

Biodiversity of ant species along a disturbance gradient in residential environments of Puerto Rico

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Published online: 10 October 2012
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Abstract One of the most effective ways to describe the successional gradient of an environment is by using measures of biodiversity. We investigated the biodiversity of ant communities (known tramp/structure invaders) in an environment undergoing urban succession to characterize how ant communities changed along a disturbance gradient. Ant community dynamics were examined within three Puerto Rican housing developments of different ages. Within each development, we assessed the ant community using biodiversity measures of richness, abundance, diversity and evenness. We also studied changes in biodiversity within each development over time as well as how biodiversity related to food preferences within the ant communities. In general, the biodiversity measures increased as the age of the housing development increased. Monthly changes in biodiversity indicated that month was a better predictor of biodiversity in the most recently disturbed development, while the biodiversity in the older developments was less predictable from month to month. The biodiversity measures also suggested that the ant community in the youngest development was comprised mostly of generalist feeders. However, the older sites' ant species appeared to have more specific feeding preferences. Based on the biodiversity measures of these ant communities, our findings suggest that the housing developments of different ages represented advancing stages of secondary succession. Furthermore, this study indicated that the succession of ant species occurs rapidly (<10 years) in urban environments, resulting in a relatively diverse ant community.

Keywords Ant community · Formicidae · Housing development · Tropical · Urban succession

Introduction

Studies of ecological succession typically focus on biodiversity changes either within a natural system (e.g. volcanic ash fields; primary succession), or in locations where human

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activities have been discontinued (abandoned agricultural fields, or clear cut forests; secondary succession). However, ecological succession also takes place in systems where human activities or structures still persist. These urban ecosystems include residential lawns and gardens, industrial sites, abandoned properties, parks and play grounds, cemeteries, and waste disposal sites (Nagle 1999). Succession in natural environments may be caused by natural or man-made disturbances. However, urban succession typically happens during and after the process of urbanization. During urbanization the previous landscape is usually denuded of vegetation, the underlying soil is graded, and structures built for human occupation. This process leaves patches of barren soil or introduced landscaping plants (surrounding a structure), within which succession can begin. Plants and animals are either slowly transported or become reestablished from surrounding locations into the urban ecosystem causing species diversity to increase (Rebele 1994).

Because an urban ecosystem is the direct result of the destruction of a previously existing ecosystem, the process of succession in urban environments is by definition, secondary succession. Throughout the stages of succession, the species composition or biological diversity of the environment is changing. Biological diversity, commonly referred to as biodiversity, is a description of the different species existing in a defined area (i.e. ecosystem, habitat, environment, community, etc.; Gaston 1996). Biodiversity is typically higher in more complex environments. Because succession ultimately results in an increase of the environmental complexity, as the communities change over time, biodiversity increases (Molles 2005).

A number of measurements have been developed to assess the biodiversity of a community. The most common metric used to describe biodiversity is species richness. Species richness is a count of the number of species in a community or habitat (Molles 2005). Species evenness is also used to quantify biodiversity and is a comparative value based on the abundances of each species. Indices of diversity have also been developed to further quantify biodiversity. These indices, such as the Shannon diversity index, use a combination of richness and evenness to calculate a diversity value for the community (Molles 2005).

Although biodiversity can be measured based on the entire species composition, some groups of species, known as indicator species, may also provide an accurate representation of the diversity within a community (Roth et al. 1994; Lindenmayer et al. 2000). These indicator species are characterized by being easily collected, and widely distributed throughout the community. Indicator species also make up a large portion of the total animal biomass. Indicator species are readily identified, and respond to environmental change in much the same way as other organisms within the community (Graham et al. 2004). One group of indicator species, whose biodiversity has been studied in many habitats, is the ants (Majer 1981, 1983, 1984; Majer et al. 1982; Rossbach and Majer 1983; Majer and Brown 1986). A classic study using ants as indicator species was conducted by Roth et al. (1994) in Costa Rica. Roth et al. (1994) quantified ant biodiversity in agricultural and forested field sites and then used these measurements to predict the overall biodiversity that could exist within different land management systems. The Roth et al. (1994) study concluded that the ant species diversity was greater at sites with fewer disturbances. Likewise, the biodiversity of other organisms was also found to be greater in sites of less disturbance. Therefore, the ant species complex was found to be a representative indicator of the overall diversity within a community.

The goal of this study was to evaluate the biodiversity of known structure invading (tramp) ant species along a disturbance gradient (time since disturbance) within an urban ecosystem. Our specific objective was to calculate and compare different measures of ant species diversity within housing developments of different ages. We hypothesized that

as the age of the housing development increased, the measures of biodiversity would also increase, thus indicating different stages in the process of succession. Measures of species richness, abundance, and diversity and evenness indices were calculated for each housing development. The biodiversity measures were then used to compare the ant species composition between housing developments representing different stages in the successional process. Monthly changes in species biodiversity were also compared between sites to determine how the annual changes in biodiversity differed along the disturbance gradient.

Additional comparisons were made to indirectly assess the biodiversity of the housing developments of different ages with regard to ant feeding preferences. In the early stages of urban succession, the housing development would provide limited microhabitats, nesting sites and food resources. We hypothesized that any ant species that became established in this environment would be a generalist in its foraging and feeding habits, activities taking advantage of all resources wherever they were available. Therefore, diversity measures would not indicate any significant feeding preferences. However, as environmental complexity increased along the disturbance gradient, the habitat would become more diverse and be able to support more ant species with particular feeding preferences.

Materials and methods

Research sites

The research sites used in this study were located in Santa Isabel, Puerto Rico as described in Brown et al. (2011). All sites were located on a large plot of land that had once been a single agricultural field (Fig. 1). The field had been cleared and converted to residential neighborhoods over the last 20 years. The study was conducted in three contiguous neighborhoods that had been constructed at different times. These neighborhoods represented a disturbance

Fig. 1 Satellite image of the three housing developments used as sample sites in Santa Isabel, Puerto Rico (November 2009; Google Earth 4.0, Google, Inc., Mountain View, CA)



gradient with regard to their time since construction, and thus we expected to identify ant communities that were indicative of the different stages of urban succession within these sites.

