ENTOMOLOGICAL
SOCIETY OF AMERICA
SHARING INSECT SCIENCE GLOBALLY

OXFORD

Community Ecology

Comparative Meta-analysis Effects of Nonnative Ants (Hymenoptera: Formicidae), Ground Beetles (Coleoptera: Carabidae), and Bark and Ambrosia Beetles (Coleoptera: Curculionidae) on Native Confamilials

Jessica A. Hartshorn[1], and David R. Coyle

Department of Forestry & Environmental Conservation, Clemson University, Clemson, SC 29634, and [1]Corresponding author, e-mail: jhartsh@clemson.edu

Abstract

Nonnative species often transform local communities to the detriment of native species. Much of the existing invasion ecology research focuses on the effects of a few extremely impactful species, and it is less clear how nonnative species which are not causing economic or ecological impacts alter closely related natives at risk of being displaced. Filling these knowledge gaps is critical because consequences of nonnative species are likely to vary depending on taxonomic scale, functional trait, and spatial or temporal niche. We conducted a meta-analysis to evaluate how biodiversity of native Formicidae (ants), Carabidae (ground beetles), and Scolytinae (bark and ambrosia beetles) species changes across a gradient of pressure from nonnative confamilials. We calculated Hill numbers for each group from data presented in literature and correlated native diversity metrics to proportion of nonnative species. Species richness of native ants was significantly negatively correlated with proportions of nonnative ants, whereas bark and ambrosia beetle metrics showed a nonsignificant negative correlation. Nonnative ground beetles had neutral effects on diversity of native ground beetles. Resulting contrasting patterns of invasive species effects on natives suggest complex biotic and abiotic factors driving effects of nonnative species in these groups. Our results suggest that a few extreme examples (e.g., red imported fire ants) drive most of the changes seen in native arthropod communities. To accurately assess impacts of invaders on native arthropod diversity, baseline data are needed, and community analyses must consider diverse functional traits of native taxa and improve the depth and breadth of community sampling.

Key words: invasive species, biodiversity, community ecology

Nonnative species are widely acknowledged to have deleterious effects on native flora and fauna communities, causing declines in species richness, evenness, and diversity (Valtonen et al. 2006, Hejda et al. 2009, Hanula and Horn 2011, Powell et al. 2011, Clark and Seewagen 2019). Despite the breadth of knowledge on the impacts of nonnative species on native ecosystems, much of the invasive species literature is focused on a relatively small number of highly influential plants, arthropods, vertebrates, and fungi (e.g., Chinese privet, *Ligustrum sinense* Lour.; emerald ash borer, *Agrilus planipennis* Fairmaire, 1888, Coleoptera: Buprestidae; wild hogs, *Sus scrofa* L., 1758; laurel wilt, *Raffaela lauricola* T.C. Harr., Fraedrich & Aghayeva). The globalization of the world's economy and rate at which goods are transported among countries—the United States is the largest importer of goods in the world (World Trade Organization 2018)—strongly suggests that nonnative species establishment and subsequent impacts will continue and are likely to increase in frequency in the future (Seebens et al. 2017). Our ability to manage these organisms is dependent on accurate predictions of interactions with native species that directly drive ecosystem processes and resulting impacts. Additionally, examining these effects at a refined taxonomic scale (e.g., species level) is necessary to identify and manage targeted nonnative species which may have the greatest and most costly effects, both in economic and ecological terms. However, initial steps are necessary to provide a baseline

understanding of family level effects before targeting certain species for investigation. Additionally, even broad analyses tend to focus on a specific region or habitat (e.g., Gandhi and Herms 2010) or on impacts to certain species (e.g., Prior and Hellman 2010). This meta-analysis will serve to investigate family-level effects across a wide range of habitats and locations.

Except for highly invasive arthropods, little is known about the impacts of nonnative arthropods on diversity of native confamilial species and the existing literature suggests inconsistent responses of native arthropods to invasion by closely related nonnatives (e.g., Eubanks et al. 2002, Cooling et al. 2015). Several factors, such as phylogenetic relationships with natives and landscape level effects, are likely to play into which and how species are affected by the establishment of a nonnative species (e.g., Krushelnycky and Gillespie 2010). Multiple hypotheses exist within invasion ecology that suggest phylogenetic distance as a factor affecting whether and how nonnative species affect closely related native (e.g., 'Adaptation' hypothesis, Duncan and Williams 2002; 'Darwin's Naturalization' hypothesis, Darwin 1809–1882). When looking at closely related native and nonnative species interactions, a few arthropod groups are well represented in the literature, namely, ants (Formicidae), ground beetles (Carabidae), and bark and ambrosia beetles (Curculionidae: Scolytinae).

Nonnative ants have been studied widely in terms of their effects on native arthropods. Argentine ants (*Linepithema humile* (Mayr), 1868) in Japan, for example, have been shown to eradicate other ant species in certain areas (Touyama et al. 2003), and the red imported fire ant (*Solenopsis invicta* Buren, 1972) can displace native ant species and reduce the diversity of the local ant communities (Kaspari 2000, Wojcik et al. 2001, Cameron et al. 2016, Wang et al. 2019) and can, conversely, positively affect species richness of ant communities as well as other arthropods (Morrison and Porter 2003). Ants have also been implicated in 'invasional meltdowns' whereby the establishment of an invasive species—in this case, the yellow crazy ant (*Anoplolepis gracilipes* (F. Smith), 1857)—directly caused a shift in a rainforest ecosystem on Christmas Island, drastically affecting at least three trophic levels (O'Dowd et al. 2003). Red imported fire ants are, however, considered beneficial in some agricultural systems due to their negative effects on native pests (Kaplan and Eubanks 2005)—so, while they may indeed antagonize native species, the economic benefit to farmers may be positive (e.g., Brinkley et al. 1991). However, agricultural systems are already highly modified which has its own suite of effects on native species (e.g., Landis et al. 2000, Vankosky et al. 2017). Because ant colonies are large and mostly sessile, it is likely more difficult for native ants to leave an area following the establishment of an invasive species (Smallwood 1982, Andersen 2008). Ants are also highly competitive (Parr and Gibb 2010) compared with ground beetles, and bark and ambrosia beetles in that they directly, and indirectly, compete for resources compared with other groups which may partition resources. These life history traits may magnify effects of nonnative ants on native ant communities.

Comparatively fewer studies are available examining nonnative ground beetle (Carabidae) impacts on native arthropod communities. Most literature examines a different relationship—the impacts of habitat type on ground beetle community composition (e.g., Werner and Raffa 2000, Goulet et al. 2004). Some studies have found positive effects of nonnative ground beetles due to their feeding on other nonnative pest species (e.g., Hannam et al. 2008), while others have shown negative effects, albeit indirectly, on native ground beetles through increased activity (e.g., Niemelä et al. 1997). Ground beetles, in contrast to ants, are relatively more mobile and live independently of one another (Holland 2002), making it much easier for them to move to a new area upon the establishment of an invasive species.

Some of the most damaging invasive insects belong to the Curculionidae; namely, the vectors of Dutch elm disease (*Scolytus multistriatus* (Marsham, 1802) and *S. schevyrewi* (Semenov-Tian-Shanskij, 1902); Knight et al. 2012) and laurel wilt (*Xyleborus glabratus* Eichhoff, 1877; redbay ambrosia beetle; Fraedrich et al. 2007) are well known for causing widespread mortality of their respective hosts. Bark and ambrosia beetles are such a threat to ecosystem health that the USDA Forest Service conducts annual targeted surveys in areas most likely to experience invasion (e.g., ports, lumber yards) and these surveys also catch a variety of native bark and ambrosia beetles (Rabaglia et al. 2019). The impacts of nonnative bark and ambrosia beetles on native plants and their associated arthropods have been widely studied in a variety of habitats (e.g., Schlarbaum et al. 1998, Evans et al. 2013) and, contrary to ants and ground beetles, no positive effects on native communities have been recorded from an invasion by a nonnative bark or ambrosia beetle. However, these studies tend to focus on certain high-impact species and broad surveys of lesser known nonnatives are not as available. Bark and ambrosia beetles fall between ants and ground beetles in their ability to move to new locations—while ground beetle and ant larvae are also largely immobile, bark and ambrosia larvae must remain inside the host plant, but adults, especially females, tend to be excellent fliers and can disperse long ranges in search of appropriate hosts (Jones et al. 2019). Some female bark and ambrosia beetles are haplo-diploid, meaning that they are able to produce offspring without the benefit of a male (e.g., Gomez et al. 2018) and this life-history trait also affects their mobility and ability to establish in new locations.

