Increased ant (Hymenoptera: Formicidae) incidence and richness are associated with alien plant cover in a small mid-Atlantic riparian forest

Daniel KJAR & Zachory PARK

Abstract

Alien plants have invaded forest habitats throughout the eastern United States (US) and may be altering native ant communities through changes in disturbance regimes, microclimate, and native plant communities. To determine if ant communities differ among sites with varying alien plant cover, we analyzed pitfall-traps and soil-core samples from a mid-Atlantic riparian forest located within a US National Park. Only one alien ant species, *Vollenhovia emeryi* WHEELER, 1906 was found in this study. Total ant incidence and, to a lesser extent, richness were positively associated with the amount of alien plant cover. Species richness estimators also predicted more ant species within sites of greater alien plant cover. Increased ant incidence and ant richness appear to be the result of greater numbers of foraging ants in areas with greater alien plant cover rather than changes in the ant species composition. We suggest alien plant presence or other factors associated with alien plant cover have led to greater ant incidence and richness in these sites.

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Introduction

Alien plant species are invading natural areas throughout the world and are changing native ecosystems (MACK & D'ANTONIO 1998, LEVINE & al. 2003, BROOKS & al. 2005, VILÀ & al. 2011, SCHOEMAN & SAMWAYS 2013). Alien plant invasion may affect native ant communities by altering resource availability, habitat structure, disturbance regime, and microclimate (THOMPSON & MCLACHLAN 2007, LINKSVAYER & JANSSEN 2008, SIMAO & al. 2010, LENDA & al. 2013, SCHOEMAN & SAMWAYS 2013). In this study, we evaluate differences in ant species incidence and richness associated with alien plant cover in a small mid-Atlantic riparian forest located within a US National Park.

Ant species rapidly respond to changing environmental conditions by altering their foraging behavior and moving their colonies (CARLSON & GENTRY 1973, SMALLWOOD 1982, HOLWAY & CASE 2000, MCGLYNN & al. 2003, LENDA & al. 2013). Environmental factors such as habitat fragmentation, soil moisture, and plant community composition have strong effects on ant communities (ANDERSEN & MAJER 2004, IVES & al. 2011) though the response may be unpredictable and context dependent (OSUNKOYA & al. 2011, SCHOEMAN & SAMWAYS 2013). The response of ants to changing environmental conditions differs depending on the specific ant community. For example, studies have demonstrated that increased soil moisture is associated with increased ant diversity in a variety of habitats (TALBOT 1934, LEVINGS 1983, LYNCH & al. 1988, SANDERS & al. 2003), but in Eastern US deciduous forests, ant diversity

was negatively associated with high soil moisture (WANG & al. 2001, THOMPSON & MCLACHLAN 2007). Ant community response to soil moisture is likely the result of predominant soil conditions and the pool of available ant species that can move into an area with a particular soil moisture regime. In arid habitats, low soil moisture probably limits ant diversity (SANDERS & al. 2003), and in areas of relatively high soil moisture, the relationship will reverse as soil becomes too saturated for many ant species to nest. Few studies have examined the ant community in habitats with consistently saturated ground in the Eastern US (ELLISON & al. 2002).

Plant communities represent both habitat structure and resource availability for ant species. Plants provide nest sites in and around fallen branches, fallen trees, litter accumulation, and roots, as well as canopy nest sites for arboreal species. Ants forage on trees and in tree leaf litter for live and dead arthropods. Some ants rely almost entirely on food sources derived from plants. For example, aphid tending is common among many subfamilies; the subgenus *Acanthomyops* tends root aphids for honeydew, and some *Pseudomyrmex* spp. consume Beltian bodies and nectar from Bullhorn Acacia trees (JANZEN 1966). The relationships among ants and plants may be reciprocal. Plant communities can determine the density of ant nests (SMALLWOOD 1982), and ants can influence plant communities by changing soil characteristics (BONTE & al. 2003), coccid tending (HOY 1964), herbivory (RAO & al. 2001), dispers-

ing seeds (CULVER & BEATTIE 1978, CHRISTIAN 2001, CARNEY & al. 2003), and by selective poisoning of plant species (FREDERICKSON & al. 2005).

Associations between ant diversity and tree diversity or tree abundance have been observed in Costa Rican coffee farms (PERFECTO & SNELLING 1995), Brazilian savannas (RIBAS & al. 2003), and Northeastern US bogs (ELLISON & al. 2002). ARMBRECHT & al. (2004) found that experimental bags containing twigs collected from multiple tree species had 80% more twig-dwelling ant species than bags containing twigs from only one tree species. However, in some cases increased tree canopy cover and vegetation complexity reduce the quality of ant nesting habitat or foraging (LASSAU & HOCHULI 2004). This response is likely dependent on the characteristics of the existing ant community and the species available for recruitment to the altered habitat.

Ant communities may change if a disturbance alters the plant community. The general pattern is an increase, or very little change, in ant richness in areas of moderate disturbance or fragmentation. This occurs because ant species which are normally excluded from a particular undisturbed habitat type, enter when the habitat is disturbed. This increases total ant richness or offsets decreased ant richness due to a loss of habitat specialists (BESTELMEYER & WIENS 1996, MITCHELL & al. 2002, BRASCHLER & BAUR 2003, HOFFMANN 2003, SOBRINHO & al. 2003). As ant communities change, a host of trophic levels may be affected, causing a cascade of effects throughout an ecosystem (WIMP & WHITMAN 2001, SIMAO & al. 2010).

Although plant communities are important in determining ant community compositions, the Eastern US ant community may be structured, to some degree, by interactions among ant species (LYNCH & al. 1980, FELLERS 1987). Habitat changes caused by or resulting in alien plant invasion may increase competition from generalist ant species such as *Aphaenogaster rudis* ENZMANN, 1947, *Lasius alienus* (FOERSTER, 1850), *Prenolepis imparis* (SAY, 1836), and *Tapinoma sessile* (SAY, 1836), and therefore result in ant community changes. In a recent review of competition and ant community structure, strong support among previous studies for competitive interactions determining ant community structure was found (CERDÁ & al. 2013). However, those authors also found the effects of abiotic and biotic factors (e.g., temperature, parasitoids, habitat complexity, disturbance) may have a greater effect on ant community structure. The importance of competition in ant community structure in disturbed habitats has been questioned by KING & TSCHINKEL (2006) in an experimental study on the red imported fire ant, *Solenopsis invicta* BUREN, 1972. After removal of *S. invicta* from sites in Florida, the authors did not find an increase in co-occurring ant species.