Site 1 was a newly constructed housing development with a post construction age of less than one year. Site 1 had the least environmental complexity of the three sites. There was no landscaping (bare soil or weedy grasses) and the houses themselves were structurally simple and of uniform design. This site would provide very few microhabitats, food resources, or nesting sites for invading ant species. At the beginning of the study, Site 1 had no human inhabitants.

Site 2 had a post construction age of approximately four years and was the residential neighborhood to the east of Site 1. The homes in Site 2 were all occupied by residents and the structures had been customized with the addition of exterior walls, closed garages, and porches. The yards contained small trees and shrubs, flowering plants, fountains, and other landscaping features that would have provided many more microhabitats, ant nesting sites and food resources than Site 1.

The third site (Site 3) was approximately eight years old. Like Site 2, the site was completely inhabited by humans and nearly all the houses were customized with unique construction features. The front yards of the properties that ranged in complexity from bare earth to elaborate landscaping with mature trees and shrubs and subterranean trash containers. The construction features and landscaping created numerous microhabitats and food resources that were exploited by ants.

Similar to Silva et al. (2007), the location of the research sites in Santa Isabel provided a unique opportunity to study the effects of succession along a disturbance gradient. With the exception of when the houses were constructed, the housing developments were nearly identical in all their environmental characteristics (soil type, climate, type of disturbance, and source of invading species, i.e. each housing development was bordered by pastureland and additional residential neighborhoods). Therefore, the study area provided a successional gradient of ant biomass accumulation and species diversity, with a single development representing a different stage in urban succession.

Sampling procedure

Thirty houses within each site were sampled to achieve a representative collection of the species distributed over the entire study site. Food based baits (one carbohydrate based; one lipid based) were used to collect ant samples. Two types of baits were provided because structure invading ant species are known to be primarily sweet feeders however, some species periodically change their feeding preferences based on their reproductive status. Cotton rope segments were soaked in one of two food attractants; peanut oil or a 25 % sucrose solution. The rope segments were then each inserted into a glass vial. A pair of baited vials, one sugar and one peanut oil, was then placed at three locations around the front exterior of each sampled house. The baits were left at the sampling locations for one hour and then collected and filled with isopropyl alcohol to kill and preserve the collected ants.

The baiting regimen was conducted twice a day over a two day period at each site. Sampling periods were between 7:00 and 10:00 am, and between 4:00 and 7:00 pm depending on seasonal daylight hours. A total of eight two-day sampling trips were conducted at approximately six week intervals so that the ants were sampled two times per season. The ant species in each vial were identified, and the number of individuals in each species was recorded.

Pitfall traps were also used to monitor for any non-structure invading ant species that may not have been detected with bait sampling. The results of the pitfall trap sampling are discussed in Brown et al. (2011) but were not included this study.

Data analysis

Four measures were selected to quantify the biodiversity of ant species in each of the housing developments: species richness (S), abundance (N), the Shannon diversity index (H), and the Shannon evenness index (E). Species richness (S) equaled the total number of ant species collected from a single house, and abundance (N) equaled the total number of ants collected from the house. The Shannon diversity index (H) was calculated for each house using the following formula:

$$H = - \sum_{i=1}^S p_i \ln p_i$$

where p_i is the proportion of the individuals of the i^{th} species, and S is the total number of species (Roth et al. 1994). The Shannon evenness index (E) was calculated for each house using:

$$E = H/H_{\max} = H/\ln S$$

where H is the Shannon diversity index, and $\ln S$ is the natural logarithm of the number of species (Roth et al. 1994).

Each house within each of the three sites was sampled at three locations around the house, using two different types of baits, at two different times during the day, for eight different months of the year, making this experiment a $3 \times 3 \times 2 \times 2 \times 8$ factorial experiment. Each measure of biodiversity (S , N , H , E) was calculated for each house ($n=30$) within a site and used as a single replication. Therefore, 96 ($3 \times 2 \times 2 \times 8$) samples were taken from each individual house within a site and pooled together. The pooled data were then used to calculate the biodiversity measures for each house within each site. The biodiversity measures were then compared using an analysis of variance (ANOVA; SAS Institute 2003). Significant differences in the biodiversity measures between sites were determined using Tukey's method of least squares means (SAS Institute 2003).

To compare the seasonal changes in biodiversity between the sites, linear regression was used to plot each biodiversity measure by month and then compare the characteristics of the regression lines to identify significant differences. For example, richness data were pooled from 12 samples for each house (samples taken from the three locations around the house, using the two bait types, during two times of the day). The pooled data for each house were then used to calculate the ant species richness for that house. The richness value of each house ($n=30$) was then averaged to calculate a mean richness value for each combination of site and month (24 values). The eight mean richness values (one for each sampling month) for each site were then analyzed using linear regression (PROC REG; SAS Institute 2003) to determine the intercept and slope (regression coefficient) of each regression line. PROC GLM (SAS Institute 2003) was used to compare the slopes of each regression line and significant differences between sites were contrasted. This procedure was then repeated for the other three biodiversity measures (abundance, diversity, and evenness).

To determine the diversity of ants feeding on each bait, the four biodiversity measures were calculated for each bait type (sugar and peanut oil), nested within each site using a two factor repeated measures ANOVA (bait, sites). For the analysis on bait type, data from 48

samples ($3 \times 2 \times 8$) were combined together for each house (from the three locations around the house, during the two times of the day, for each of the eight months). The pooled data for each house were then used to calculate the biodiversity measures for that individual house. The biodiversity measures of each house ($n=30$) were then statistically analyzed to determine differences in the measures of biodiversity from each bait type. Significant differences in the biodiversity measures between baits, nested within sites, were determined using Tukey's method of least squares means (SAS Institute 2003).

Results

Biodiversity measures of each site

Ant sampling throughout the year resulted in the collection and identification of 243,252 ants from a total of 8,640 bait samples. A total of 19 species were identified from the bait samples collected at all three sites and an additional six species were identified from pitfall trap samples (Table 1; Brown et al. 2011). Measures of biodiversity were calculated from bait sample data only.