Because different taxa seem to have varying effects on native species, the lack of a keen understanding of native arthropod responses to the presence and relative abundance of closely related nonnative taxa may limit our ability to predict the potential economic and ecological impacts of invasion. Refining management priorities and attempting to alleviate some of the negative effects of nonnative arthropods relies on the examination of these nonnative species through a fine lens while also considering a wide range of interactions with closely related native species. Our objective was to quantify the effects of nonnative species in three arthropod groups on native confamilial diversity through a meta-analysis, focusing on ants, ground beetles, and bark and ambrosia beetles in North America. We predict that diversity metrics of all three families will be inversely correlated with the proportion of nonnative species in the sampled community.

Methods

Data Collection

Here we define 'nonnative' as any organism which originated outside of North America and 'invasive' as a nonnative organism which causes significant impacts either economically or ecologically. To identify suitable arthropod families for use in this study, we searched for peer-reviewed articles in Google Scholar and Web of Science using the search terms 'invasive species', 'nonnative', 'species abundance', 'exotic species', and 'arthropod' alone and in combination. Initial searches indicated that Carabidae, Formicidae, and Scolytinae (Curculionidae) would be well represented in the literature and result in sufficient data for this study (at least 10 studies per Family or Subfamily taxa). We then added the terms 'Scolytinae',

'Scolytidae' (to identify older literature), 'bark beetle', 'ambrosia beetle', 'Formicidae', 'ant', 'and', 'Carabidae', and 'ground beetle' to refine our results. We did not set a date range for results.

Publications were included if they met the following criteria: studies were conducted in North America, all reported organisms were identified to species, abundance data were extractable directly from the publication or could be obtained by contacting the corresponding author, and at least one nonnative species that had an abundance of one or more individuals was reported in the study. Only adult insects were included in the study because immature arthropods often have vastly different life histories than adults and are much less represented in the literature. Within individual publications, individual collection events at multiple sites and/or years were considered independent data points if they were reported separately, were spatially (e.g., sites were multiple km apart) or temporally independent (e.g., multiple years apart) and had at least 100 individuals per collecting event which were all identified to species. In cases where fewer than 100 individuals were collected across multiple collection events, counts were combined assuming sites did not change, and collections were in a short period of time (e.g., consecutive years). Within a study, all habitats were included except treatments that significantly altered arthropod communities (e.g., pesticide application) were excluded from analyses. Each replication within each study was considered a single 'data point'.

Data Analyses

Cumulative proportion of all nonnative species was calculated for each data point by dividing the total number of nonnative individuals by the total number of individuals captured. Nonnative species were then removed from each dataset and Hill numbers ([Hill 1973](#)) were calculated:

N_0 = species richness; number of unique species
N_1 = exp(H); effective number of species
N_2 = Reciprocal of Simpson's Index; diversity considering richness and evenness

with H representing Shannon's Index and N_2 being equal to $1/(p_1^2 + p_2^2 + \cdots + p_n^2)$. Nonnative species were removed to identify impacts on native species only. Evenness was also calculated for each data point and each taxon (sans nonnative species) by dividing Shannon's Index by species richness (H/N_0). Hill numbers were chosen as they describe multiple aspects of community composition and are regularly used to estimate diversity at and above the family level (e.g., [Roth et al. 1994](#), [Hoback et al. 1999](#)). N_0 refers to the number of unique species in the sample while the effective number of species (N_1) refers to the number of equally abundant species needed that would result in the same mean abundance observed in the sample. Finally, N_2 measures the probability that two random individuals from the same sample will belong to the same species. In all cases, the higher the value, the higher the diversity of the sample.

To account for differences in collection methods, the proportion of nonnatives and all three Hill numbers were compared across habitat types, sampling methods, and sampling effort for papers that used only a single sampling type and a single habitat. Sampling methods are detailed in respective papers ([Table 1](#)). Briefly, all ground beetles were collected by pitfall trap. Ants were collected through a variety of traps including pitfall as well as leaf litter sifting, baited traps, woody debris dissection, hand collection, UV light traps, and mercury vapor traps. Bark and ambrosia beetles were collected mostly with Lindgren funnel traps and intercept panel traps. Other methods of bark and ambrosia beetle collection included sticky traps, window pane traps, malaise traps, hand collections, sweep net, fogging, and dissecting trap trees. A linear mixed effects model was created for

each diversity index with proportion of nonnative species serving as the independent variable using the 'nlme' package ([Pinheiro et al. 2020](#)). To account for variation among publications, 'publication' was included as a random effect in each model. All statistical analyses were performed in R 4.0.2 ([R Core Team 2020](#)).

Results

In total, 86 publications and 191 individual data points were identified across three insect groups ([Supp Appendix 1 [online only]](#)). Ants were represented by 72 data points across 25 publications; Carabidae was represented by 80 data points across 41 publications; and Scolytinae was represented by 39 data points across 20 publications. Publications represented a range of sampling methods and habitats for each arthropod group ([Table 1](#)). Non-native species collected are reported in respective publications ([Supp Appendix 2 [online only]](#)).

Among all groups, [Naumann and Higgins (2015](#), Formicidae) had the lowest Hill numbers with species richness (N_0) at two, N_1 at 1.00, and N_2 at 0.82. The upper range of Hill numbers was more variable with the highest species richness at 102 ([Goulet et al. 2004](#), Carabidae), N_1 at 47.74 ([Clark et al. 2011](#), Formicidae), and N_2 at 30.47 ([Byers et al. 2000](#), Formicidae, 1995 data). Scolytinae had the lowest average values of Hill Numbers (N_0 = 21 ± 3; N_1 = 6.21 ± 1.41; N_2 = 4.38 ± 1.07). Evenness ranged from 0.0068 ([Naumann and Higgins 2015](#); Formicidae, red alder site) to 1.00 ([Clark et al. 2011](#), Formicidae) with ants having the highest average value (0.61 ± 0.02) and Carabidae having the lowest average value (0.32 ± 0.06).

Forests and prairies had the lowest proportion of nonnatives, while nurseries had the highest (F = 5.38, P = 0.0001). Sampling method was not significant, but only narrowly so, with regards to proportion of nonnatives (F = 2.12, P = 0.054). Prairies had significantly higher N_0, whereas urban sites had significantly lower N_0 compared with other habitat types (F = 4.26, P = 0.0012). Bottle traps had the lowest N_0, whereas window traps had the highest N_0 (F = 2.40, P = 0.03). However, these were also the least frequently used trap types and the N_0 of the most commonly used trap types did not differ. Forest and prairie sites had the highest N_1 and nurseries had the lowest N_1 (F = 4.04, P = 0.002). Window traps had the highest N_1, whereas trap trees had the lowest N_1 (F = 2.26, P = 0.041). However, these were again the least used sampling methods and the more commonly used sampling methods did not differ significantly from each other. Sampling method, habitat type, and sampling effort did not significantly affect N_2. Forests and urban sites had the highest evenness, while prairies had the lowest evenness (F = 16.81, P < 0.0001). Lindgren funnel traps had the highest evenness, while pitfall traps had the lowest evenness (F = 4.34, P = 0.0005).

Within ant data collected from the literature, the proportion of nonnative species ranged from 0.0001 ([Skvarla 2015](#)) to 1.00 ([Naumann and Higgins 2015](#), red alder). Species richness (N_0) ranged from two ([Naumann and Higgins 2015](#), red alder site, Philpott et al. 2014, G2 sites) to 72 ([Skvarla 2015](#)) with an average of 22 (±2). N_1 ranged from 1.0047 ([Naumann and Higgins 2015](#), red alder) to 47.74 ([Clark et al. 2011](#)) with an average of 7.50 (±1.0230). N_2 ranged from 0.76 ([Naumann and Higgins 2015](#), red alder) to 11.49 ([Toennisson et al. 2011](#)) with an average of 6.55 (±0.9321). Evenness ranged from 0.0068 ([Naumann and Higgins 2015](#), red alder) to 1.00 ([Clark et al. 2011](#)) with an average of 0.62 (±0.07).