Alien plants may facilitate changes in ant communities by altering ant habitats through changing disturbance intensity, rate, and type; reducing native plant diversity; changing soil moisture; and stopping usual habitat succession (MACK & D'ANTONIO 1998). Alien vines in the Dyke Marsh Preserve (DMP) forest appear to reduce native plant diversity (KJAR & BARROWS 2004), weaken mature trees, and stop usual forest succession after a tree falls by shading out tree saplings (THOMAS 1980). In this study, we sampled ant species from sites throughout a forest invaded by four alien vines and five other alien plant species. The sampling was in a small forest (4.4 hectare area sampled) at a fine scale (40 sites). Here we test whether changes in ant incidence and ant richness are associated with alien plant cover. We also test whether increasing alien plant cover is associated with changes in the incidence of select ant species and groups of ant species.

Materials and methods

Dyke Marsh Preserve (DMP) is part of the George Washington Memorial Parkway (GWMP) in Fairfax County, Virginia, USA (latitude N 38° 46', longitude W 77° 03'). The GWMP is a US National Park bordering the western shore of the Potomac River. The DMP is 3.5 km long; 500 m wide at its widest point on an east-west transect, and located 15 km south of the Ronald Reagan Washington National Airport. The preserve has areas of flood-plain forests, open tidal freshwater marsh, and swamp forests (JOHNSTON 2000, BARROWS & al. 2005). All of our sampling sites were within the DMP forest (Fig. 1). The part of the forest used in this study is 1 - 2 m above sea level, had standing water only during floods, and may be considered a flood-plain forest, or low forest. This forest type is common along tidal rivers in the mid-Atlantic. The mid-Atlantic region of the US includes the District of Columbia and the states of: Delaware, Maryland, New Jersey, New York, Pennsylvania, Virginia, and West Virginia.

The study forest is dominated by *Liquidambar styraciflua* L. (Sweetgum) and a dense understory of *Lindera benzoin* (L.) BLUME (Spicebush) and *Viburnum dentatum* L. (Smooth Arrowwood). Other trees common in the forest include *Acer negundo* L. (Boxelder), *Acer rubrum* L. (Red Maple), *Fraxinus americana* L. (White Ash), *Liriodendron tulipifera* L. (Tulip Tree), *Nyssa sylvatica* (MARSH.). (Tupelo), *Quercus palustris* MÜNCHH. (Pin Oak), *Quercus phellos* L. (Willow Oak), *Quercus rubra* L. (Red Oak), *Sassafras albidum* (NUTT.) NEES (Sassafras), and *Ulmus americana* L. (American Elm) (KJAR 2005).

A plant survey of 60 sites (including the 40 used for this study) found nine alien and 42 native forest-floor plant species (excluding trees over 1 m tall), and 16 native tree species. Alien plants made up more than 40% of all plant cover (KJAR 2005). The most common alien plant, *Lonicera japonica* THUNB. (Japanese Honeysuckle), was found in 80% of the study sites (Fig. 1).

We selected 60 random sites within the DMP using a geographical information system (GIS) and aerial photography with the cooperation of the National Park Service GIS coordinator of the GWMP. We used the computer program ArcView™ 3 (ESRI 2001) and the National Park Services' AlaskaPak extension (NATIONAL PARK SERVICE 2002), which randomly selects any number of points within a polygon and creates a list of coordinates for each point. Sites were in a predefined area of the forest whose borders were at least 10 m from trails or roads. This area was bordered by the Mt. Vernon Trail on the west, Haul Road and the Potomac River on the east, a large tidal channel on the south, and an area overtaken by *Ampelopsis brevipedunculata* (MAXIM.) TRAUTV. (Porcelainberry) vines on the north.

We used a Trimble™ backpack global positioning system (GPS) to locate each of the sites in the forest. Forty of the 60 sites in the plant census were used in this study.
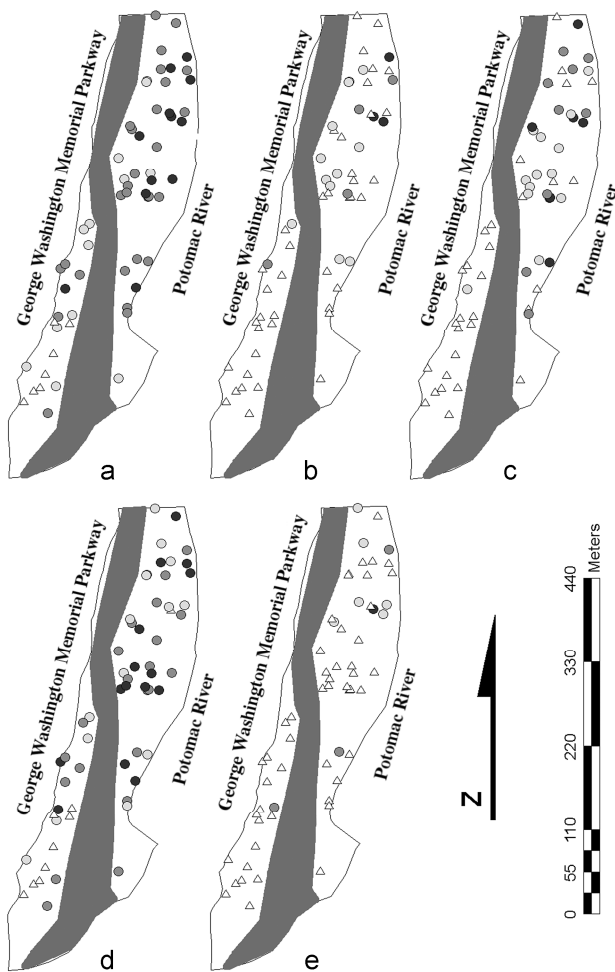
Fig. 1: Plant cover in study sites in a riparian forest of Dyke Marsh Wildlife Preserve, VA: (a) all alien plants, (b) *Ampelopsis brevipedunculata*, (c) *Celastrus orbiculatus*, (d) *Lonicera japonica*, (e) *Clematis terniflora*. Alien plant cover is in four categories: not present 0% (triangle), low 1 - 33% (light circle), medium 34 - 66% (grey circle), high 67 - 100% (black circle). The tidal channel bisecting the study site is represented by the greyed in area of the map.

