

# Intermediate disturbance promotes invasive ant abundance



Merav Vonshak\*, Deborah M. Gordon<sup>1</sup>

Department of Biology, Stanford University, Stanford, CA 94305-5020, USA

## ARTICLE INFO

### Article history:

Received 10 October 2014

Received in revised form 19 March 2015

Accepted 21 March 2015

Available online 21 April 2015

### Keywords:

*Linepithema humile*  
Urban–rural gradient  
Biological invasions  
Urban ecology  
Biodiversity

## ABSTRACT

Urban habitats are undergoing a faunal and floral homogenization process worldwide. We investigated how such homogenization influences ant communities. We monitored ant species richness and abundance in natural, semi-natural, urban, and agricultural habitats for one year, along an urban–rural gradient in the San Francisco Bay Area, and examined which human-related and other environmental variables most affect ant distribution. We investigated whether alien ant species have an advantage in human-modified habitats. We found that distance from buildings was the most important factor affecting ant distribution. In total, we recorded 17 ant species, of which four were non-native. Native ant species richness was highest in natural habitats, and alien species richness was highest in urban habitats. Remarkably, in a sample of 19,450 ant workers at food baits, the highest ant abundance across all seasons was in the semi-natural habitat where usually only the invasive Argentine ant (*Linepithema humile*), representing 81% of all ants seen at baits, and the native winter ant (*Prenolepis imparis*) were present. Agricultural habitats had a surprisingly high number of native and alien species. It appears that the invasive Argentine ant creates a favorable ecological community in semi-natural environments, where they compete successfully with the native species, and do not face the increased competition with other alien species that they encounter in urban habitats. Even well protected natural habitat may be favorable for invasive species, due to its proximity to human disturbance.

© 2015 Elsevier Ltd. All rights reserved.

## 1. Introduction

One of the most significant global ecological changes of the 20th century is the shift of human populations from rural to urban dwelling. While in 1900 only 10% of the population was living in cities, today it is more than 50% (Grimm et al., 2008). During the urbanization process, cropland, pastures, and forests were converted into highly modified urban and suburban environments (Ehrensfield, 1970), resulting in high densities of food, water, energy, pollution, and garbage (Godron and Forman, 1983; McDonnell et al., 2008). These long-lasting, extreme habitat modifications (Marzluff and Ewing, 2001) lead to biological homogenization through habitat degradation and species loss (McKinney, 2006). In addition, the proportion of species that are invasive is higher in cities than in rural or forest areas (Rebele, 1994; Mack et al., 2000). However, urban habitats now account for an important part of the world's biodiversity, for example when they contain indigenous plant species (McDonnell and Hahs, 2013).

Among alien species, occurring outside of their natural range, invasive alien species become established and threaten native biological diversity (IUCN, 2000), and are one of the greatest threats to biodiversity worldwide (Mack et al., 2000). Many opportunistic mammals and bird species, native and non-native alike, thrive on the high resource availability in human modified habitats (i.e., Fedriani et al., 2001). Ants are using the same anthropogenic resources to create large populations that have high impact on their ecosystem.

Ants are an important component of natural ecosystems. Invasive species of ants often have substantial impact on many other organisms, including plants, which in turn can lead to substantial agricultural damage (Holway et al., 2002). Urbanization may change ant species composition (Philpott et al., 2010), through the loss of nesting habitat, decreased soil moisture, and soil disturbance such as tilling (Uno et al., 2010). The loss of native species might facilitate the establishment of non-native species (Holway and Suarez, 2006; Carpintero, 2003).

The only invasive ant in our study system is the Argentine ant, *Linepithema humile*, first identified in California in 1907 (Newell and Barber, 1913), and today the most abundant species in many urban, agricultural, and even natural wetlands in northern California (Ward, 2005). *L. humile* displaces almost the entire

\* Corresponding author. Tel.: +1 650 725 6791.

E-mail addresses: [mvonshak@stanford.edu](mailto:mvonshak@stanford.edu) (M. Vonshak), [dmgordon@stanford.edu](mailto:dmgordon@stanford.edu) (D.M. Gordon).