Within Carabidae data collected from the literature, the proportion of nonnative species ranged from 0.0002 ([French et al. 2004](#)) to 0.96 ([Lalonde et al. 2012](#)). Species richness (N_0) ranged from 9 ([Hatten et al. 2007](#), CTB) to 102 ([Goulet et al. 2004](#)) with an average of 35 (±8). N_1 ranged from 1.28 ([Blubaugh et al. 2011](#), 2005 data)

Table 1. Summary of literature used in data analyses including habitat type sampled, sampling methods used, and number of replicates per paper

Citation	Number of replications	Trapping method	Habitat
Family: Formicidae			
Choate and Drummond (2012)	1	Pitfall, leaf litter, baits, hand collection	Agricultural field
Clark et al. (2011)	1	Pitfall, baits, hand collection, malaise, UV light traps, mercury vapor trap, bee bowls	Woodland, shrub, field
Cumberland and Kirkman (2012)[a]	2	Pitfall	Forest
Davis and Zigler (2012)	3	Pitfall	Forest
Graham et al. (2004)	3	Pitfall	Forest
Gouchnour et al. (2019)	3	Pitfall, leaf litter, woody debris dissection, baits, hand collection	Urban
Guénard and Dunn (2010)[a]	2	Pitfall	Forest
Holway (1998)[a]	2	Pitfall, baits	Forest
Ivanov et al. (2011)[a]	3	Leaf litter, baits	Urban
King and Tschinkel (2006)[a]	4	Pitfall	Agricultural field
King and Tschinkel (2013)[a]	1	Pitfall	Forest
Lubertazzi and Tschinkel (2003)	12	Pitfall	Forest
Martelli et al. (2004)	1	Leaf litter	Forest
Menke et al. (2011)	1	Pitfall	Urban
Menzel and Nebeker (2008)[a]	1	Baits	Forest
Naumann and Higgins (2015)[a]	3	Pitfall	Forest
Pećarević et al. (2010)	1	Pitfall	Urban
Philpott et al. (2013)	10	Pitfall	Urban
Porter and Savignano (1990)[a]	2	Pitfall, baits	Agricultural field
Rowles and Silverman (2010)[a]	2	Pitfall, hand collection	Forest
Skvarla (2015)	1	Pitfall	Forest
Stuble et al. (2011)[a]	3	Pitfall	Forest
Toennisson et al. (2011)	1	Pitfall	Urban
Verble and Yanoviak (2013)	10	Leaf litter, baits, hand collection	Forest
Wang et al. (2000)	2	Pitfall	Forest
Family: Carabidae			
Belaoussoff et al. (2003)	1	Pitfall	Agricultural field
Bergmann et al. (2012)	1	Pitfall	Forest
Blubaugh et al. (2011)	2	Pitfall	Forest, prairie
Bourassa et al. (2008)	1	Pitfall	Turf
Bourassa et al. (2010)	3	Pitfall	Agricultural field
Brunke et al. (2009)	1	Pitfall	Agricultural field
Byers et al. (2000)	5	Pitfall	Agricultural field
Cárdenas and Buddle (2009)	1	Pitfall	Forest
Carmona and Landis (1999)	1	Pitfall	Agricultural field
Clark et al. (2006)	1	Pitfall	Agricultural field
Comeau et al. (2012)	1	Pitfall	Agricultural field
Cutler et al. (2012)	2	Pitfall	Agricultural field
Ellsbury et al. (1998)	1	Pitfall	Agricultural field
Firlej et al. (2012)	2	Pitfall	Agricultural field
French et al. (2004)	1	Pitfall	Agricultural field
Gagne and Fahrig (2010)	6	Pitfall	Urban, forest
Gandhi et al. (2008)	8	Pitfall	Forest
Gandhi et al. (2011)	4	Pitfall	Forest
Gandhi et al. (2014)	1	Pitfall	Forest
Gardiner et al. (2010)	1	Pitfall	Agricultural field
Goulet et al. (2004)	1	Pitfall	Agricultural field
Hartley et al. (2010)	1	Pitfall	Urban, prairie
Hatten et al. (2007)	9	Pitfall	Agricultural field
Hummel et al. (2012)	1	Pitfall	Agricultural field
Kleintjes et al. (2002)	1	Pitfall	Prairie
Koivula and Spence (2006)	1	Pitfall	Forest
Lalonde et al. (2012)	3	Pitfall	Agricultural field
Larsen and Williams (1999)	3	Pitfall	Prairie
Larsen and Work (2003)	1	Pitfall	Prairie
Larsen et al. (2003)	3	Pitfall	Prairie
Leslie et al. (2014)	3	Pitfall	Agricultural field
Melnychuk et al. (2003)	1	Pitfall	Agricultural field
Niwa and Peck (2002)	1	Pitfall	Forest
Petrillo and Witter (2009)	1	Pitfall	Forest

Table 1. Continued

Citation	Number of replications	Trapping method	Habitat
Riley and Brown (2011)	1	Pitfall	Forest
Russell et al. (2017)	4	Pitfall	Agricultural field
Rykken et al. (1997)	1	Pitfall	Forest
Skvarla (2015)	1	Pitfall	Forest
Smith et al. (2004)	2	Pitfall	Agricultural field
Trager et al. (2013)	1	Pitfall	Forest
Werling and Gratton (2008)	1	Pitfall	Agricultural field
Werner and Raffa (2000)	2	Pitfall	Forest
Family: Curculionidae: Scolytinae			
Atkinson et al. (1988)	2	Sticky trap, window trap	Forest
Coyle et al. (2005)	1	Lindgren funnel	Forest
Coyle et al. (2015)	2	Lindgren funnel	Forest
Dodds et al. (2010)	3	Lindgren funnel, intercept trap, malaise	Forest
Dodds et al. (2015)	1	Lindgren funnel, intercept trap, SLAM trap	Forest
Dodds et al. (2019)	1	Lindgren funnel, SLAM trap	Forest
Dodds (2011)	2	Lindgren funnel	Forest
Gandhi et al. (2010)	1	Lindgren funnel	Urban
Grant et al. (2003)	1	Hand collecting, sweep net, beat sheet, light trap, canopy fogging, malaise, Manitoba trap, pitfall	Prairie
Johnson et al. (2014)[a]	1	Lindgren funnel	Forest
Kendra et al. (2011)[a]	1	Lindgren funnel	Forest
Miller and Duerr (2008)	1	Lindgren funnel	Forest
Miller and Rabaglia (2009)	8	Lindgren funnel	Forest
Oliver and Mannion (2001)	1	Lindgren funnel	Nursey
Pfammatter et al. (2011)	3	Lindgren funnel	Forest
Reding et al. (2010)	4	Bottle trap	Nursery
Reed and Muzika (2010)[a]	2	Lindgren funnel	Forest
Reed et al. (2015) [a]	1	Trap trees	Forest
Turnbow and Franklin (1980)	1	–	–
Weber and McPherson (1991)	1	Window trap	Forest
Zylstra et al. (2010)[a]	1	Trap trees	Forest

[a]Paper focused on invasive species.

to 18.11 (Gandhi et al. 2011, Willow 1981 site) with an average of 8.50 (±1.57). N_2 ranged from 1.2802 (Blubaugh et al. 2011, 2005 data) to 30.47 (Byers et al. 2000, 1995 data) with an average of 6.38 (±1.7890). Evenness ranged from 0.02 (Goulet et al. 2004) to 0.80 (Gagne and Fahrig 2010) with an average of 0.32 (±0.06).

Within Scolytinae data collected from the literature, the proportion of nonnative species ranged from 0.0004 (Pfammatter et al. 2011, 2007 data) to 1.00 (Atkinson et al. 1988, window traps). Species richness (N_0) ranged from 5 (Reding et al. 2010, 2007 data) to 55 (Weber and McPherson 1991) with an average of 21 ± 3. N_1 ranged from 1.65 (Reding et al. 2010, 2009 data) to 13.38 (Turnbow and Franklin 1980) with an average of 6.21 (±1.41). N_2 ranged from 1.29 (Reding et al. 2010, 2009 data) to 8.96 (Pfammatter et al. 2011, 2007 data) with an average of 4.38 (±1.07). Evenness ranged from 0.23 (Reding et al. 2010) to 0.91 (Reed and Muzika 2010, 2008 data) with an average of 0.10 (±0.02).

Increasing proportions of nonnative confamilials was significantly correlated with a decrease in ant species richness ($t_{47} = -2.90, P = 0.0052$) and no diversity index for either Carabidae or Scolytinae was significantly affected by the proportion of nonnative species present (Table 2).

Discussion

We predicted that standard diversity metrics would be inversely correlated with the proportion of nonnative species, as is common in much of the invasive species literature (e.g., Simberloff 2005, Molnar et al. 2008, Pyšek and Richardson 2010, Clark and Seewagen 2019). However, we found no impact of nonnative species on most of the diversity metrics we examined. Instead, we found widely varying effects of invasion that were often unique to each diversity index and arthropod group. And, while statistically significant effects were not discernable for most groups and diversity measures, descriptive statistics did show some patterns. For instance, the 'red alder' site from Naumann and Higgins (2015) had the highest proportion of nonnative ants and the lowest value for all Hill numbers and evenness while Skvarla (2015) had the lowest proportion of nonnative ants and the highest species richness. The Naumann and Higgins (2015) 'red alder' site was one of three that had known populations of the invasive European fire ant (*Myrmica rubra* L., 1758), whereas the Skvarla (2015) data were collected in protected National Forest and National Park land in the Ozark Mountains, Arkansas.