Sites were chosen if they were not saturated with water and at least 3 m from any other site (Fig. 1). Twenty sites were excluded from the analysis presented here due to their location near a tidal channel that floods during high tides. Although the statistical analysis based on 60 sites produced identical models with a better fit, we used the more conservative analysis based on 40 sites due to the impact of tidal flooding on trap sampling.

We conducted a plant census in early August 2002 and 2003. A 12-cm-diameter pitfall trap located at the center of each site provided a reference point for each plant census. We counted all plants within a 1 m × 1 m quadrat of the pitfall trap using a frame of nine equal quadrats. The frame was aligned to the north and south during both surveys to make sure the same areas were surveyed during both years. The frame was placed over the site and the presence or absence of any plant species below 1.5 m tall was recorded, yielding a score of 0 - 9 for each plant species at each site. This method of determining coverage is advantageous because it produces a proportional coverage estimate, as well as a coverage estimate for each plant species independent of the scores of other species. Percent invasion by alien plant species was determined as the proportion of alien plant coverage to the total plant coverage at a site (Fig. 1).

All tree species with a diameter at breast height (DBH, 130 cm from the ground) greater than 3 cm and within 3 m of the center of each site were recorded during the August 2002 plant census. The number of each species and their DBHs were recorded.

A cylindrical soil core (70 mm diameter × 70 mm deep) was taken 1.5 m from each site in the third week of June, August, and October of 2002 and 2003. The samples were stored in sealed plastic bags until wet weights were taken approximately 1 - 3 h after removal from the forest. Arthropods were extracted from the soil cores in Berlese funnels containing a 5 mm mesh plastic screen and allowed to air dry for five days in a room under 24 h of fluorescent lighting. Heat was not applied during extraction because test runs had found unacceptable mortality of diplurans, symphylans, and other soft-bodied arthropods before extraction. Examination of test core material found all ants moved down into jars of killing fluid (95% ethanol) by the end of the extraction period. The soil was then placed in a drying oven at 80 °C for 5 h and weighed. Percent soil moisture was then averaged for each sample site across the three sampling events for each year (n = 6 soil samples for each site). Soil moisture is highly variable among sample sites within the DMP forest. This is due to the presence of a tidal channel in the forest that parallels the river and the contours of the forest floor, rather than proximity to the river's edge.

Forty pitfall traps were run for 24 h, on the same clear day in the last week of June, August, and October during 2002 and 2003. A single collar and funnel pitfall trap was used at each study site (KJAR & BARROWS 2004). This pitfall trap design results in a high arthropod-per-trap-hour catch (KJAR 2002), and prevents non-target vertebrates from injuring themselves or damaging the trap. All pitfall traps were in position one month before the study began and remained capped and in place throughout both years of the study. The killing fluid used in the pitfall traps was 95% ethanol. All species were classified as either rare or common, and were also classified as multiple-habitat or forest species based on a survey of published studies and species lists for the eastern US (KJAR 2009). KJAR (2009) contains a detailed description of the trap catches from this study and distribution of these ants in the DMP and mid-Atlantic region. Ants were identified using published keys, the US National Museum of Natural History ant collection, and with the help of Dr. David Smith (formerly of the USDA), and Terry Nuhn (USDA). Voucher specimens were deposited with the GWMP. Due to the current unresolved taxonomic issues associated with *Aphaenogaster rudis* we will refer to the form that we collected at the DMP as *A. rudis* complex (UMPHREY 1996).

We used all subsets regression, generalized linear models, and the Akaike Information Criterion (AIC) to determine the model that best fit the dependent variables: ant richness, ant incidence, *Aphaenogaster rudis* complex incidence, *Prenolepis imparis* incidence, *Nylanderia faisonensis* (FOREL, 1922) incidence, multiple-habitat ant incidence,

Tab. 1: Ant species nest locations, feeding behaviors, and habitats, Dyke Marsh Preserve, Virginia. The group identity abbreviations are: C, common ant species; R, rare ant species; F, forest ant group; MH, multiple-habitat ant group. Within nest location, cavity includes spaces within twigs, fruits, fallen logs and branches, and any arboreal ant nest. *Solenopsis molesta* and *Vollenhovia emeryi* are not included in either the common or rare ant group due to their alien status or habitat preference. Abundance is the abundance of a species in all samples combined. Incidence is the number of samples in which a particular species occurred.

Species	Group	Nest location			Feeding behavior		Habitat		Abundance	Incidence
		Soil	Litter	Cavity	Generalist	Specialist	Forest	Field		
Aphaenogaster rudis complex	C, MH	×	×	×	×		×	×	1011	187
Prenolepis imparis	C, MH	×			×		×	×	829	99
Nylanderia faisonensis	R, F		×	×	×		×		717	168
Pyramica rostrata	R, F		×			×	×		114	21
Lasius alienus	C, MH	×	×	×	×		×	×	83	61
Myrmecina americana	C, F	×		×		×	×		77	25
Temnothorax curvispinosus	C, F			×	×		×		65	28
Ponera pennsylvanica	C, MH	×		×	×		×	×	60	35
Tapinoma sessile	C,MH	×	×	×	×		×	×	51	32
Stenamma brevicorne	R, MH	×	×	×	×		×	×	35	28
Aphaenogaster fulva	R, F		×	×	×		×		28	13
Brachymyrmex depilis	R, MH	×			×		×	×	27	7
Myrmica punctiventris	C, MH	×		×	×		×	×	21	12
Camponotus chromaiodes	R, F			×	×		×		18	6
Pyramica ohioensis	R, F		×			×	×		13	8
Crematogaster cerasi	R, MH	×	×	×	×		×	×	8	8
Lasius umbratus	R, MH	×		×	×		×	×	7	2
Solenopsis molesta	MH	×	×	×	×			×	5	2
Stenamma impar	R, F	×		×	×		×		4	4
Proceratium silaceum	R, F			×		×	×		3	3
Vollenhovia emeryi	MH			×	×		×	×	3	3
Camponotus pennsylvanicus	R, MH			×	×		×	×	2	1
Crematogaster pilosa	R, F			×	×		×		2	2
Aphaenogaster tennesseensis	R, F			×	×		×		1	2
Stigmatomma pallipes	R, F	×				×	×		1	1
Camponotus castaneus	R, MH			×	×		×	×	1	1
Camponotus nearcticus	R, MH			×	×		×	×	1	1