Repeated measures ANOVA determined that the species richness (S) and abundance (N) between the sites was significantly different (richness: $F=64.27$; $df=2, 58$; $P<0.0001$; abundance: $F=9.48$; $df=2, 58$; $P=0.0003$). The Tukey-Kramer test of least significant difference (LSD) indicated that significantly fewer species were collected per house at Site 1 compared with Site 2 ($P<0.0001$) and Site 3 ($P<0.0001$). However, the number of species collected at Site 2 and 3 did not differ significantly from each other ($P=0.0957$; Fig. 2). Similarly, the Tukey-Kramer LSD test also indicated that the mean abundance of ants collected per house at Site 1 was significantly less than at Site 2 ($P=0.0003$) and Site 3 ($P=0.0076$). However, the number of ants collected at Site 2 and 3 did not differ significantly from each other ($P=0.5508$; Fig. 3).

Species diversity (H) and evenness (E) were significantly different between the test sites (diversity: $F=27.33$; $df=2, 58$; $P<0.0001$; evenness: $F=13.38$; $df=2, 58$; $P<0.0001$). LSD comparisons of diversity revealed that each site was significantly different from the other two (Fig. 4). Site 1 was significantly less diverse than Site 2 ($P=0.0003$) and Site 3 ($P<0.0001$), and Site 2 was less diverse than Site 3 ($P=0.0062$). LSD comparisons conducted on evenness indices indicated Sites 1 and 2 were not significantly different from each other ($P=0.1496$). However, the evenness index for Site 3 was significantly greater than those of Site 1 and 2 (Site 1 and 3: $P<0.0001$; Site 2 and 3: $P=0.0056$).

Monthly biodiversity measures

Mean monthly biodiversity measures were calculated for each site in order to plot regression lines representing changes in biodiversity over the course of the test period. The regression lines for each site were used to determine the correlation between each biodiversity measure and month (Figs. 5, 6, 7, 8). The rate of change (slope) of the biodiversity measure with respect to time (month) was also determined using linear regression. Richness (Fig. 5), abundance (Fig. 6), and diversity indices (Fig. 7) had a positive correlation (R value) with the sampling month in all three sites. However, evenness indices in Sites 2 and 3 indicated that evenness and month had a negative correlation (Fig. 8). In contrast, the R value calculated for Site 1 indicated that evenness indices and sampling month were positively correlated. Overall, the strongest correlations (R values) between biodiversity measures and

Table 1 Species list for ants collected in housing developments of Santa Isabel, Puerto Rico. Species collected in each housing development are indicated with an “X” (Brown et al. 2011)

Subfamily and Species Name	Common Name	Origin ^a	Housing Development Age		
			One year	Four years	Eight years
Dolichoderinae					
<i>Tapinoma melanocephalum</i> Fabricius	Ghost ant	Old World	X	X	X
<i>Tapinoma rasenum</i> Smith & Lavigne ^b		Native			X
<i>Dorymyrmex antillana</i> Forel ^b		New World	X		
Formicinae					
<i>Brachymyrmex</i> sp. 1 Mayr	Rover ant	New World	X	X	X
<i>Brachymyrmex</i> sp. 2 Mayr ^b	Rover ant	New World	X	X	
<i>Paratrechina longicornis</i> Forel	Crazy ant	Old World	X	X	X
Myrmicinae					
<i>Cardiocondyla emeryi</i> Forel		Old World	X	X	X
<i>Crematogaster steinheili</i> Forel ^c	Acrobat ant	New World		X	
<i>Cyphomyrmex minutus</i> Mayr ^c		New World		X	X
<i>Monomorium destructor</i> Jerdon	Destructive trailing ant	Old World	X	X	X
<i>Monomorium floricola</i> Jerdon	Bicolored trailing ant	Old World		X	X
<i>Pheidole fallax</i> Mayr	Big-headed ant	New World	X	X	X
<i>Pheidole megacephala</i> Fabricius ^b	Big-headed ant	Old World	X	X	X
<i>Pheidole moerens</i> Wheeler	Big-headed ant	Native	X	X	X
<i>Pheidole subarmata</i> Mayr	Big-headed ant	New World		X	X
<i>Solenopsis corticalis</i> Forel		New World	X	X	X
<i>Solenopsis globularia</i> Creighton		New World	X	X	X
<i>Solenopsis invicta</i> Buren	Red imported fire ant	New World	X	X	X
<i>Solenopsis pygmaea</i> B Forel ^c		Native		X	X
<i>Strumigenys louisianae</i> Roger		New World		X	X
<i>Tetramorium simillimum</i> Smith ^c		Old World		X	X
<i>Wasmannia auropunctata</i> Roger ^b	Little fire ant	New World			X
Ponerinae					
<i>Hypoponera punctatissima</i> Roger ^c		Old World	Pitfall trap only. Not in a site.		
<i>Odontomachus ruginodis</i> Smith		New World	X	X	X
Pseudomyrmecinae					
<i>Pseudomyrmex simplex</i> Smith ^c		New World			X

R. R. Snelling and J. A. Torres, unpublished data^a; Collected only in bait samples^b; Collected only in pitfall traps^c

sampling month (goodness-of-fit) occurred in Site 1. The weakest correlations occurred in Site 3. In other words, sampling month was a strong predictor of biodiversity in Site 1, but a weak predictor of biodiversity in Site 3.

Contrast comparisons were used to determine whether there was a significant difference in the slopes (regression coefficients) for each biodiversity measure, S , N , H , and E between the three study sites. There was a significant difference in the regression coefficients for diversity (H) (Fig. 7; $F=5.44$; $df=2$; $P=0.0142$) but not richness (S) (Fig. 5; $F=2.57$; $df=2$;

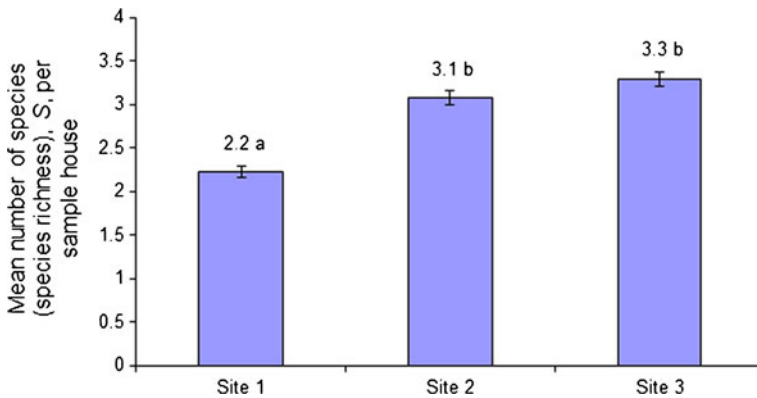


Fig. 2 Mean number of ant species (species richness) collected from sample houses ($n=30$) at different aged housing sites (one, four, and eight years old) in Puerto Rico. Means followed by different letters are significantly different

$P=0.1042$) or evenness (E) (Fig. 8; $F=1.18$; $df=2$; $P=0.3305$). Although there was not a statistical difference between the regression coefficients of abundance (N) at the $P\leq 0.05$ level, abundance regression coefficients were significant at the $P\leq 0.06$ level (Fig. 6; $F=3.30$; $df=2$; $P=0.0600$).