Several factors may contribute to our inconsistent results. While the random effect of 'publication' was not a significant factor in any model, targeted sampling of specific nonnatives within publications likely affected our results. Two of the 41 Carabidae publications (5%), 4 of the 20 Scolytinae publications (20%), and 11 of 25 Formicidae publications (44%) focused specifically on nonnative species. This is unsurprising because research focusing on an impactful invasive species likely has a greater chance of being supported

Table 2. Summary of statistical coefficients

Family	Index	Mean (± SE)	t-value	P-value	R^2
Formicidae	N_0 (richness)	22 (± 2)	–2.8959	**0.0052***	0.0251
	N_1 (Exp(H))	7.4992 (± 1.0230)	–1.3891	0.1714	0.0036
	N_2 (1/Simpson's)	4.7207 (± 0.7801)	1.6628	0.1030	0.0396
	Evenness	0.6185 (± 0.0680)	0.4247	0.6730	0.1662
Carabidae	N_0 (richness)	35 (± 8)	–1.2163	0.2305	0.0117
	N_1 (Exp(H))	8.5004 (± 1.5735)	–0.6862	0.4962	0.0059
	N_2 (1/Simpson's)	6.3823 (± 1.7890)	–0.6737	0.5041	0.0059
	Evenness	0.3180 (± 0.0634)	1.5469	0.1292	0.0114
Scolytinae (literature)	N_0 (richness)	21 (± 3)	–0.9951	0.3336	0.0062
	N_1 (Exp(H))	6.2080 (± 1.4133)	–0.6369	0.5327	0.0081
	N_2 (1/Simpson's)	4.3824 (± 1.0663)	–1.2707	0.2210	0.0405
	Evenness	0.5961 (± 0.0661)	0.5701	0.5761	0.0081

*Significance.

than pure biodiversity work. This increase in focus on nonnative species corresponds to increasing effects on native confamilials.

Time since invasion is another factor impacting the effects of nonnatives on native communities. While some species do have accurate and specific timelines for introduction (e.g., red imported fire ants were introduced in the 1940s; Tschinkel 2006), the specific introduction event for many species is not known or is unclear (e.g., redbay ambrosia beetle), and this prevented our use of 'time since invasion' as a reliable independent variable. Each of these studies is a snapshot of disturbance and species causing the most significant effects may be newer to their environment, thus causing rapid initial declines in native communities. Long-term ecological studies that follow invasions and the effects on native flora and fauna are necessary to answer these long-standing questions.

Previous meta-analyses (e.g., Kenis et al. 2009, Cameron et al. 2016) suggest that invader trophic level significantly affects the directionality and size of nonnative impacts, and that increasing the number of nonnative species does not necessarily translate to an increase in effects on native diversity. For instance, the brown tree snake (*Boiga irregularis* (Merrem, 1802)) is a classic example of a single nonnative species which altered several ecological guilds in places where it has invaded (Wiles et al. 2003, Colvin et al. 2005, Rodda and Savidge 2007). Impacts of these magnitudes have been seen with some introduced arthropods (e.g., Davis et al. 2008, Herms and McCullough 2014, Nisbet et al. 2015), so the overall negative correlation between species richness and proportion of nonnative ants that we found makes sense.

Landscape effects may also play a role in whether, and how, nonnative species affect natives. For example, studies that show significant negative impacts of nonnative ants on native ant species have mostly occurred on islands and have investigated species which are not yet present, or widespread, in North America. Future arrival of these species to the continent may change this relationship. One such example is Alluaud's little yellow ant, *Plagiolepis alluaudi* Emery, 1894, which has recently established in southern Florida, and has already been implicated in the displacement of a native ant species in that area (Chouvenc et al. 2018). Other landscape effects like edge effects (e.g., Holway 2005) and patch size (e.g., Vercken et al. 2011) also affect how nonnatives impact native species through varying disturbance regimes or elevated densities of predators. Examples like these deserve long-term monitoring to determine how these effects may play out over time.

Ecological niche—including feeding, spatial, and temporal partitioning—is also a factor in how nonnatives are received in their new environment. Nonnative arthropod generalist predators (AGPs) tend to have wide-ranging effects on native arthropods due to their complex trophic interactions. Because AGPs feed on herbivores, predators, detritivores, and sometimes plant material, they can negatively affect communities through consumptive and nonconsumptive effects. This leads to complex and unpredictable impacts on native communities (Snyder and Evans 2006). For example, many ants are omnivorous, feeding on a variety of plants and animal matter, including other arthropods, and this trait allows them to fill multiple niches, easily assimilate into many habitat types, and have multi-trophic effects by preying on, and competing with, other predators and herbivores (Crowder and Snyder 2010). Additionally, trophic position has a significant effect on both the size and directionality of impacts by nonnative species and, overall, increasing the number of nonnative species does not necessarily lead to an increase in their impacts on native diversity measures (Cameron et al. 2016). Determining the effects of one species is made more difficult due to intraguild predation which has been shown to dampen trophic cascades; therefore, knowing the composition of entire communities is necessary to determining the effects of one species on others (Finke and Denno 2004, Finke and Denno 2005).

Spatial and temporal partitioning and stratification also likely play a role in the effects of nonnatives on native species. Compared with bark and ambrosia beetles and ground beetles (Wallin and Ekbom 1994) that travel great distances for food and hosts and occur individually or in small groups, ant colonies are fairly sessile and can consist of tens of thousands of individuals (e.g., Pedersen et al. 2006, Andersen 2008) in set locations, only moving when necessary (e.g., because of disturbance, death of the queen, or for mating). These characteristics may allow nonnative ants to have faster, and more intense, impacts on native arthropods compared with more motile nonnative species arthropods or those with specialized diets (e.g., Snyder and Evans 2006). Carabidae can fill multiple niches with some species being highly specialized (e.g., the Rhysodini tribe which feeds on ameboid stages of slime molds), some being omnivorous, and others predatory, and are known to travel great distances. Some of these characteristics may lead to a longer lag time between nonnative establishment and impacts on natives and their cumulative effects make it difficult to predict impacts based on family.

An additional layer of complexity is that these spatial and temporal niches may shift over time and be affected by the introduction of a nonnative species. Much like the studies which look at overall effects of nonnative species on native diversity, there is a wide range of results when looking at shifts in temporal or spatial partitioning

among closely associated species. Most of this work has been done on nonarthropod animals; for example, Harrington et al. (2009) showed that otters and polecats in the United Kingdom shifted their feeding behavior from nocturnal to diurnal in the presence of American mink, an established nonnative predator. Flowering phenology has also been shown to shift when nonnative species enter a naïve system, allowing the introduced plant species to reduce competition and fill a previously unfilled temporal niche (Godoy et al. 2009). Nonnative fish in China, however, showed no patterns of niche partitioning with native and nonnative goby fish overlapping in terms of diet and feeding activity (Guo et al. 2017). What literature exists for insects has mixed results, with both positive and negative associations, high turnover of native and nonnative species at varying locations, and significant seasonal variation in niche separation (e.g., Albrecht and Gotelli 2001, Coccia et al. 2016). Native species that are able to adapt with behavioral shifts, such as these will likely be less impacted by the establishment and spread of nonnative species.

Finally, each species and publication objective necessitated a different sampling method and habitat type (Table 1). While ant sampling was highly variable among publications and included hand collecting, pitfall traps, baits, and leaf litter sifting, it was also the only group to show any statistical significance. Comparatively, ground beetle collections were largely consistent (pitfall traps in agricultural fields and forests) and did not show any significance among any diversity index measured. Bark and ambrosia beetle collections were also fairly consistent and consisted mostly of Lindgren funnel traps baited with various lure types and host volatiles, and yet, no significant correlation was found between diversity metrics and proportion of nonnative species.

Our results demonstrate the complexity of nonnative species relationships with, and impacts on, native confamilial species. Other interactions are likely occurring such as the 'Identity Effect' which means that a single nonnative species may drive community changes while many others are able to co-exist without causing significant changes (e.g., Emery and Gross 2006). Ants in particular are known for their high levels of competitive exclusion and several studies have demonstrated dominance among certain nonnative ant species relative to native ant communities (Parr 2008, Arnan et al. 2018). This competitive exclusion may occur through competition for resources and interference with native ant foraging (e.g., Human and Gordon 1996) or may be a result of interactions with environmental and habitat factors (e.g., Philpott et al. 2010).

The least frequently used sampling methods produced unsurprisingly extreme results for N_0 and N_1 and it is likely that additional sampling would eliminate this significance. The most commonly used sampling methods, Lindgren funnel traps and pitfalls, had the highest and lowest evenness measures, respectively. Considering that evenness and all Hill numbers were not significantly correlated with proportion of nonnatives for ground beetles or bark and ambrosia beetles, the differences in evenness and Hill numbers associated with sampling method and habitat are likely due to these human-related and environmental factors.

Our results suggest that these complex interactions cannot adequately be assessed by relatively simple indices at the family or subfamily level, and thus, it is essential that research progresses beyond these standard measures of diversity to estimate impacts of nonnative species on native communities by assessing both taxonomic and functional diversity. These suggestions have been previously noted (e.g., Schlaepfer 2018) and our analyses support those conclusions. Using these indices may result in an underestimation of impacts to natives, potentially impacting management and conservation decisions.