forest ant incidence, common ant incidence and rare ant incidence (R STATISTICS PACKAGE 2015). Ant incidence was used rather than abundance due to behavioral effects in ant pitfall trap catches (LONGINO & al. 2002). Incidence is a measure of absence or presence at a site during any sampling event. Incidence of each ant species was then summed across all sampling events (n = 6 sampling events). The independent variables in our analysis included: native plant cover, total plant cover, invasive plant cover, tree number, and soil moisture. Native plant cover, total plant cover, and invasive plant cover were transformed using the natural log before analysis. We determined the top three models for each dependent variable using the Bayesian Information Criterion (BIC) values of the all subsets regressions (R STATISTICS PACKAGE 2015). Bayesian Information Criterion penalizes models more heavily as the number of variables increases; whereas, Akaike Information Criterion does not penalize models as the number of variables grow (DZIAK & al. 2005, VRIEZE 2012).

The variables from these models were then used to create Generalized Linear Models in R. We selected the best model for each dependent variable using AIC. If the AIC values of two models were within two points of each other, the model with fewer independent variables was chosen. We used multiple regressions to determine the adjusted R^2 and statistical significance of the final models. Linear re-

Tab. 2: The nine models that best fit each dependent variable based on Bayesian and Akaike Information Criterion. Adjusted R^2 and significance were determined using a general linear model regression.

Dependent variable	Model	Adjusted R^2	P
Total ant richness	Alien plant cover	0.113	0.018
Total ant incidence	Alien plant cover	0.248	0.004
	Tree number		
	Soil moisture		
Aphaenogaster rudis complex incidence	Total plant cover	0.262	0.003
	Alien plant cover		
	Tree number		
Prenolepis imparis incidence	Soil moisture	0.171	0.005
Nylanderia faisonensis incidence	Alien plant cover	0.201	0.006
	Tree number		
Multiple-habitat ant group incidence	Alien plant cover	0.275	0.002
	Tree number		
	Soil moisture		
Forest ant group incidence	Alien plant cover	0.215	0.004
	Tree number		
Common ant group incidence	Soil moisture	0.173	0.004
Rare ant group incidence	Alien plant cover	0.221	0.004
	Tree number		

gressions were used to evaluate relationships among pairs of variables. We created rank abundance curves using incidence values of each ant species for areas of high alien plant cover and low alien plant cover. All data and R code used in this analysis is available for download (Appendix S1 - S5, as digital supplementary material to this article, at the journal's web pages).

We used EstimateS (COLWELL 2013) to evaluate further the connection between invasive plant cover and ant species richness. Three different species accumulation curves were done with EstimateS; the first contained all of the ant richness data (27 species and 40 observations), the second only those sites where plant invasion was greater than or equal to ten (based on the plant census) (27 species and 21 observations), and the third only those sites where invasive plant cover was less than ten (27 species and 19 observations). We compared multiple species estimators (Chao 2, ICE, and the first order Jackknife) to determine the estimated species richness for each grouping. The same grouping of sites was used in generating ant species rank abundance curves, however, average ant incidence per site was used rather than simple summation due to the difference in group size.

Results

We obtained 3193 ants from 27 species in pitfall traps and soil cores during this two year study (Tab. 1). The reduction of the dataset to 40 sites resulted in the loss of two species from the analysis: *Brachymyrmex depilis* EMERY, 1893 and *Crematogaster pilosa* EMERY, 1895. Eight species were included in the common ant group, 17 species in the rare ants, 15 species in the multiple-habitat ants, and 12 species in the forest ants (Tab. 1). We found nine alien plant species during the plant census; none of the trees were alien species. The four alien plants with the most coverage at the sample sites were *Ampelopsis brevipedunculata*, *Celastrus orbiculatus* THUNB., *Lonicera japonica*, and *Clematis terniflora* L. (Fig. 1). KJAR (2005) contains detailed information on the plant and tree survey results. All alien plant species found in this study are common invasive species in urban forests in the mid-Atlantic region.

In all models produced in this study invasive plant cover and tree number, when present in a model, had a positive coefficient, although no model for any dependent variable exceeded an R^2 value of 0.275 (Tab. 2). Soil moisture had a negative coefficient in all models where this variable was present. Although foraging may not be greatly influenced by soil moisture, it does influence nest site selection in many ant species (TALBOT 1934, ELLISON & al. 2002) and in all cases soil moisture had a negative effect on ant incidence and richness in this study. Tree number was positively associated with ant incidence and ant species richness in all models that included it as a variable. Due to the strong connection between tree richness and the number of trees in a site (linear regression, $R^2 = 0.85$, $P < 0.001$, n = 60), the variable tree number likely represents a variety of correlated environmental variables such as canopy cover, resource abundance, and resource diversity.

The model that best explained *Aphaenogaster rudis* complex incidence contained the variables total plant cover, invasive plant cover, and tree number. In this model total plant cover had a negative effect on *A. rudis* complex incidence, but invasive plant cover and tree number had a positive effect. The models for *Prenolepis imparis* and the common ant group contained only soil moisture. The models for forest ants, rare ants, and *Nylanderia faisonensis* included invasive plant cover and tree number. The model for multiple-habitat ants included invasive plant cover and tree number as well as soil moisture. The model with the best fit for ant incidence included invasive plant cover, tree number, and soil moisture. The model for ant richness contained only invasive plant cover. Of the nine models included in this study, invasive plant cover was present in seven (Tab. 2). The incidence of the common ant group was not negatively associated with the incidence of the rare ant group (linear regression, $R^2 = 0.031$, $P = 0.274$, n = 40). The mean, standard deviation, and range of all variables measured at each site in this study are included in Table 3.