Diversity index (H) comparisons between each site indicated that the slope of the regression line for Site 1 was significantly greater than the slope of the lines for Site 2 and 3 (Site 1 and 2: $P=0.0183$; Site 1 and 3: $P=0.0067$; Fig. 7). However, the slopes of the regression lines for Site 2 and Site 3 were not significantly different ($P=0.6465$). Abundance (N) comparisons ($P\leq 0.06$) indicated that the slopes of the regression lines for Site 2 and Site 3 were significantly different ($P=0.0205$), but that the slope for Site 1 was not significantly different from either Site 2 or Site 3 (Site 1 and 2: $P=0.1247$; Site 1 and 3: $P=0.3652$).

Bait preferences

Analysis of ant species sampled at each of the baits (sugar or oil) was conducted to determine whether the ant species in each site had any feeding preferences. Repeated

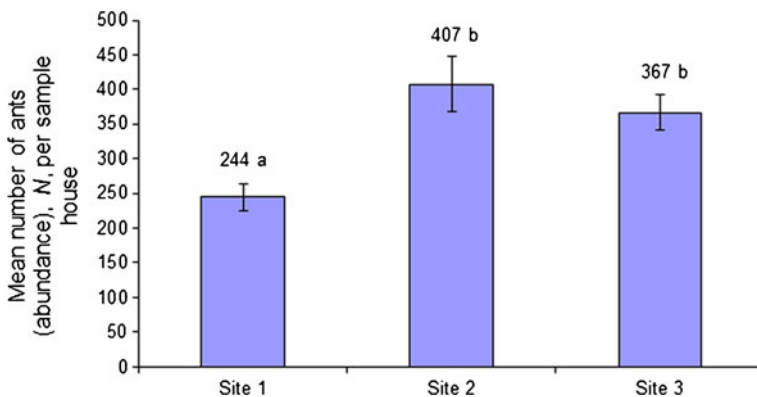


Fig. 3 Mean number of ants (abundance) collected from sample houses ($n=30$) at different aged housing sites (one, four, and eight years old) in Puerto Rico. Means followed by different letters are significantly different

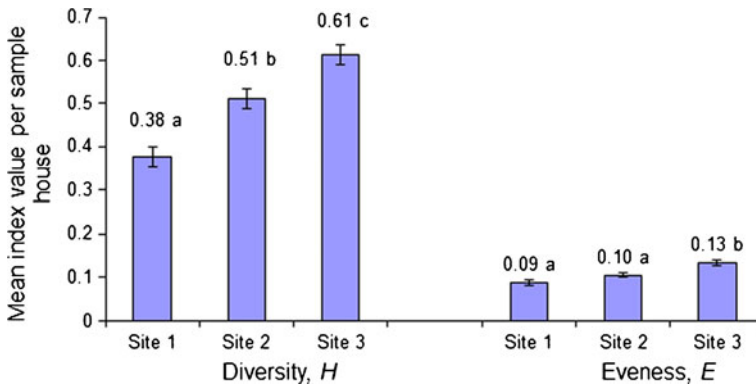


Fig. 4 Mean diversity and evenness indices averaged across all sample houses ($n=30$) at different aged housing sites (one, four, and eight years old) in Puerto Rico. Means followed by different letters are significantly different

measures ANOVA was used to determine whether there was a difference in the biodiversity measures, S , N , H , and E between the two bait types. Species richness (S) was found to be significantly different for each bait type ($F=8.76$; $df=2, 118$; $P=0.0003$). Comparison tests indicated that significantly more species were collected from sugar baits at Site 2 and 3 than from the peanut oil baits (Fig. 9). However, there was no significant difference between the species richness values calculated for sugar and peanut oil baits placed at Site 1. At all three sites, there was no significant difference in the abundance of ants (N) collected from the different types of baits ($F=0.53$; $df=2, 118$; $P=0.5913$).

Diversity (H) and evenness (E) indices calculated for bait type, nested within each site, were also significantly different (diversity: $F=3.30$; $df=2, 118$; $P=0.0402$; evenness: $F=3.30$; $df=2, 118$; $P=0.0403$). LSD tests comparing diversity indices indicated that the diversity index calculated for ants collected in sugar baits was significantly greater than those indices calculated for peanut oil baits in both Sites 2 and 3. However, there was no significant difference between diversity index values calculated for sugar and peanut oil

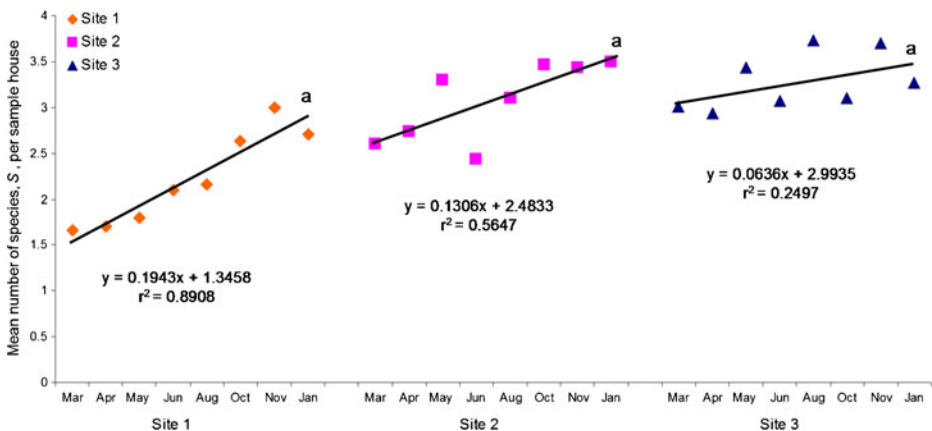


Fig. 5 Mean number of species (species richness) collected at each sample house ($n=30$) during each sample period (month) from the three sites in Puerto Rico. The regression line of each site is represented by the solid black line. The slopes of the regression lines were not statistically different