<sup>1</sup> Tel.: +1 650 725 6364.

non-cryptic ant fauna in its invasive range, excelling in food discovery (Sanders et al., 2003; Human and Gordon, 1996; Holway, 1999; Gordon and Heller, 2013), and also affects other invertebrates, vertebrates, and plants (Human and Gordon, 1997; Holway et al., 2002).

Urban–rural gradients provide an opportunity to study the effect of human impact on natural processes such as species dispersal or biotic homogenization, while measuring human influence directly (McDonnell and Pickett, 1990). Here we examine the factors affecting native and invasive ant distributions along a gradient of human disturbance in the San Francisco Bay Area, California (following Blair, 1996). The Bay Area has undergone major developmental pressure in the past few decades, but pockets of native plant communities remain. It is likely that alien ants are initially introduced into and establish in urban areas where propagule pressure and survival rates are higher, and competition with native species is lower (Carpintero, 2003). Natural habitats thus serve as a native species source, while urban habitats serve as a non-native species source. In addition, it is likely that the agricultural sites we studied, an organic struck farm and a tree nursery, serve as an alien species source, as potted plants are one of the most common methods of invasive ants' spread (Holway et al., 2002), while the abundant plant parasites provide the ants carbohydrate-rich food.

Our main hypothesis was that alien ant species have an advantage in disturbed habitats, as well as in agricultural habitats, while native species have an advantage in preserved habitats. This would lead to higher abundances and species richness of native species in preserved habitats, and higher species richness of alien species in urban habitats (illustrated in Fig. 1). We expected that the outcome would depend on conditions, and considered two possibilities. (1) Invasive species abundances may peak in urban habitats, if they benefit from garbage and suburban gardening (Fig. 1A), or (2) invasive species abundances may peak in semi-natural habitats if they manage to eliminate competing native species and find alternative resources (Fig. 1B).

## 2. Methods

### 2.1. Study sites

The study was conducted in Silicon Valley, in the San Francisco Bay Area of northern California. We set a non-linear gradient along an 8 km grid of human disturbance between Jasper Ridge Biological Preserve (JRBP) and the business district of the city Palo Alto. Eight out of a total of 12 sites were on Stanford University land, all of which have undergone some development in the past 100 years (Blair, 1996; Blair and Launer, 1997). Habitat type at all sites was similar, an oak-dominated community that included coast live oaks (*Quercus agrifolia*) and/or valley oaks (*Q. lobata*) and grassland. At urban sites PA 8–10, in downtown Palo Alto, there are no grasslands, so plots with cultivated lawns were chosen instead. At each site we established three 25 × 25 m plots, located at least 200 m apart. The two most urbanized sites, Urb. 9 and Urb. 10, had three 4 × 150 m sidewalk plots (Fig. B1).

Compared with other sites, as expected, natural sites were most distant from human disturbance and had the least human intervention. Each of the natural sites was paired with a semi-natural site, within 400–860 m, in close proximity to a building, with other similar habitat attributes (Table 1, additional info at Table B1). One of the agricultural sites was at Hidden Villa (Agr. 12), an educational organic farm 5 km distant from the nearest site. Agr. 12 plots were extensively managed; one plot (#3) was converted into a plant material dumpsite after about 9 months of survey. We