Species accumulation curves based on all sites resulted in an ant species richness estimate that is close to previous estimates in this forest based on these data combined with an earlier survey (KJAR 2005). The total species list for the study site (based on multiple surveys) includes 31 species, but four species were not found in this study; *Lasius claviger* (ROGER, 1862), *Myrmica latifrons* STÄRCKE, 1927, *Camponotus subbarbatus* EMERY, 1893, and *Lasius subumbratus* VIERECK, 1903 (KJAR 2009). EstimateS ana-

Tab. 3: Mean, standard deviation, and range of all variables measured at each site.

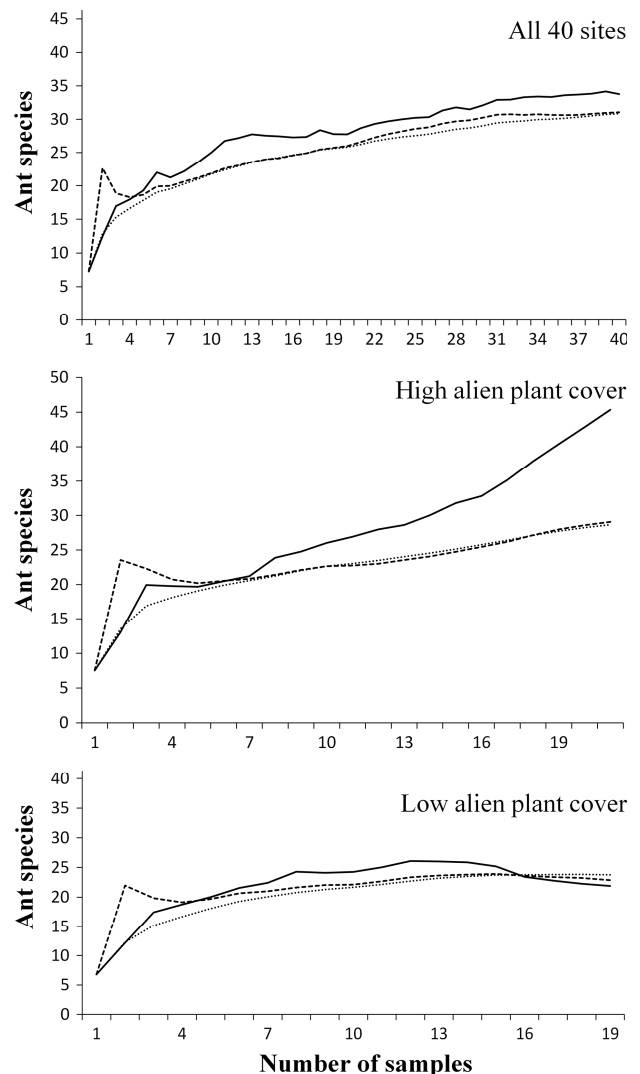| Variables	Mean ± SD	Minimum	Maximum
Native plant cover	9.69 ± 6.40	1.00	25.53
Invasive plant cover	10.75 ± 5.00	4.00	27.90
Total plant cover	20.48 ± 7.50	7.03	43.38
Tree number	2.10 ± 1.75	0.00	08.00
Soil moisture (in %)	0.26 ± 0.04	0.20	00.34
Aphaenogaster rudis complex incidence	4.48 ± 1.88	0.00	07.00
Nylanderia faisonensis incidence	4.00 ± 1.88	0.00	08.00
Prenolepis imparis incidence	2.45 ± 1.48	0.00	06.00
Total ant richness	7.10 ± 1.74	3.00	11.00
Total ant incidence	17.15 ± 5.18	4.00	25.00
Forest group incidence	0.52 ± 1.28	0.00	08.00
Multiple-habitat group incidence	0.76 ± 1.53	0.00	08.00
Common group incidence	1.36 ± 1.76	0.00	07.00
Rare group incidence	0.38 ± 1.13	0.00	08.00

Fig. 2: EstimateS (COLWELL 2013) species accumulation curves generated using the estimators Chao 2 (solid line), Jack 1 (dotted line), and ICE (dashed line).

lysis of all 40 sites together resulted in a Chao 2, first-order Jackknife (Jack), and ICE of 34, 31, and 31 species respectively compared to the 25 observed species (Fig. 2). The group of sites with high alien plant cover (alien plant cover ≥ 10) had 22 observed species, while the group with low alien plant cover (alien plant cover < 10) had 20 observed ant species. Sites with high alien plant cover resulted in a higher estimate of ant species richness than those sites with low alien plant cover. For the high alien plant cover group, ICE and Jack estimators both plateau at 29 total species, but Chao2 does not reach an asymptote. The low alien plant cover group resulted in species estimates near 23 species for all estimators (Fig. 2). Observed ant richness was 21 species in the ≥ 10 alien plant cover group and 22 species in the < 10 alien plant cover group. Ant species rank abundance curves were similar for both alien plant cover groups and the low alien plant cover group had lower incidences for most ant species (Fig. 3).

Discussion

The DMP forest ant community is predominantly composed of the more common mid-Atlantic US ants (KJAR 2009). The ant species in the study forest are common in degraded forest habitat, forest, and in open fields. Species

found only in forests are much less abundant, and many rare forest species were not present in our samples (see KJAR 2009 and Tab. 1). We believe the ant community in this study reflects the frequent large-scale forest disturbance in the DMP (e.g., hurricanes), which may restrict the ant community to more generalist species regardless of alien plant invasion. Such species are more likely to do well in areas that are invaded by alien plants than forest specialists. MITCHELL & al. (2002) and SOBRINHO & al. (2003) suggest that increased diversity in disturbed or fragmented forest may be due to the establishment of such generalist ant species.