One issue with community assessment is the sheer volume of data and time required to do so. Further, baseline data for preinvasion diversity is often not available, so comparisons with 'untouched' systems may not be possible. Long-term datasets are key to answering these questions and mitigating future impacts by nonnative species. Within the invasion ecology community, researchers can and should work together to share data and revisit previously measured sites.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

References Cited

Albrecht, M. and N. J. Gotelli. 2001. Spatial and temporal niche partitioning in grassland ants. Oecologia 126: 134–141.

Andersen, A. N. 2008. Not enough niches: non-equilibrial processes promoting species coexistence in diverse ant communities. Austr. Ecol. 33: 211–220.

Arnan, X., A. N. Andersen, H. Gibb, C. L. Parr, N. J. Sanders, R. R. Dunn, E. Angulo, F. B. Baccaro, T. R. Bishop, R. Boulay, *et al*. 2018. Dominance-diversity relationships in ant communities differ with invasion. Glob. Chan. Biol. 24: 4614–4625.

Atkinson, T. H., J. L. Foltz, and M. D. Connor. 1988. Flight patterns of phloem- and wood-boring Coleoptera (Scolytidae, Platypodidae, Curculionidae, Buprestidae, Cerambycidae) in a north Florida slash pine plantation. Environ. Entomol. 17: 259–265.

Belaoussoff, S., P. G. Kevan, S. Murphy, and C. Swanton. 2003. Assessing tillage disturbance on assemblages of ground beetles (Coleoptera: Carabidae) by using a range of ecological indices. Biodiv. Conserv. 12: 851–882.

Bergmann, D. J., D. Brandenburg, S. Petit, and M. Gabel. 2012. Habitat preferences of ground beetle (Coleoptera: Carabidae) species in the northern Black Hills of South Dakota. Environ. Entomol. 41(5): 1069–1076.

Blubaugh, C. K., V. A. Caceres, I. Kaplan, J. Larson, C. S. Sadoff, and D. S. Richmond. 2011. Ground beetle (Coleoptera: Carabidae) phenology, diversity, and response to weed cover in a turfgrass ecosystem. Environ. Entomol. 40: 1093–1101.

Bourassa, S., H. A. Cárcamo, F. J. Larney, and J. R. Spence. 2008. Carabid assemblages (Coleoptera: Carabidae) in a rotation of three different crops in southern Alberta, Canada: a comparison of sustainable and conventional farming. Environ. Entomol. 37: 1214–1223.

Bourassa, S., H. A. Cárcamo, J. R. Spence, R. E. Blackshaw, and K. Floate. 2010. Effects of crop rotation and genetically modified herbicide-tolerant corn on ground beetle diversity, community structure, and activity density. Can. Entomol. 142: 143–159.

Brinkley, C. K., R. T. Ervin, and W. L. Sterling. 1991. Potential beneficial impact of red imported fire ant to Texas cotton production. Biol. Ag. Hort. 8: 145–152.

Brunke, A. J., C. A. Bahlai, M. K. Sears, and R. H. Hallett. 2009. Generalist predators (Coleoptera: Carabidae, Staphylinidae) associated with millipede populations in sweet potato and carrot fields and implications for millipede management. Environ. Entomol. 38(4): 1106–1116.

Byers, R. A., G. M. Barker, R. L. Davidson, E. R. Hoebeke, and M. A. Sanderson. 2000. Richness and abundance of Carabidae and Staphylinidae (Coleoptera), in northeastern dairy pastures under intensive grazing. Great Lakes Entomol. 33: 81–106.

Cameron, E. K., V. Montserrat, and M. Cabeza. 2016. Global meta-analysis of the impacts of terrestrial invertebrate invaders on species, communities and ecosystems. Global Ecol. Biogeog. 25: 596–606.

Cárdenas, A. M. and C. M. Buddle. 2009. Introduced and native ground beetle assemblages (Coleoptera: Carabidae) along a successional gradient in an urban landscape. J. Ins. Conserv. 13: 151–163.

Carmona, D. M. and D. A. Landis. 1999. Influence of refuge habitats and cover crops on seasonal activity-density of ground beetles (Coleoptera: Carabidae) in field crops. Environ. Entomol. 28: 1145–1153.

Choate, B. and F. A. Drummond. 2012. Ant diversity and distribution (Hymenoptera: Formicidae) throughout Maine lowbush blueberry field in Hancock and Washington Counties. Environ. Entomol. 41: 222–232.

Chouvenc, T., R. H. Scheffrahn, and J. Warner. 2018. Establishment of Alluaud's little yellow ant, Plagiolepis alluaudi Emery (Hymenoptera: Formicidae: Formicinae): first continental New World record. Fla. Entomol. 101: 138–140.

Clark, R. E. and C. L. Seewagen. 2019. Invasive Japanese barberry, *Berberis thunbergii* (Ranunculales: Berberidaceae), is associated with simplified branch-dwelling and leaf-litter arthropod communities in a New York forest. Environ. Entomol. 48: 1071–1078.

Clark, S., K. Szlavecz, M. A. Cavigelli, and F. Purrington. 2006. Ground beetle (Coleoptera: Carabidae) assemblages in organic, no-till, and chisel-till cropping systems in Maryland. Environ. Entomol. 35: 1034–1312.

Clark, A. T., J. J. Rykken, and B. D. Farrell. 2011. The effects of biogeography on ant diversity and activity on the Boston Harbor Islands, Massachusetts, U.S.A. PLoS One 6: e28045.

Coccia, C., B. Fry, F. Ramirez, L. Boyero, S. E. Bunn, C. Diz-Salgado, M. Walton, L. Le Vay, and A. J. Green. 2016. Niche partitioning between invasive and native corixids (Hemiptera, Corixidae) in south-west Spain. Aqua. Sci. 78: 779–791.

Colvin, B. A., M. W. Fall, L. A. Fitzgerald, and L. L. Loope. 2005. Review of brown tree snake problems and control programs. USDA National Wildlife Research Center, Fort Collins, CO, pp. 1–68.

Comeau, C., J. P. Privé, and G. Moreau. 2012. Effects of reflective groundcovers on ground beetles (Coleoptera: Carabidae) in red raspberry (*Rubus idaeus*) cropping systems. J. Appl. Entomol. 137: 264–274.

Cooling, M., D. A. Sim, and P. J. Lester. 2015. Density-dependent effects of an invasive ant on a ground-dwelling arthropod community. Environ. Entomol. 44: 44–53.

Coyle, D. R., D. C. Booth, and M. S. Wallace. 2005. Ambrosia beetle (Coleoptera: Scolytidae) species, flight, and attack on living eastern cottonwood trees. J. Econ. Entomol. 98: 2049–2057.

Coyle, D. R., C. L. Brissey, and K. J. K. Gandhi. 2015. Species characterization and responses of subcortical insects to trap-logs and ethanol in a hardwood biomass plantation. Agric. For. Entomol. 17: 258–269.

Crowder, D. W. and W. E. Snyder. 2010. Eating their way to the top? Mechanisms underlying the success of invasive insect generalist predators. Biol. Invasions. 12: 2857–2876.

Cumberland, M. S. and L. K. Kirkman. 2012. The effects of disturbance on the red imported fire ant (*Solenopsis invicta*) and the native ant community. For. Ecol. Mgmt. 279: 27–33.

Cutler, G.C., J. M. Renkema, C. G. Majka, J. M. Sproule. 2012. Carabidae (Coleoptera) in Nova Scotia, Canada wild blueberry fields: prospects for biological control. Can. Entomol. 144: 808.820.

Darwin, C. 1809–1882. On the origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life. J. Murray, 1859, London.

Davis, R. A. and K. S. Zigler. 2012. Ant (Hymenoptera: Formicidae) communities of the southern Cumberland plateau. Ann. Entomol. Soc. Am. 105: 484–492.

Davis, N. E., D. J. O'Dowd, P. T. Green, and R. Mac Nally. 2008. Effects of an alien ant invasion on abundance, behavior, and reproductive success of endemic island birds. Cons. Biol. 22: 1165–1176.

Dodds, K. J. 2011. Effects of habitat type and trap placement on captures of bark (Coleoptera: Scolytidae) and longhorned (Coleoptera: Cerambicidae) beetles in semiochemical-baited traps. J. Econ. Entomol. 104: 879–888.

Dodds, K. J., G. D. Dubois, and E. R. Hoebeke. 2010. Trap type, lure placement, and habitat effects on Cerambycidae and Scolytinae (Coleoptera) catches in the northeastern United States. J. Econ. Entomol. 103: 698–707.

Dodds, K. J., J. D. Allison, D. R. Miller, R. P. Hanavan, and J. Sweeney. 2015. Considering species richness and rarity when selecting optimal survey traps: comparisons of semiochemical baited flight intercept traps for Cerambycidae in eastern North America. Agric. For. Entomol. 17: 36–47.

Dodds, K. J., M. F. DiGirolomo, and S. Fraver. 2019. Response of bark beetles and woodborers to tornado damage and subsequent salvage logging in northern coniferous forests of Maine, USA. For. Ecol. Mgmt. 450: e117489.