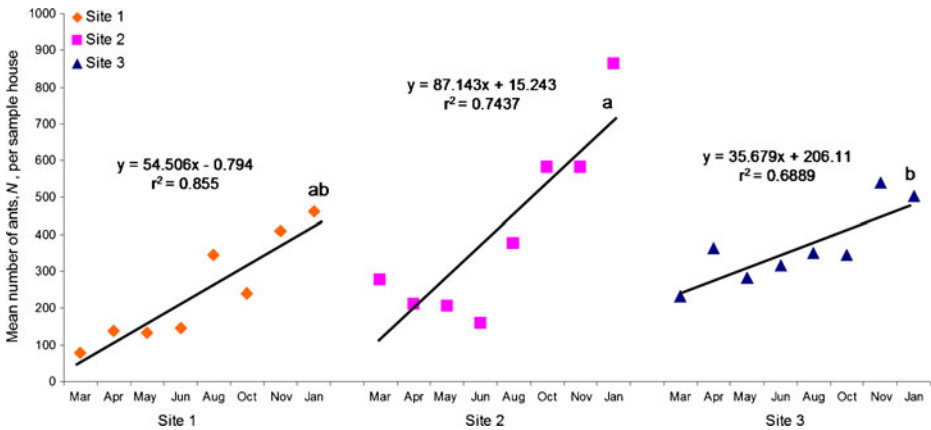


Fig. 6 Mean number of ants (abundance) collected at each sample house ($n=30$) during each sample period (month) from the three sites in Puerto Rico. The regression line of each site is represented by the solid black line. Statistically different slopes (at the $P<0.06$) are indicated by a different letter located at the end of the regression line

baits in Site 1 (Fig. 10). LSD tests comparing the evenness indices (E) calculated for the two bait types were found to be different only in Site 2 (Fig. 11). Within Site 2, the species evenness index calculated for sugar baits were significantly greater than that of the peanut oil baits (Tukey-Kramer, $P=0.0002$).

Discussion

Biodiversity measures of each site

There were measurable differences in ant biodiversity over the gradient of housing development ages. The observed trend of ant biodiversity increasing with increased housing

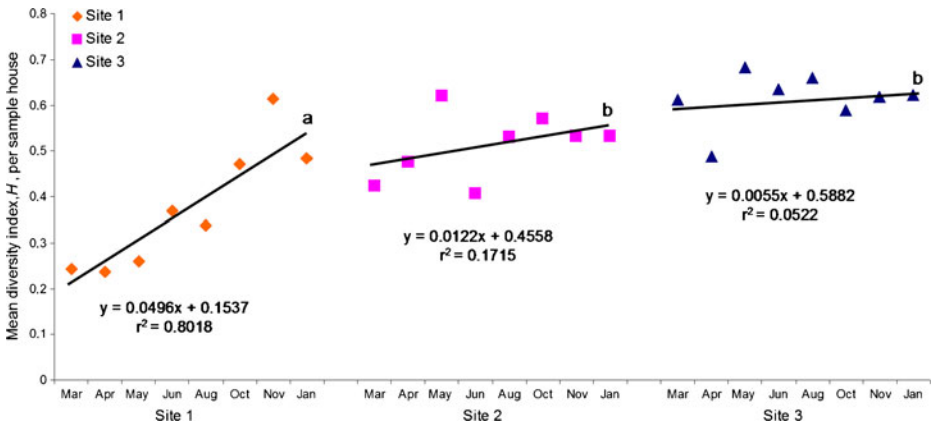


Fig. 7 Mean diversity index of each sample house ($n=30$) during each sample period (month) from the three sites in Puerto Rico. The regression line of each site is represented by the solid black line. Statistically different slopes are indicated by a different letter located at the end of the regression line

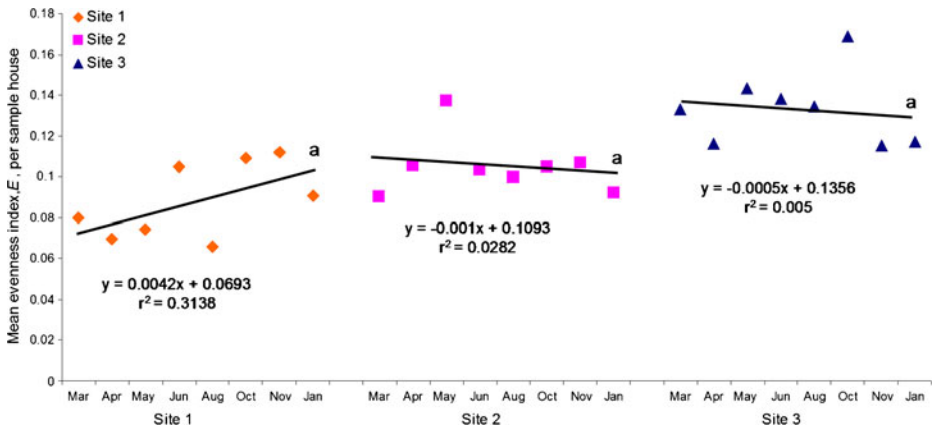


Fig. 8 Mean evenness index of each sample house ($n=30$) during each sample period (month) from the three sites in Puerto Rico. The regression line of each site is represented by the solid black line. The slopes of the regression lines were not statistically different

development age supported the hypothesis that biodiversity increases during urban succession. Osorio-Perez et al. (2007), came to a similar conclusion when they examined the succession of ant species in secondary forests of Puerto Rico. Osorio-Perez et al. (2007) found that early successional forests (0–5 year since last disturbance) had the least biodiversity while both mid and late successional forests (25–35 year and >60 year, respectively) were significantly more diverse. Although the mid to late successional forests had very similar species compositions, the mid-successional forest was actually found to have greater biodiversity (authors measured species richness) than even the late-successional forests (>60 year).