Habitat changes resulting in the displacement of normally competitive ant species may be a mechanism for an increase in ant richness in areas of alien plant invasion. In this study, the incidence of the common ant group was not associated with the amount of alien plant cover, and incidences of rare and forest ant groups were positively associated with the amount of alien plant cover. *Nylanderia faisonensis*, the only individual species of the rare ant group with great enough trap capture for individual analysis, had increased incidence in areas of high alien plant
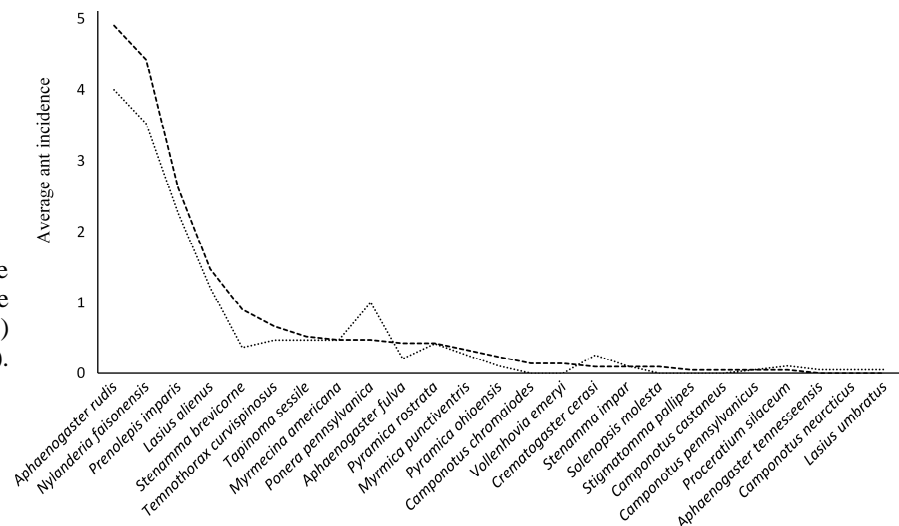
Fig. 3: Ant species rank abundance curve based on average ant incidence per site in areas of high (dashed line) and low alien plant cover (dotted line).

cover (Tab. 2). The common ant group in this study consists of species that recruit quickly and frequently in great numbers, particularly when compared to the rare ant group. If competitive interactions between groups are structuring this community we would expect the rare ant group to increase in incidence as the competitive common ant group decreases. However, in this study the rare ant group was not associated with changes in the common ant group (linear regression, $R^2 = 0.031$, $P = 0.274$, n = 40).

Prenolepis imparis and *Aphaenogaster rudis* complex are common, generalist ants found throughout the US in forested habitats (HEADLEY 1943, TALBOT 1965, HERBERS & al. 1985). The incidence of *A. rudis* complex, an ant species likely to compete throughout the warm season with all other generalists (LYNCH & al. 1980, FELLERS 1987, LUBERTAZZI 2012), was positively associated with the amount of alien plant cover. Alien plant cover did not predict the incidence of the abundant and competitive ant species, *P. imparis* (Tab. 2). Of all ant species in this study, *P. imparis* has the largest range and is found in many diverse habitats across North America (TALBOT 1943, CREIGHTON 1950, LYNCH & al. 1980, FELLERS 1987, TSCHINKEL 1987). It is therefore not surprising that it appears unaffected by alien plant cover in this study. In this forest it appears that the displacement of competitive species in areas of alien plant invasion allowing for greater densities of less competitive species cannot explain the increase in ant incidence and richness in areas of alien plant invasion in this forest.

The ant species rank abundance curves for areas with low versus high alien plant cover demonstrate that the members of the ant community do not appear to be changing. Instead the incidence of most ant species increases in areas with greater alien plant cover (Fig. 3). There was turnover at the tail of the curve where trap incidences were less than three, but the absence from traps with this low overall incidence makes analysis of these species questionable. We believe more intensive trapping would have resulted in the eventual capture of those rarer species. Greater trap effort would shift the curves upward and add a longer tail (predicted by the species estimators), but we do not believe increased trapping effort would change the ant species rank order. We did not find species turnover or large rank abundance differences between groups for those ants whose trap incidences were greater than four

(Fig. 3). Therefore, we believe these data show that the increased ant incidence and richness we are observing in areas with greater alien plant cover is simply a greater incidence of all foraging ants rather than changes in ant species composition.

Areas that have been invaded by alien plants in the DMP forest are often covered by a dense growth of alien vines, possibly increasing the surface area available for ant foraging. However, total plant cover was not a significant predictor of incidences of any ant species or group besides *Aphaenogaster rudis* complex, and in that case it had a negative coefficient (Tab. 2). Therefore, if alien plants are facilitating increases in ant incidence and richness, it seems likely that the presence of alien plants may represent increased resource availability or some other correlated factor rather than simply more plant cover. The more common alien plant species in this study produce large numbers of fruits and nectar-containing flowers. In areas with a low abundance of alien plants, the herbaceous ground cover of this forest is sparse and tends to be dominated by *Lindera benzoin* L. (Spicebush) and *Toxicodendron radicans* (L.) KUNTZE (Poison Ivy). The addition of plants which flower several times a year (*Lonicera japonica*), and have numerous fruits (*Ampelopsis brevipedunculata*; *Celastrus orbiculatus*), may be used directly by some ant species or may increase prey species abundance in areas with these alien plants. However, due to the observational nature of this study we cannot use these data to determine if alien plant cover is directly facilitating the increased incidence of ants. We believe observations on the use of alien plant resources by native ants (including plant feeding homopterans tended by these ants) and isolating disturbance from alien plant cover in analysis will be a critical part of any further study aimed at understanding the relationship of increased incidence of ant species in areas of high alien plant cover.

Conclusion

Total ant incidence and to a lesser extent, richness, were positively associated with the amount of alien plant cover. The findings of this study also suggest that these changes are not the result of release from competitive ant species in such areas or the addition of generalist ant species. Increased ant incidence and ant richness appears to be the

result of greater numbers of foraging ants in areas with greater alien plant cover rather than changes in the ant species composition. These differences may be the result of increased resource availability, disturbed habitat, or some other factor correlated with alien-plant cover.

Acknowledgments

References

ANDERSEN, A.N. & MAJER, J.D. 2004: Ants show the way Down Under: invertebrates as bioindicators in land management. – Frontiers in Ecology and the Environment 2: 291-298.

ARMBRECHT, I., PERFECTO I. & VANDERMEER, J. 2004: Enigmatic biodiversity correlations: ant diversity responds to diverse resources. – Science 304: 284-286.