Duncan, R. P. and P. A. Williams. 2002. Ecology-Darwin's naturalization hypothesis challenged. Nature 416: 608–609.

Ellsbury, M. M., J. E. Powell, F. Forcella, W. D. Woodson, S. A. Clay, and W. E. Riedell. 1998. Diversity and dominant species of ground beetle assemblages (Coleoptera: Carabidae) in crop rotation and chemical input systems for the northern Great Plains. Ann. Entomol. Soc. Am. 91: 619–625.

Emery, S. M. and K. L. Gross. 2006. Dominant species identity regulates invasibility of old-field plant communities. Oikos 115: 549–558.

Eubanks, M. D., S. A. Blackwell, C. J. Parrish, Z. D. Delamar, and H. Hull-Sanders. 2002. Intraguild predation of beneficial arthropods by red imported fire ants in cotton. Environ. Entomol. 31: 1168–1174.

Evans, J., B. R. Scheffers, and M. Hess. 2013. Effect of laurel wilt invasive on redbay populations in a maritime forest community. Biol. Invasions. 16: 1581–1588.

Finke, D. L. and R. F. Denno. 2004. Predator diversity dampens trophic cascades. Nature 429: 407–410.

Finke, D. L. and R. F. Denno. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. Ecol. Lett. 8: 1299–1306.

Firlej, A., A-E. Gagnon, S. Laurin-Lemay, and J. Brodeur. 2012. Diversity and seasonal density of carabid beetles (Coleoptera: Carabidae) in relation to the soybean aphid in soybean crop in Québec, Canada. Can. Entomol. 144: 542–554.

French, B. W., L. D. Chandler, M. M. Ellsbury, B. W. Fuller, and M. West. 2004. Ground beetle (Coleoptera: Carabidae) assemblages in a transgenic corn–soybean cropping system. Environ. Entomol. 33: 554–563.

Gagne, S. A. and L. Fahrig. 2010. The trade-off between housing density and sprawl area: minimizing impacts to Carabid beetles (Coleoptera; Carabidae). Ecol. Soc. 15(4): 12.

Gandhi, K. J. K. and D. A. Herms. 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biol. Invasions. 12: 389–405.

Gandhi, K. J. K., D. W. Gilmore, S. A. Katovich, W. J. Mattson, J. C. Zasada, and S. J. Seybold. 2008. Catastrophic windstorm and fuel-reduction treatments alter ground beetle (Coleoptera: Carabidae) assemblages in a North American sub-boreal forest. For. Ecol. Mgmt. 256: 1104–1123.

Gandhi, K. J., A. I. Cognato, D. M. Lightle, B. J. Mosley, D. G. Nielsen, and D. A. Herms. 2010. Species composition, seasonal activity, and semiochemical response of native and exotic bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) in northeastern Ohio. J. Econ. Entomol. 103: 1187–1195.

Gandhi, K. J. K., M. E. Epstein, J. J. Koehle, and F. F. Purrington. 2011. A quarter of a century succession of epigaeic beetle assemblages in remnant habitats in an urbanized matrix (Coleoptera, Carabidae). ZooKeys 147: 667–689.

Gandhi, K. J. K., A. Smith, D. M. Hartzler, and D. A. Herms. 2014. Indirect effects of emerald ash borer-induced ash mortality and canopy gap formation on epigaeic beetles. Environ. Entomol. 43: 546–555.

Gardiner, M. M., D. A. Landis, C. Gratton, N. Schmidt, M. O'Neal, E. Mueller, J. Chacon, and G. E. Heimpel. 2010. Landscape composition influences the activity density of Carabidae and Arachnida in soybean fields. Biol. Cont. 55: 11–19.

Graham, J. H., H. H. Hughie, S. Jones, K. Wrinn, A. J. Krysik, J. J. Duda, D. C. Freeman, J. M. Emlen, J. C. Zak, D. A. Kovacic, et al. 2004. Habitat

disturbance and the diversity and abundance of ants (Formicidae) in the Southeastern Fall-Line Sandhills. J. Ins. Sci. 4: 1–15.

Grant, J. F., A. J. Mayor, P. L. Lambdin, and G. J. Wiggins. 2003. New species records and incidence of bark beetles and ambrosia beetles (Coleoptera: Scolytidae) from the barrens of middle Tennessee, USA. Nat. Areas J. 23: 278–283.

Godoy, O., P. Castro-Diez, F. Valladares, and M. Costa-Tenorio. 2009. Different flowering phenology of alien invasive species in Spain: evidence for the use of an empty temporal niche? Plant Biol. 11: 803–811.

Gomez, D. F., R. J. Rabaglia, K. E. O. Fairbanks, and J. Hulcr. 2018. North American Xyleborini north of Mexico: a review and key to genera and species (Coleoptera, Curculionidae, Scolytinae). Zookeys 768: 19–68.

Gouchnour, B. M., D. R. Suiter, and D. Booher. 2019. Ant (Hymenoptera: Formicidae) faune of the marine port of Savannah, Garden City, Georgia (USA). J. Entomol. Sci. 54: 417–429.

Goulet, H., L. LesageL, N. J. Bostanian, C. Vincent, and J. Lasnier. 2004. Diversity and seasonal activity of ground beetles (Coleoptera: Carabidae) in two vineyards of southern Quebec, Canada. Ann. Entomol. Soc. Amer. 97: 1263–1272.

Guénard, B. and R. R. Dunn. 2010. A new (old), invasive ant in the hardwood forests of eastern North America and its potentially widespread impacts. PLoS One 5: e11614.

Guo, Z., J. Liu, S. Lek, Z. Li, F. Zhu, J. Tang, R. Britton, and J. Cucherousset. 2017. Coexisting invasive gobies reveal no evidence for temporal and trophic niche differentiation in the sublittoral habitat of Lake Erhai, China. Ecol. Freshw. Fish 26: 42–52.

Hannam, J. J., J. K. Lieherr, and A. E. Hajek. 2008. Climbing behavior and aphid predation by *Agonum muelleri* (Coleoptera: Carabidae). Can. Entomol. 140: 203–207.

Hanula, J. L. and S. Horn. 2011. Removing an exotic shrub from riparian forests increases butterfly abundance and diversity. For. Ecol. Manage. 262: 674–680.

Harrington, L. A., A. L. Harrington, N. Yamaguchi, M. D. Thom, P. Ferreras, T. R. Windham, and D. W. Macdonald. 2009. The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific competition. Ecology 90: 1207–1216.

Hartley, J. D., M. J. Koivula, J. R. Spence, R. Pelletier, and G. E. Ball. 2010. Effects of urbanization on ground beetle assemblages (Coleoptera, Carabidae) of grassland habitats in western Canada. Ecography. 30: 673–684.

Hatten, T. D., N. A. Bosque-Pérez, J. R. Labonte, S. O. Guy, and S. D. Eigenbrode. 2007. Effects of tillage on the activity density and biological diversity of carabid beetles in spring and winter crops. Environ. Entomol. 36: 356–368.

Hejda, M., P. Pyšek, and V. Jarošík. 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. J. Ecol. 97: 393–403.

Herms, D. A. and D. G. McCullough. 2014. Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annu. Rev. Entomol. 59: 13–30.

Hill, M. O. 1973. Diversity and evenness: A unifying notation and its consequences. Ecology 54: 427–432.

Hoback, W., T. Svatos, S. Spomer, and L. Higley. 1999. Trap color and placement affects estimates of insect family-level abundance and diversity in a Nebraska salt marsh. Entomol. Exp. Appl. 91: 393–402.

Holland, J. M. 2002. Carabid beetles: their ecology, survival, and use in agroecosystems, pp. 1–40. *In* J. Holland (ed.), The agroecology of carabid beetles. Intercept.

Holway, D. A. 1998. Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. Oecologia 116: 252–258.

Holway, D. A. 2005. Edge effects of an invasive species across a natural ecological boundary. Biol. Conserv. 121: 561–567.

Human, K. G. and D. M. Gordon. 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. Oecologia 105: 405–412.

Hummel, J. D., L. M. Dosdall, G. W. Clayton, K. N. Harker, and J. T. O'donovan. 2012. Ground beetle (Coleoptera: Carabidae) diversity, activity density, and community structure in a diversified agroecosystem. Environ. Entomol. 41: 72–80.

Ivanov, K., O. M. Lockhart, J. Keiper, and B. M. Walton. 2011. Status of the exotic ant *Nylanderia flavipes* (Hymenoptera: Formicidae) in northeastern Ohio. Biol. Invasions. 13: 1945–1950.

Johnson, C. W., R. S. Cameron, J. L. Hanula, and C. Bates. 2014. The attractiveness of manuka oil and ethanol, alone and in combination, to *Xyleborus glabratus* (Coleoptera: Curculionidae: Scolytinae) and other Curculionidae. Fla. Entomol. 97: 861–864.