Similar to Osorio-Perez et al. (2007), Site 1 (the one year old site) in our study had the lowest overall biodiversity measures of the three sites, indicative of an early stage of succession (Figs. 2–4). Both Site 2 and Site 3 had greater richness and abundance values

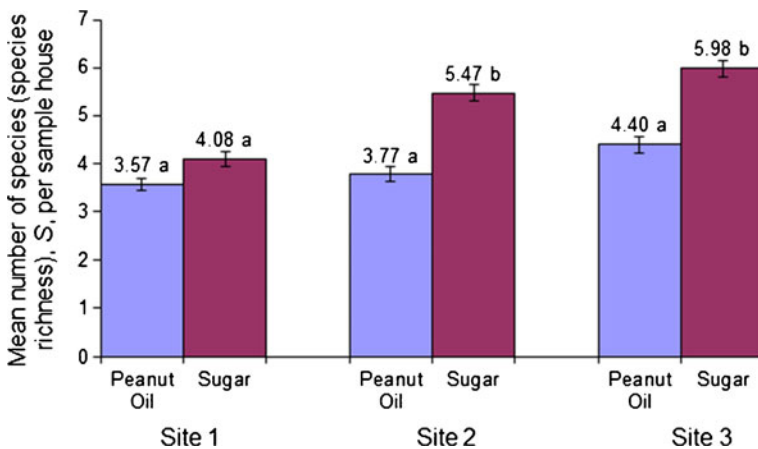


Fig. 9 Mean number of species (species richness) collected from sample houses ($n=30$) at different aged housing sites (one, four, and eight years old) and bait types in Puerto Rico. Means followed by different letters are significantly different

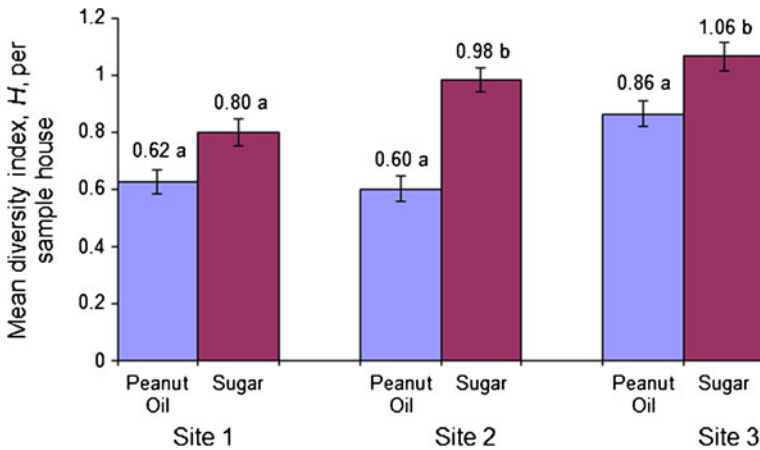


Fig. 10 Mean diversity index averaged across all sample houses ($n=30$) at different aged housing sites (one, four, and eight years old) and bait types in Puerto Rico. Means followed by different letters are significantly different

than Site 1, yet the total number of ants (abundance) and total number of species (richness) collected from Site 2 and Site 3 were not significantly different from each other (Figs. 2–3). As expected, the index values for diversity and evenness were greater for Site 3 than the other two sites. These greater index values are indicative of an environment in the later stages of succession.

Interestingly, Osorio-Perez et al. (2007) found the greatest ant species richness existed in mid-successional forests with species richness becoming reduced in late-successional forests. The reason for the greater richness in the mid-successional forests was due to the fact that these forests had greater food availability (due to more sunlight reaching the forest floor) and a greater number of habitat niches (more herbaceous plants instead of mature trees) than late-successional forests. In our study, both Site 2 and Site 3 had the greatest species

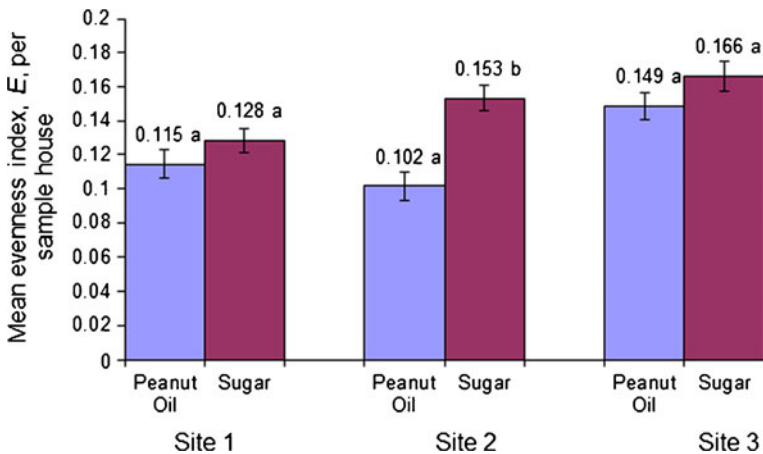


Fig. 11 Mean evenness index averaged across all sample houses ($n=30$) at different aged housing sites (one, four, and eight years old) and bait types in Puerto Rico. Means followed by different letters are significantly different

richness, although Site 3 had the greatest diversity index values (which include measures of both species richness and relative abundance). The high diversity index value calculated for Site 3 was most likely due to Site 3 having had the greatest time interval since the last disturbance (eight years post construction). Site 3 was also more environmentally complex than the other two sites (i.e. extensive landscaping, mature trees and shrubs, and man-made artifacts; personal observation). Similar studies on urban succession by MacKay (1993) and Majer (1983) also found that ant species invasion of disturbed sites usually occurred rapidly (within 8–10 years after the disturbance) with the number of established species increasing as the sites aged. Both the 1983 and 1993 studies concluded that as the time interval increased since the last disturbance, the number of plant and animal species (ants demonstrably) colonizing the site also increased.