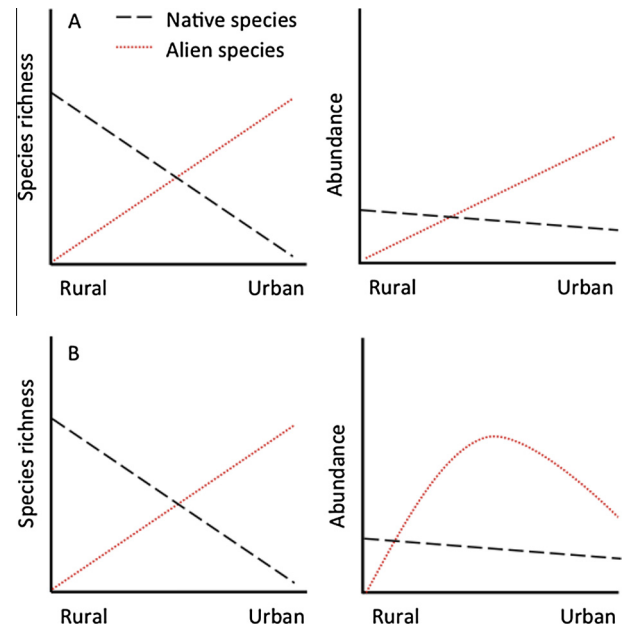


Fig. 1. Hypotheses for ant abundance along urban–natural gradients: (A) alien species abundances peak at urban sites and (B) alien species abundances peak at semi-natural sites.

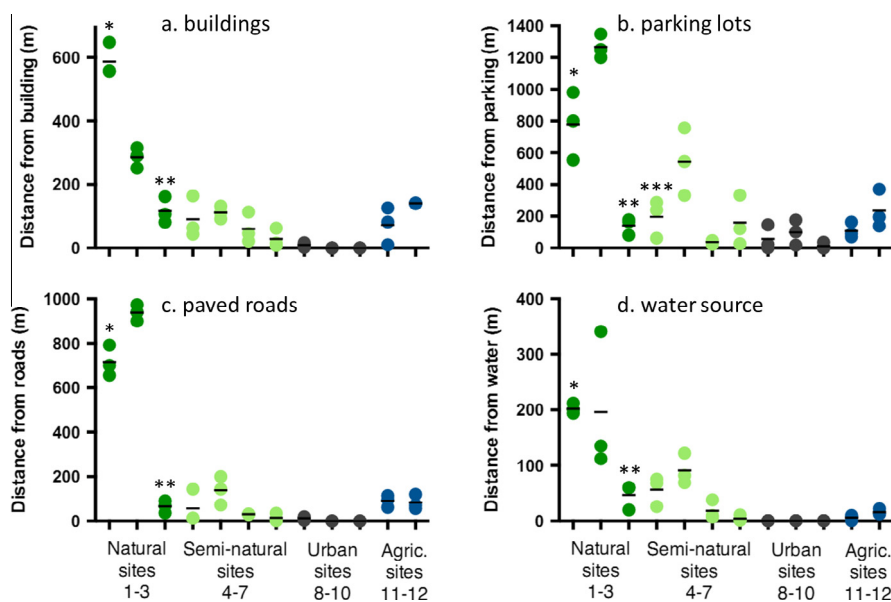
compared results among the 4 types of land use (Nat., SemN., Urb., and Agr.), and, in some cases, among all 12 sites.

### 2.2. Ant survey

We surveyed ants 12 times, once a month for one year, from spring 2011 to winter 2012. We defined seasons as: Spring: April–June, Summer: July–early September, Fall: late September–December, Winter: January–March.

In each plot we estimated ant species richness and abundance by using three methods. (1) Visual search. Visual search was conducted by MV only, and was performed for 15 min, by systematically surveying the entire plot, searching on the ground, under stones and logs, and on vegetation. (2) Bait stations. Bait stations consisted of a 5 cm diameter cardboard disc, with honey and tuna fish, a mixture of carbohydrates and protein as bait (Human and Gordon, 1996). Four baits were placed at the corners of each plot, and were checked after 30 min. In a preliminary study we used similar baits at the same plots, and found no significant difference among 15, 30 min and 120 min intervals. (3) Beating vegetation. At each plot, we chose 3 plants and struck each plant 10 times with a stick over a beating sheet. The selected plant species were the dominant ones at the plot. In plots Urb. 9 and Urb. 10 we did not strike plants, as most of the plants were on private property.

