Biological Station Director Jim Costa. We thank three anonymous reviewers for helpful comments on the manuscript.

Data accessibility The data generated and analyzed for the current study will be available in the SUNY Buffalo State Digital Commons (https://digitalcommons.buffalostate.edu/biology_data/7/) upon manuscript acceptance.

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