In spite of the significant differences in richness, abundance, and diversity values between Site 1 and Site 2, evenness values were not significantly different between those two sites (Fig. 4). These similar evenness values indicated that the species in Site 1 and Site 2 had similar relative abundances. Additionally, the significantly greater evenness value for Site 3 indicated that Site 3 had a more even distribution of species abundances than Site 1 or Site 2. Because evenness tends to be reduced when a site is dominated by a few species (Roth et al. 1994), the reduced evenness values of Site 1 and Site 2 could be attributed to the presence of three dominant species (*Solenopsis invicta*, *Brachymyrmex sp.*, and *Pheidole sp.*). These three species accounted for over 75 % of the total number of ants collected from Sites 1 and 2. However, at Site 3, only one species had a large relative abundance (*Solenopsis invicta*, 46.37 %) while 10 other species had similar relative abundances (1–13 %). The large number of similar relative abundance values was responsible for Site 3 having the greater evenness index (Brown 2009). The greater species evenness in Site 3 also indicated that Site 3 represented a later successional stage than Sites 1 or 2. Similarly, Graham et al. (2004) found that at sites of light disturbance (representing a late-successional stage characterized by heavy vegetative ground and canopy cover), ant species evenness indices were significantly greater than indices calculated for sites with heavy disturbance (representing an earlier successional stage).

Monthly biodiversity measures

In our study, monthly changes in the biodiversity measures differed with housing development age. In other words, the time since disturbance at each site influenced how the biodiversity changed or did not change throughout the year. The relatively high R^2 values determined for the biodiversity measures in Site 1 indicated that month was a better predictor of the biodiversity in Site 1 than in Sites 2 or 3. Furthermore, the relatively low R^2 values for each biodiversity measure in Site 3, indicated that sampling month was a poor predictor of biodiversity in the oldest (more stable) site. This general trend of decreasing R^2 values from Sites 1 > 2 > 3 indicated there was less predictability in the biodiversity measures from month to month as the sites aged.

We hypothesized that there would be a positive correlation between month and the biodiversity measures in the early stage of succession (Site 1). This is because new species were moving into the environment and increasing their numbers. During later stages of succession (Sites 2 and 3) we expected fewer species additions to occur because most niches would be occupied. So the biomass of the sites would be near carrying capacity. This hypothesis was supported by the linear regression and contrast analysis which determined that with regard to diversity, Site 1 experienced the greatest overall increase over time.

However, it is interesting to note that there was no difference between the three sites with regard to species richness. Instead, there was a general trend of increasing monthly richness values throughout the test period in each site. This increase in richness may be attributed to the fact that the number of species collected from each house in the three sites increased as the site aged over the year. This increase in richness can occur if either more species move into the site, or if the species already present at the site spread out to more houses. In either case, an increase in the mean number of species present at an individual sample house would cause the richness of that sample house to increase. Brown (2009) found that new species additions were not common in any site during the test. However, the expansion of existing species to additional sample houses was documented in all three sites throughout the year (Brown unpublished data). Therefore, it was concluded that the overall increased richness observed over the test period was the result of species which were already in the site, expanding their foraging range to additional houses.

There was also a general trend of increasing ant abundance within each site throughout the test period. Because sample means in March were relatively low when compared to later months of the year, we concluded that these increases in abundance were attributed to an annual colony growth cycle (Holldobler and Wilson 1990). The greatest abundance values were calculated for the period between October and January, indicating the onset of the breeding season for the colony in which colony numbers reach a peak (Holldobler and Wilson 1990). The most likely environmental factor related to the maximum colony abundance during this time is the onset of the rainy season in Puerto Rico (August through December). Increases in colony growth due to the onset of the rainy season would also explain the increased richness values as a larger number of ants would cause foraging ranges to expand and thus, ants were collected from a greater number of houses throughout the sites (Brown unpublished data).

Interestingly, the slope of the regression line for abundance values in Site 2 was significantly greater than the slope of the regression line for Site 3 at the $P \geq 0.06$ level. The greater slope of Site 2 indicated that the rate in which ant abundance increased over the year was greater in Site 2 than in Site 3. This significant difference in the rate of increasing ant abundance suggested that these sites represented different stages of succession. The large increases in ant abundance in Site 2 indicated that resources were still available to support additional biomass. The general increases in ant abundance in Site 3 appeared to be much more stable over the year. Site 3 likely had fewer resources available to support additional biomass because most resources were already at carrying capacity. The possibility that Site 3 was already at carrying capacity may have prevented the production of a large number of additional ant workers in Site 3. The hypothesis that Site 3 was at or near carrying capacity was also supported by rank-abundance curves (Brown et al. 2011) and diversity indices.

The regression analysis for diversity indices also indicated that diversity increased with each sampling period in all sites. Similar to the richness analysis, the positive diversity slopes were due to the species expanding throughout the site and increasing their numbers at each house within the sites. Although all three sites had positive slopes (indicating increasing diversity), the slope of Site 1 was significantly greater than Site 2 and 3. The greater regression coefficient for Site 1 implies that the ant species were expanding their range and numbers more rapidly throughout Site 1 than in the other two sites. Because Site 1 was recovering from a recent disturbance (construction of the development), we would expect new and hardy species (*Solenopsis invicta*) to have little competition for territory, and to rapidly increase their range over a period of several months.

Sites 2 and 3 had more consistent measures of diversity over the test period, indicating little change in the number and abundance of species collected from one sampling period to

the next. The relatively flat slope of the regression line indicated that no new species were moving into the older sites, and those species which were already present were no longer expanding their range. The reason for this stasis in biodiversity was most likely due to the fact that there were few available resources in these fully inhabited sites. Similar to our study, Majer (1983) documented the rapid establishment of 29 new ant species in rehabilitated mines in Northern Australia within 1.5 years. However, at mining sites that had been rehabilitated for longer periods (between 3.5 and 7.5 year), the addition of new species were much less frequent (in one site only three new species were collected over a two year period). Both the current study and the Majer (1983) study provide evidence that the ant species complex in older sites is more stable than sites which have been more recently disturbed.

The regression and contrast analysis for species evenness indices indicated no significant difference between the three sites. Therefore, the rate at which evenness was changing over the test period was the same across all three sites. Although the rates of change were not significantly different, the slope for Site 1 was slightly positive while the slopes for Sites 2 and 3 were slightly negative. These differences in slopes suggested that species evenness was increasing in Site 1 as the year progressed. However in Sites 2 and 3, the negative slopes suggested that evenness may have been decreasing over the year. The ability of some species (e.g. *S. invicta*; Tschinkel 2006) to produce a greater number of workers than other species over the course of the year could be the cause of this negative correlation between evenness and the month of the year in the older sites. However, it must be considered that the slopes for the three sites were not significantly different, and the R^2 values for Sites 2 and 3 were very low indicating that the slope of the regression lines were not necessarily good predictors of the evenness trends.