All ants were counted, up to a maximum of 100 workers, and identified at the site, or preserved in 90% ethanol and taken to the laboratory for further identification. Three of the ant taxa were identified to the genus level only (*Camponotus*, *Crematogaster*, and *Temnothorax*), as species identification in the field was not possible, and we did not want to influence biodiversity by removing large numbers of ants from the sites. The cryptic species *Solenopsis molesta* and *Hypoponera* sp. were found only once during the entire study. Since our sampling methods were not suitable for detecting cryptic species, we decided to omit these species from all analyses. Only the Argentine ant, *L. humile*, could be regarded as an invasive species in this study, as it is the only species found in semi-natural (or natural) habitats. The other three alien species were confined to urban and agricultural habitats.



**Fig. 2.** Distances of study plots from buildings, roads, parking lots, and water sources by site (1–12). Black lines represent average value per site, asterisks represent significant differences between sites, colors represent land uses (dark green = Nat., light green = SemN., grey = Urb., blue = Agr.). Graphs differ in the distance scale represented on the y axis.

**Table 1**

Full site list, including general and specific land use classification and location (see Fig. B1 for a map, and Table B1 for more details).

Site name	Land use	Location	Specific land use
Nat. 1	Natural	Jasper ridge	Biological preserve
Nat. 2	Natural	The dish	Academic reserve
Nat. 3	Natural	Stanford campus	Oak park
SemN. 4	Semi-natural	Jasper ridge	Biological preserve
SemN. 5	Semi-natural	The dish	Academic reserve
SemN. 6	Semi-natural	Stanford campus	Oak park
SemN. 7	Semi-natural	Stanford campus	Residential neighborhood
Urb. 8	Urban	Palo alto	City parks
Urb. 9	Urban	Palo alto	Residential neighborhood
Urb. 10	Urban	Palo alto	Business district
Agr. 11	Agricultural	Boething tree land	Plant nursery
Agr. 12	Agricultural	Hidden villa	Organic farm

### 2.3. Environmental data

Using Bing Map Hybrid 2010 aerial photos on ArcMap 10.0, we measured land cover of trees and shrubs, grassland or lawn, unpaved roads, and impervious area (paved road or pavement). For each plot we measured distance from disturbances such as buildings, roads, street parking or parking lots, and water sources. We measured air and ground temperature and humidity every 10 min using i-button data-loggers during baiting sessions, placed on the ground and on vegetation at about 0.5–1 m height (Hygrochron i-Buttons, Maxim, Dallas, TX). Canopy cover photos and soil characteristics were used in summer 2012 to measure human disturbance at each plot. Average canopy openness percentage, expressed as the proportion of sky hemisphere not obscured by vegetation or buildings when viewed from a single point (Jennings et al., 1999), was analyzed from hemispherical canopy photographs taken using a digital camera (Nikon Coolpix 4500, 4MP) with a fisheye lens (fisheye converter FC-E8 0.21×). Five pictures were taken at random locations at each plot, with the camera placed in a horizontal position on a tripod at a height of 1.1 m. Photos were analyzed using Gap Light Analyzer (GLA) free software (Frazer et al., 1999). The average soil penetrability per

plot was measured by releasing a 25 cm stake into a 1 m pipe at 10 random points per plot and measuring how deeply the stake was embedded into the soil (as in Jones et al., 2006).

In order to compare soil attributes among sites, we collected soil samples from five randomly located points within each plot (following Jones et al., 2006). At each sampling point we collected two 100 g samples: from depths of 0–5 cm and 5–10 cm; each group of five random samples was mixed together. Soil pH was measured at the same day in the lab, after crushing large soil particles and removing stones and large pieces of organic matter. 20 g soil was mixed with 40 g DI water, and pH was measured after 10 min using indicator paper. To calculate soil humidity, the rest of the 500 g sample of soil was weighed before and after it was air-dried for a week. To measure soil organic content, a subsample of 5–7 g dried soil was further grounded and oven-dried in a furnace for 16 h at 375 °C. We weighed the soil before and after being dried.

### 2.4. Statistical analyses

To test for difference among sites along the urban–rural gradient, among land uses, in distance from human disturbance, or in land cover, we used One-way ANOVAs followed by Tukey HSD post hoc tests, with either site or land use as a main effect categorical predictor. Similar tests were conducted for soil characteristics such as soil humidity and pH.