Jones, K. L., V. A. Shegelski, N. G. Marculis, A. N. Wijerathna, and M. L. Evenden. 2019. Factors influencing dispersal by flight in bark beetles (Coleoptera: Curculionidae: Scolytinae): from genes to landscapes. Can. J. For. Res. 49: 1024–1041.

Kaplan, I. and M. D. Eubanks. 2005. Aphids alter the community-wide impact of fire ants. Ecology 86: 1640–1649.

Kaspari, M. 2000. Do imported fire ants impact canopy arthropods? Evidence from simple arboreal pitfall traps. Southw. Nat. 45: 118–122.

Kendra, P. E., J. S. Sanchez, W. S. Montgomery, K. E. Okins, J. Niogret, J. E. Peña, N. D. Epsky, and R. R. Heath. 2011. Diversity of Scolytinae (Coleoptera: Curculionidae) attracted to avocado, lychee, and essential oil lures. Fla. Entomol. 94: 123–130.

Kenis, M., M. A. Auger-Rozenberg, L. Timms, C. Péré, M. J. W. Cock, J. Settele, S. Augustin, and C. Lopez-Vaamonde. 2009. Ecological effects of invasive alien insects. Biol. Invasions. 11: 21–45.

King, J. R. and W. R. Tschinkel. 2006. Experimental evidence that the introduced fire ant, *Solenopsis invicta*, does not competitively suppress co-occurring ants in a disturbed habitat. J. Anim. Ecol. 75: 1370–1378.

King, J. R. and W. R. Tschinkel. 2013. Experimental evidence for weak effects of fire ants in a naturally invaded pine-savanna ecosystem in north Florida. Ecol. Entomol. 38: 68–75.

Kleintjes, P. K., A. M. Christensen, W. J. Barnes, and L. A. Lyons. 2002. Ground beetles (Coleoptera: Carabidae) inhabiting stands of reed canary grass *Phalaris arundinacea* on islands in the lower Chippewa River, Wisconsin. Great Lakes Entomol. 35: 14.

Koivula, M. and J. R. Spence. 2006. Effects of post-fire salvage logging on boreal mixed-wood ground beetle assemblages (Coleoptera, Carabidae). For. Ecol. Mgmt. 236: 102–112.

Krushelnycky, P. D. and R. G. Gillespie. 2010. Correlates of vulnerability among arthropod species threatened by invasive ants. Biodiv. Conserv. 19: 1971–1988.

Lalonde, O., A. Légère, F. C. Stevenson, M. Roy, and A. Vanasse. 2012. Carabid beetle communities after 18 years of conservation tillage and crop rotation in a cool humid climate. Can. Entomol. 144: 645–657.

Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Ann. Rev. Entomol. 45: 175–201.

Larsen, K. J. and J. B. Williams, 1999. Influence of fire and trapping effort on ground beetles in a reconstructed tallgrass prairie. Nature. 31: 75–86.

Larsen, K. J. and T. W. Work. 2003. Differences in ground beetles (Coleoptera: Carabidae) of original and reconstructed tallgrass prairies in northeastern Iowa, USA, and impact of 3-year spring burn cycles. J. Ins. Conserv. 7: 153–166.

Larsen, K. J., T. T. Work, and F. F. Purrington. 2003. Habitat use patterns by ground beetles (Coleoptera: Carabidae) of northeastern Iowa. Pedobiology. 47: 288–299.

Leslie, T. W., D. J. Biddinger, J. R. Rohr, A. G. Hulting, D. A. Mortensen, and S. J. Fleischer. 2014. Examining shifts in Carabidae assemblages across a forest-agriculture ecotone. Environ. Entomol. 43: 18–28.

Lubertazzi, D. and W. R. Tschinkel. 2003. Ant community change across a ground vegetation gradient in north Florida's longleaf pine flatwoods. J. Ins. Sci. 3: 1–17.

Martelli, M. G., M. M. Ward, and A. M. Fraser. 2004. Ant diversity sampling on the southern Cumberland Plateau: a comparison of litter sifting and pitfall trapping. Southeast. Nat. 3(1): 113–126.

Melnychuk, N. A., O. Olfert, B. Youngs, and C. Gillott. 2003. Abundance and diversity of Carabidae (Coleoptera) in different farming systems. Agric. Ecosyst. Environ. 95: 69–72.

Menke, S. B., B. Guénard, J. O. Sexton, M. D. Weiser, R. R. Dunn, and J. Silverman. 2011. Urban areas may serve as habitat and corridors for

dry-adapted, heat tolerant species; an example from ants. Urban Ecosyst. 14: 135.163.

Menzel, T. O. and T. E. Nebeker. 2008. Distribution of hybrid imported fire ants (Hymenoptera: Formicidae) and some native ant species in relation to local environmental conditions and interspecific competition in Mississippi forests. Ann. Entomol. Soc. Am. 101(1):119–127.

Miller, D. R. and D. A. Duerr. 2008. Comparison of arboreal beetle catches in wet and dry collection cups with Lindgren multiple funnel traps. J. Econ. Entomol. 101: 107–113.

Miller, D. R. and R. J. Rabaglia. 2009. Ethanol and (–)-α-pinene: Attractant kairomones for bark and ambrosia beetles in the southeastern US. J. Chem. Ecol. 35: 435–448.

Molnar, J. L., R. L. Gamboa, C. Revenga, and M. D. Spalding. 2008. Assessing the global threat of invasive species to marine biodiversity. Front. Ecol. Environ. 6: 485–492.

Morrison, L. W. and S. D. Porter. 2003 Positive association between densities of the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), and generalized ant and arthropod diversity. Environ. Entomol. 32: 548–554.

Naumann, K. and R. J. Higgins. 2015. The European fire ant (Hymenoptera: Formicidae) as an invasive species: impact on local ant species and other epigaeic arthropods. Can. Entomol. 147: 592–601.

Niemelä, J., J. R. Spence, and H. Cárcamo. 1997. Establishment and interactions of carabid populations: an experiment with native and introduced species. Ecography. 20: 643–652.

Nisbet, D., D. Kreutzweiser, P. Sibley, and T. Scarr. 2015. Ecological risks posed by emerald ash borer to riparian forest habitats: A review and problem formulation with management implications. For. Ecol. Manage. 358: 165–173.

Niwa, C. G. and R. W. Peck. 2002. Influence of prescribed fire on Carabid beetle (Carabidae) and spider (Araneae) assemblages in forest litter in southwestern Oregon. Environ. Entomol. 31: 785–796.

O'Dowd, D. J., P. T. Green, and P. S. Lake. 2003. Invasional meltdown on an oceanic island. Ecol. Lett. 6: 812–817.

Oliver, J. B. and C. M. Mannion. 2001. Ambrosia beetle (Coleoptera: Scolytidae) species attacking chestnut and captured in ethanol-baited traps in middle Tennessee. Environ. Entomol. 30: 909–918.

Parr, C. L. 2008. Dominant ants can control assemblage species richness in a South African savanna. J. Anim. Ecol. 77: 1191–1198.

Parr, C. L. and H. Gibb. 2010. Competition and the role of dominant ants. Ant Ecol. 77–96.

Pećarević, M., J. Danoff-Burg, and R. R. Dunn. 2010. Biodiversity on Broadway—enigmatic diversity of the societies of ants (Formicidae) on the streets of New York City. PLoS One. 5(10): e13222.

Pedersen, J. S., M. J. B. Krieger, V. Vogel, T. Giraud, and L. Keller. 2006. Native supercolonies of unrelated individuals in the invasive argentine ant. Evolution. 60: 782–791.

Petrillo, H. A. and J. A. Witter. 2009. Habitat distribution of Carabid beetles (Coleoptera: Carabidae) in northern hardwood forests of Michigan. Great Lakes Entomol. 42: 139–157.

Pfammatter, J. A., D. R. Coyle, A. M. Journey, T. L. Pahs, J. C. Luhman, V. J. Cervenka, and R. L. Koch. 2011. Bark beetle (Coleoptera: Curculionidae: Scolytinae) community structure in northeastern and central Minnesota. Great Lakes Entomol. 44: 163–176.

Philpott, S. M., I. Perfecto, I. Armbrecht, and C. L. Parr. 2010. Ant diversity and function in disturbed and changing habitats. Ant Ecol. 1: 137–156.

Philpott, S. M., J. Cotton, P. Bichier, R. Friedrich, L. Moorhead, S. Uno, and M. Valdez. 2013. Local and landscape drivers of arthropod abundance, richness, and trophic composition in urban habitats. Urban Ecosyst. 17: 513–532.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2020. nlme: linear and non-linear mixed effect modles. R package version 3.1–149, https://CRAN.R-project.org/package=nlme. Accessed 1 July 2020.

Porter, S. D. and D. A. Savignano. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. Ecology. 71(6): 2095–2106.

Powell, K. I., J. M. Chase, and T. M. Knight. 2011. A synthesis of plant invasion effects on biodiversity across spatial scales. Am. J. Bot. 98: 539–548.