Bait preferences

Newly disturbed habitats have few resources, and species that establish these barren environments must be hardy enough to make use of the resources that are available. In other words, early successional habitats have less environmental complexity (Molles 2005) and successful pioneer species must be generalists with regard to their food and shelter needs. Not surprisingly the dominant pioneer ant species in Site 1, the red imported fire ant, is a well documented generalist feeder that prefers to nest in disturbed habitats. As habitats increase in complexity, a greater variety of food resources become available. Habitats in the later stages of succession tend to have greater environmental complexity with regard to food and nesting resources (Molles 2005), and are able to support a greater diversity of ant species. Therefore, these later stage habitats are able to support ant species with specialized nesting and feeding preferences. Sites that contain species known to have specialized feeding or foraging habits are indicative of a habitat that has a relatively high level of food source diversity as well as habitat complexity.

MacKay (1993), studied the ant species succession at a nuclear waste site in New Mexico. MacKay (1993) determined that five of the pioneer ant species that established the site were scavengers and generalist feeders. MacKay (1993) referred to these generalist species as “weedy” species that could survive well on limited resources. Similar to MacKay (1993), Majer (1983) also identified many generalist, ground-foraging ant species in the early stages of bauxite mine rehabilitation.

In contrast to the generalist species found in newly and profoundly disturbed habitats, ants with specialized feeding preferences tend to colonize habitats that are in the later stages of succession where more resources are available. In our study, species bait preferences

within the three different sites were indicative of the resources available in those sites. At Site 1, there was no difference in the richness values calculated for ants feeding on sugar or peanut oil baits. Therefore, we could not identify a feeding preference among ant species at Site 1, and concluded that those species were most likely generalist species. Because Site 1 was the most recently disturbed of the three sites, it represented the earliest stage of succession characterized by the recent invasion of founding species. The plant fauna of Site 1 was extremely limited with only grasses and other weedy plant species observed inhabiting the site. No other (flowering) plants were observed. However, in pitfall traps placed throughout Site 1, we collected additional small arthropod species (beetles, millipedes, spiders) which may have provided additional food sources for newly established ant colonies (Brown 2009). These limited plant and animal food resources at Site 1, could only support generalist feeders and not those species that would require a more specialized diet (Smith 1965; Majer 1983; Klotz 2004).

At Sites 2 and 3, the species richness and diversity indices calculated for the sugar baits were significantly greater than those calculated for peanut oil baits. This preference for sugar based foods most likely developed after the establishment or intentional planting of flowering plants which provide nectar, or ornamental plants with extrafloral nectaries in the sites. The presence of these plants throughout the landscaping allowed for additional sweet feeders, such as *P. longicornis* and *T. melanocephalum* (Klotz 2004), to become established.

Overall, the richness and diversity indices calculated for baits at Site 1 indicated that the founding species (*S. invicta*; *Brachymyrmex*) were generalist feeders. However, as succession progressed (at Sites 2 and 3), the subsequent ant species (e.g. *P. longicornis*) were more specialized in their preference for carbohydrate based food sources (Majer 1983; Majer and Brown 1986). The gradation from the generalist species in Site 1, to the more specific sweet feeders in Site 2 and 3 are indicative of the greater number of food resources (complexity) available within those sites.

Conclusions

The results of this study (i.e. measuring changes in ant biodiversity over time since disturbance) documented major differences in the biodiversity across housing developments of different ages. While there may be many factors influencing these differences in biodiversity (e.g. seasonal rainfall), we determined the most significant influence on biodiversity was housing development age (the time since the last disturbance). As the age of the housing development increased, we observed that the environmental complexity of the site increased. Most importantly, we documented that the overall ant diversity of the site also increased with housing development age. Although the houses were subjected to continual disturbances due to human activities, these impacts were small in scale and tended to increase the food resources and nest sites (addition of trash containers, landscaping, and pet waste) rather than reduce them. Homes and properties at the older sites (Sites 2 and 3) had greater environmental complexity than in the one year old site. Thus, the older sites provided a greater diversity of microhabitats (niches) and food resources. Ant species diversity has been determined to be an excellent indicator of the overall diversity of an environment (Majer et al. 1982; Van Schagen 1986; Roth et al. 1994; Osorio-Perez et al. 2007). Therefore, the increase in ant biodiversity measures from Site 1 to Site 3 correlated with the disturbance gradient and the increasing environmental complexity of each site as it increased in age. Thus the one year old site also represented an early stage of succession and the two older sites were indicative of the later stages of succession.

Overall, this study determined that species succession in Puerto Rican housing developments occurs relatively rapidly. The ant biomass accumulation and calculated diversity indices for each site along the disturbance gradient indicated that these urban housing developments were stabilizing with respect to succession within eight years. Note that Majer (1983) and MacKay (1993) also found that ant succession on rehabilitated land occurred within 7.5 and 10 years, respectively. The species richness and diversity indices calculated for Site 1 had increased to a value similar to those for Sites 2 and 3 by the end of the test period. The rapid establishment of the ant species was attributed to the invasion from the surrounding habitats, and the invasive characteristics of the majority of species collected (Brown 2009). Because there was no significant difference in richness values for Site 2 and 3, it was determined that either all available niches were filled within four years of the initial disturbance or that there were no additional ant species within the surrounding areas that were available, or capable of establishing in these housing developments.

Acknowledgements We would like to thank those individuals who contributed to this research project. Donald Bieman, of the San Pedrito Institute, helped us to choose the research sites and provided on-site assistance collecting samples. Alan Harms, of Mycogen Seeds Research Station, supplied us with weather data for the area. Tim McCoy, David Moore, Hamilton Allen, and Tamara Sutphin, of the Dodson Urban Pest Management Laboratory, also contributed their assistance processing the samples. We would also like to thank Roy Snelling and Juan Torres for providing a copy of their manuscript on the ants of Puerto Rico for ant identification. Additionally, Matthew Buffington and Mark Deyrup offered their taxonomic assistance with ant identifications. Dr. Eric Smith, of the Virginia Tech Department of Statistics, contributed a great amount of time and guidance with the statistical analysis.

Ethical standards The authors declare that the experiments comply with the current laws of the country in which they were performed.

Conflict of interest The authors declare that they have no conflict of interest.

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