BARROWS, E.M., MCINTYRE, A.M. & FLINT, O.S. 2005: Alderfly (Neuroptera: Sialidae) flight periods and habitats in Dyke Marsh Wildlife Preserve, Virginia, USA. – Proceedings of the Washington Entomological Society 107: 693-699.

BESTELMEYER, B.T. & WIENS, J.A. 1996: The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. – Ecological Applications 6: 1225-1240.

BONTE, D., DEKONINCK, W., PROVOOST, S., COSIJNS, E. & HOFFMANN, M. 2003: Microgeographical distribution of ants (Hymenoptera: Formicidae) in coastal dune grassland and their relation to the soil structure and vegetation. – Animal Biology 53: 367-377.

BRASCHLER, B. & BAUR, B. 2003: Effects of experimental small-scale grassland fragmentation on spatial distribution, density, and persistence of ant nests. – Ecological Entomology 28: 651-658.

BROOKS, M.L., D'ANTONIO, C.M., RICHARDSON, D.M., GRACE, J.B., KEELEY, J.E., DITOMASO, J.M., HOBBS, R.J., PELLANT, M. & PYKE, D. 2005: Effects of invasive alien plants on fire regimes. – Bioscience 54: 677-688.

CARLSON, D.M. & GENTRY, J.B. 1973: Effects of shading on the migratory behavior of the Florida harvester ant, *Pogonomyrmex badius*. – Ecology 54: 452-453.

CARNEY, S.E., BYERLEY, M.B. & HOLWAY, D.A. 2003: Invasive Argentine ants (*Linepithema humile*) do not replace native ants as seed dispersers of *Dendromecon rigida* (Papaveraceae) in California, USA. – Oecologia 135: 576-582.

CERDÁ, X., ARNAN, X. & RETANA, J. 2013: Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology? – Myrmecological News 18: 131-147.

CHRISTIAN, C.E. 2001: Consequences of a biological invasion reveal the importance of mutualism for plant communities. – Nature 413: 635-639.

COLWELL, R.K. 2013: EstimateS: statistical estimation of species richness and shared species from samples. Version 9. – <http://purl.oclc.org/estimates>, retrieved on 23 January 2015.

CREIGHTON, W.S. 1950: The ants of North America. – Bulletin of the Museum of Comparative Zoology at Harvard College 104: 1-569.

CULVER, D.C. & BEATTIE, A.J. 1978: Myrmecochory in *Viola*: dynamics of seed-ant interactions in some West Virginia species. – The Journal of Ecology 66: 53-72.

DZIAK, J., LI, R. & COLLINS, L. 2005: Critical review and comparison of variable selection procedures for linear regression (Technical report). – < http://sites.stat.psu.edu/~jdziak/classical.pdf>, retrieved on 10 June 2015.

ELLISON, A.M., FARNSWORTH, E.J. & GOTELLI, N.J. 2002: Ant diversity in pitcher-plant bogs of Massachusetts. – Northeastern Naturalist 9: 267-284.

ESRI, INC. 2001: Version 3.1.380. – ESRI, Inc., Redlands, CA.

FELLERS, J.H. 1987: Interference and exploitation in a guild of woodland ants. – Ecology 68: 1466-1478.

FREDERICKSON, M.E., GREENE, M.J. & GORDON, D.M. 2005: "Devil's gardens" bedevilled by ants. – Nature 437: 495-496.

HEADLEY, A.E. 1943: The ants of Ashtabula County, Ohio (Hymenoptera: Formicidae). – Ohio Journal of Science 43: 22-31.

HERBERS, J.M., ADAMOWICZ, S.C. & HELMS, S.D. 1985: Seasonal changes in social organization of *Aphaenogaster rudis* (Hymenoptera: Formicidae). – Sociobiology 10: 1-15.

HOFFMANN, B.D. 2003: Responses of ant communities to experimental fire regimes on rangelands in the Victoria River District of the Northern Territory. – Austral Ecology 28: 182-196.

HOLWAY, D.A. & CASE, T.J. 2000: Mechanisms of dispersed central-place foraging in polydomous colonies of the Argentine ant. – Animal Behaviour 59: 433-441.

HOY, J.M. 1964: Animal modification of native vegetation: the effects of insects on natural vegetation. – Proceedings of the New Zealand Ecological Society 11: 56-59.

IVES, C.D., HOSE, G.C., NIPPERESS, D.A. & TAYLOR, M.P. 2011: Environmental and landscape factors influencing ant and plant diversity in suburban riparian corridors. – Landscape and Urban Planning 103: 372-382.

JANZEN, D.H. 1966: Coevolution of mutualism between ants and acacias in Central America. – Evolution 20: 249-275.

JOHNSTON, D.W. 2000: The Dyke Marsh Preserve ecosystem. – Virginia Journal of Science 51: 223-272.

KING, J.R. & TSCHINKEL, W.R. 2006: Experimental evidence that the introduced fire ant, *Solenopsis invicta*, does not competitively suppress co-occurring ants in a disturbed habitat. – Journal of Animal Ecology 75: 1370-1378.

KJAR, D.S. 2002: Variation in terrestrial arthropod and vascular plant diversity in a mid-Atlantic low deciduous forest. – MSc thesis, Georgetown University, Washington, DC, 70 pp.

KJAR, D.S. 2005: Studies on the ants, alien and native plants, and ant sampling methods in a U. S. National Park. – PhD thesis, Georgetown University, Washington, DC, 165 pp.

KJAR, D.S. 2009: The ant community of a riparian forest in the Dyke Marsh Preserve, Fairfax County, Virginia, and a checklist of mid-Atlantic Formicidae. – Banisteria 33: 3-17.

KJAR, D.S. & BARROWS, E.M. 2004: Arthropod community heterogeneity in a mid-Atlantic forest highly invaded by alien organisms. – Banisteria 24: 26-37.

LASSAU, S.A. & HOCHULI, D.F. 2004: Effects of habitat complexity on ant assemblages. – Ecography 27: 157-164.

LENDA, M., WITEK, M., SKORKA, P., MORON, D. & WOYCIECHOWSKI, M. 2013: Invasive alien plants affect grassland ant communities colony size and foraging behavior. – Biological Invasions 15: 2403-2414.