Prior, K. M. and J. J. Hellman. 2010. Impact of an invasive oak gall wasp on a native butterfly: a test of plant-mediated competition. Ecology 91: 3284–3293.

Pyšek, P. and D. M. Richardson. 2010. Invasive species, environmental change and management, and health. Annu. Rev. Environ. Res. 35: 25–55.

R Core Team. 2020. R: A language and environmental for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. https://www.r-project.org/. Accessed 1 July 2020.

Rabaglia, R. J., A. I. Cognato, E. R. Hoebeke, C. W. Johnson, J. R. Labonte, M. E. Carter, and J. J. Vlach. 2019. Early detection and rapid response: a 10-year summary of the USDA Forest Service program of surveillance for non-native bark and ambrosia beetles. Am. Entomol. 65: 29–42.

Reding, M. E., C. M. Ranger, J. B. Oliver, and P. B. Schultz. 2010. Monitoring attack and flight activity of *Xylosandrus* spp. (Coleoptera: Curculionidae: Scolytinae): the influence of temperature on activity. J. Environ. Hort. 28: 85–90.

Reed, S. E. and R. M. Muzika. 2010. The influence of forest stand and site characteristics on the composition of exotic dominated ambrosia beetle communities (Coleoptera: Curculionidae: Scolytinae). Environ. Entomol. 39: 1482–1491.

Reed, S. E., J. Juzwik, J. T. English, and M. D. Ginzel. 2015. Colonization of artificially stressed black walnut trees by ambrosia beetle, bark beetle, and other weevil species (Coleoptera: Curculionidae) in Indiana and Missouri. Environ. Entomol. 44: 1455–1464.

Riley, K. N. and R. A. Browne. 2011. Changes in ground beetle diversity and community composition in age structured forests (Coleoptera, Carabidae). ZooKeys. 147: 601.

Rodda, G. H. and J. A. Savidge. 2007. Biology and impacts of pacific island invasive species. 2. Boiga irregularis, the brown tree snake (Reptilia: Colubridae). Pac. Sci. 61: 307–324.

Roth, D. S., I. Perfecto, and B. Rathcke. 1994. The effects of management systems on ground-foraging ant diversity in Costa Rica. Ecol. Appl. 4: 423–436.

Rowles, A. D. and J. Silverman. 2010. Argentine ant invasion associated with loblolly pines in the southeastern United States: minimal impacts but seasonally sustained. Environ. Entomol. 39(4): 1141–1150.

Russell, M. C., J. Lambrinos, E. Records, and G. Ellen. 2017. Seasonal shifts in ground beetle (Coleoptera: Carabidae) species and functional composition maintain prey consumption in Western Oregon agricultural landscapes. Biol. Contr. 106: 54–63.

Rykken, J. J., D. E. Capen, and S. P. Mahabir. 1997. Ground Beetles as Indicators of Land Type Diversity in the Green Mountains of Vermont. Conserv. Biol. 11: 522–530.

Schlaepfer, M. A. 2018 Do non-native species contribute to biodiversity?. PLoS Biol. 16: e2005568.

Schlarbaum, S. E., F. Hebard, P. C. Spaine, and J. C. Kamalay. 1998. Three American tragedies: chestnut blight, butternut canker, and Dutch elm disease. *In* Proceedings of Exotic Pests in Eastern Forests. USDA Forest Service and Tennessee Exotic Pest Plant Council, pp. 45–54.

Seebens, H., T. M. Blackburn, E. E. Dyer, P. Genovesi, P. E. Hulme, J. M. Jeschke, S. Pagad, P. Pyšek, M. Winter, M. Arianoutsou, *et al.* 2017. No saturation in the accumulation of alien species worldwide. Nat. Commun. 8: 14435–14444.

Simberloff, D. 2005. Non-native species do threaten the natural environment. J. Agric. Environ. Ethics. 18: 595–607.

Skvarla, M. J. 2015. Sampling terrestrial arthropod biodiversity: A case study in Arkansas. Dissertation, University of Arkansas, Fayetteville, AR.

Smallwood, J. 1982. Nest relocation in ants. Insect. Sociaux 29: 138–147.

Smith, R. F., J. E. Cossentine, S. M. Rigby, and C. S. Sheffield. 2004. Species of ground beetle (Coleoptera: Carabidae) in organic apple orchards of British Columbia. J. Entomol. Soc. Brit. Col. 101: 93–100.

Snyder, W. E. and E. W. Evans. 2006. Ecological effects of invasive arthropod generalist predators. Annu. Rev. Ecol. Evol. Syst. 37: 95–122.

Stuble, K. L., K. Kirman, C. R. Carroll, and N. J. Sanders. 2011. Relative effects of disturbance on red imported fire ants and native ant species in a longleaf pine ecosystem. Conserv. Biol. 25(3): 618–622.

Toennisson, T. A., N. J. Sanders, W. E. Klingeman, and K. M. Vail. 2011. Influences on the structure of suburban ant (Hymenoptera: Formicidae)

communities and the abundance of Tapinoma sessile. Environ. Entomol. 40: 1397–1404.

Touyama, Y., K. Ogata, and T. Sugiyama. 2003. The Argentine ant, *Linepithema humile*, in Japan: assessment of impact on species diversity of ant communities in urban environments. Entomol. Sci. 6: 57–62.

Trager, M. D., T. E. Ristau, S. H. Stoleson, R. L. Davidson, and R. E. Acciavatti. 2013. Carabid beetle responses to herbicide application, shelterwood seed cut and insect defoliator outbreaks. For. Ecol. Manage. 289: 269–277.

Turnbow, R. H. and R. T. Franklin. 1980. Flight activity by Scolytidae (Coleoptera) in the northeast Georgia Piedmont (Coleoptera). J. Ga. Entomol. Soc. 15: 26–37.

Valtonen, A., J. Jantunen, and K. Saarinen. 2006. Flora and lepidoptera fauna adversely affected by invasive *Lupinus polyphyllus* along road verges. Biol. Conserv. 133: 389–396.

Vankosky, M. A., H. A. Cárcamo, H. A. Catton, A. C. Costamagna, and R. De Clerck-Floate. 2017. Impacts of the agricultural transformation of the Canadian Prairies on grassland arthropods. Can. Entomol. 149: 718–735.

Verble and Yanoviak. 2013. Short-term effects of prescribed burning on ant (Hymenoptera: Formicidae) assemblages in Ozark forests. Ann. Entomol. Soc. Am. 106(2): 198–203.

Vercken, E., A. M. Kramer, P. C. Tobin, and J. M. Drake. 2011. Critical patch size generated by Allee effect in gypsy moth, *Lymantria dispar* (L.). Ecol. Lett. 14: 179–186.

Wallin, H. and B. Ekbom. 1994. Influence of hunger level and prey densities on movement patterns in three species of Pterostichus beetles (Coleoptera: Carabidae). Environ. Entomol. 23: 1171–1181.

Wang, C., J. Strazanac, and L. Butler. 2000. Abundance, diversity, and activity of ants (Hymenoptera: Formicidae) in oak-dominated mixed Appalachian forests treated with microbial pesticides. Environ. Entomol. 29: 579–586.

Wang, L., Y. Xu, L. Zeng, and Y. Lu. 2019. Impact of the red imported fire ant *Solenopsis invicta* Buren on biodiversity in South China: a review. J. Int. Agri. 18: 788–796.

Weber, B. C. and J. E. McPherson. 1991. Seasonal flight patterns of Scolytidae (Coleoptera) in black walnut plantations in North Carolina and Illinois. Coleop. Bull. 45: 45–56.

Werling, B. P. and C. Gratton. 2008. Influence of field margins and landscape context on ground beetle diversity in Wisconsin (USA) potato fields. Agric. Ecosyst. Environ. 128: 104–108.

Werner, S. M. and K. F. Raffa. 2000. Effects of forest management practices on the diversity of ground-occurring beetles in mixed northern hardwood forests of the Great Lakes Region. For. Ecol. Manage. 139: 135–155.

Wiles, G. J., J. Bart, R. E. Beck, and C. F. Aguon. 2003. Impacts of the brown tree snake: patterns of decline and species persistence in Guam's avifauna. Cons. Biol. 17: 1350–1360.

Wojcik, D. P., C. R. Allen, R. J. Brenner, E. A. Forys, D. P. Jouvenaz, and R. S. Lutz. 2001. Red imported fire ants: impact on biodiversity. Am. Entomol. 47: 16–23.

World Trade Organization. 2018. World Trade Organization Statistical Review 2018. https://www.wto.org/english/res_e/statis_e/wts_e.htm. Accessed 1 July 2020.

Zylstra, K. E., K. J. Dodds, J. A. Francese, and V. Mastro. 2010. *Sirex noctilio* in North America: the effect of stem-injection timing on the attractiveness and suitability of trap trees. Agric. For. Entomol. 12: 243–250.