LEVINE, J.M., VILÀ, M., D'ANTONIO, C.M., DUKES, J.S., GRIGULIS, K. & LAVOREL, S. 2003: Mechanisms underlying the impacts of exotic plant invasions. – Proceedings of the Royal Society B-Biological Sciences 270: 775-781.

LEVINGS, S.C. 1983: Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: some causes of patchy species distributions. – Ecological Monographs 53: 435-455.

LINKSVAYER, T.A. & JANSSEN, M.A. 2008: Traits underlying the capacity of ant colonies to adapt to disturbance and stress regimes. – Systems Research and Behavioral Science 26: 315-329.

LONGINO, J.T., CODDINGTON, J. & COLWELL, R.K. 2002: The ant fauna of a tropical rain forest: Estimating species richness three different ways. – Ecology 83: 689-702.

LUBERTAZZI, D. 2012: The biology and natural history of *Aphaenogaster rudis*. – Psyche 2012: 11 pp.

LYNCH, J.F., BALINSKY, E.C. & VAIL, S.G. 1980: Foraging patterns in three sympatric species, *Prenolepis imparis*, *Nylanderia melanderi* and *Aphaenogaster rudis*. – Ecological Entomology 5: 353-371.

LYNCH, J.F., JOHNSON, A.K. & BALINSKY, E.C. 1988: Spatial and temporal variation in the abundance and diversity of ants (Hymenoptera: Formicidae) in the soil and litter layers of a Maryland forest. – The American Midland Naturalist 119: 31-44.

MACK, M. & D'ANTONIO, C.M. 1998: Impacts of biological invasions on disturbance regimes. – Trends in Ecology & Evolution 13: 195-198.

MCGLYNN, T.P., SHOTELL, M.D. & KELLY, M.S. 2003: Responding to a variable environment: home range, foraging behavior, and nest relocation in the Costa Rican rainforest ant *Aphaenogaster araneoides*. – Journal of Insect Behavior 16: 687-701.

MITCHELL, C.E., TURNER, M.G. & PEARSON, S.M. 2002: Effects of historical land use and forest patch size on myrmecochores and ant communities. – Ecological Applications 12: 1364-1377.

NATIONAL PARK SERVICE 2002: AlaskaPak: Functions pack extensions for ArcView 3x National Park Service Alaska Support Office. – <http://www.nps.gov/akso/gis/av31/akpak.htm>, retrieved on 3 June 2002.

OSUNKOYA, O.O., POLO, C. & ANDERSEN, A.N. 2011: Invasion impacts on biodiversity: responses of ant communities to infestation by cat's claw creeper vine, *Macfadyena unguis-cati* (Bignoniaceae) in subtropical Australia. – Biological Invasions 13: 2289-2302.

PERFECTO, I. & SNELLING, R. 1995: Biodiversity and the transformation of a tropical agroecosystem: ants in coffee plantations. – Ecological Applications 5: 1084-1097.

R CORE TEAM 2013: R: a language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna; <http://www.R-project.org/>, retrieved on 10 September 2014.

RAO, M., TERBORGH, J. & NUNEZ, P. 2001: Increased herbivory in forest isolates: implications for plant community structure and composition. – Conservation Biology 15: 624-633.

RIBAS, C.R., SCHOEREDER, J.H., PIC, M. & SOARES, S.M. 2003: Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. – Austral Ecology 28: 305-314.

SANDERS, N.J., MOSS, J. & WAGNER, D. 2003: Patterns of ant species richness along elevational gradients in an arid ecosystem. – Global Ecology and Biogeography 12: 93-102.

SCHOEMAN, C.S. & SAMWAYS, M.J. 2013: Temporal shifts in interactions between alien trees and the alien Argentine ant on native ants. – Journal of Insect Conservation 17: 911-919.

SIMAO, M.C.M., FLORY, S.L. & RUDGERS, J.A. 2010: Experimental plant invasion reduces arthropod abundance and richness across multiple trophic levels. – Oikos 119: 1553-1562.

SMALLWOOD, J. 1982: Nest relocations in ants. – Insectes Sociaux 29: 138-147.

SOBRINHO, T.G., SCHOEREDER, J.H., SPERBER, C.F. & MADUREIRA, M.S. 2003: Does fragmentation alter species composition in ant communities (Hymenoptera: Formicidae)? – Sociobiology 42: 329-342.

TALBOT, M. 1934: Distribution of ant species in the Chicago Region with reference to ecological factors and physiological toleration. – Ecology 15: 416-439.

TALBOT, M. 1943: Population studies of the ant, *Prenolepis imparis* SAY. – Ecology 24: 31-44.

TALBOT, M. 1965: Populations of ants in a low field. – Insectes Sociaux 12: 19-46.

THOMAS, L.K. 1980: The impact of three exotic plant species on a Potomac island. – National Park Service Scientific Monograph Series 13: 1-179.

THOMPSON, B. & MCLACHLAN, S. 2007: The effects of urbanization on ant communities and myrmecochory in Manitoba, Canada. – Urban Ecosystems 10: 43-52.

TSCHINKEL, W.R. 1987: Seasonal life history and nest architecture of a winter-active ant, *Prenolepis imparis*. – Insectes Sociaux 34: 143-164.

UMPHREY, G.J. 1996: Morphometric discrimination among sibling species in the *fulva-rudis-texana* complex of the ant genus *Aphaenogaster* (Hymenoptera: Formicidae). – Canadian Journal of Zoology 74: 528-559.

VILÀ, M., ESPINAR, J.L., HEJDA, M., HULME, P.E., JAROŠIK, V., MARON, J.L., PERGL, J., SCHAFFNER, U., SUN, Y. & PYŠEK, P. 2011: Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. – Ecology Letters 14: 702-708.

VRIEZE, S.I. 2012: Model selection and psychological theory: a discussion of the differences between the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC). – Psychological Methods 17: 228-243.

WANG, C., STRAZANAC, J. & BUTLER, L. 2001: Association between ants (Hymenoptera: Formicidae) and habitat characteristics in oak-dominated mixed forests. – Environmental Entomology 30: 842-848.

WIMP, G.M. & WHITMAN, T.G. 2001: Biodiversity consequences of predation and host plant hybridization on an aphid-ant mutualism. – Ecology 82: 440-452.