To test for differences in ant species richness and abundance among sites and land use types, we used main effect ANOVA and Tukey HSD post hoc tests, with season and land use type, or season and site as categorical predictors. To compare ant species richness among sampling methods, we used data collected from 10 sites using visual search, baiting, and beating vegetation.

To measure seasonal effects in ant activity patterns we compared ant abundances recorded from baits. For species richness we used the total number of times a species was observed, both by baits and visual search per sampling event (0 = the species was not found, 1 = the species was found using one method, 2 = the species was found using two methods). The number of ant workers at the bait stations was used as a measure of ant

abundance. We used Primer 5 software to calculate Shannon diversity index on the square root transformed data. We used Statistica 10 (StatSoft, 2011) for all statistical analyses.

We used ordination techniques to analyze the relationship among human-related environmental variables and ant occurrence. For the analyses, we used visual search and baits data only, from 12 sites. We pooled together the three samples per season. To determine whether human-related environmental variables affect ant distribution, we performed a redundancy analysis (RDA) using CANOCO 4.5 for Windows (ter Braak and Šmilauer, 2002). RDA is a constrained form of principal components analysis (PCA) (Lepš and Šmilauer, 1999), where the canonical ordination vectors are linear combinations of the response variables (Legendre and Legendre, 1998). We first performed forward selection using the 36 plots as co-variables. We used a Monte Carlo permutation test to test the significance of each variable, and then ran the model with the significant variables only, to determine the percentage of community composition explained by each variable (as in Lepš and Šmilauer, 2003).

### 3. Results

Ant communities differed greatly in diversity and richness across the urban to natural gradient. Using visual search and baits, we found that natural sites had the highest number of native species and no alien species, while the urban sites had the highest number of alien species, as well as some native species (Fig. 3). While natural sites had a diverse community of native species, most semi-natural sites had only two species, one native and one alien, and urban and agricultural sites had a mixture of native and alien species (Fig. 4). Agricultural sites had a surprisingly high number of native species and only 1–2 alien species. *L. humile* was very common at certain plots, while *Cardiocondyla mauritanica* was found infrequently. However, the average number of species was low, as most species were rarely found. In semi-natural habitats, *L. humile* was the only alien species found (Fig. 5). Using the plant-shaking method only in 10 of the 12 sites (excluding Urb. 9 and 10), we found similar trends in species richness across the gradient (Fig. B7).

Ant species richness showed a bimodal distribution, with one peak at the least disturbed natural habitats and a second peak at the most disturbed urban sites, while the lowest number of species was found in the semi-natural and agricultural habitats (ANOVA, with land use and season as factors:  $F = 41.7$ ,  $df = 3$ ,  $P < 0.0001$ ; Tukey,  $df = 425$ ,  $P < 0.005$ , Fig. 3). We found a total of 17 ant species, four of them alien. Most species were omnivores and ground nesting (Table 2). When we compared sites, the natural sites and Urb. 9 had the highest species richness, and SemN. 4 (JRBP) and Agr. 12 had the lowest number of species, with mostly *L. humile* present (main effect ANOVA, with site and season as factors:  $F = 21.6$ ,  $df = 3$ ,  $P < 0.0001$ ; Tukey,  $df = 425$ ,  $P < 0.005$ ). Agr. 12 had a few additional rare species. SemN. 5, located 0.8 km away from Nat. 2, but very close to buildings, had a higher number of species compared with other semi-natural sites. In this site, located in a reserve near buildings, we found *L. humile* more than once in only one of the three replicate plots, while the two other plots supported a diverse ant community.

The abundance of ants was highest at the semi-natural sites across all seasons, with the highest peak in summer (Main effect ANOVA,  $F = 34.28$ ,  $df = 3$ ,  $P < 0.0001$ ; Tukey,  $df = 1721$ ,  $P < 0.0001$ , Fig. 6). Remarkably, *L. humile* was responsible for most of this trend (with 15,779 workers estimated, accounting for 81.13% of the individuals observed at baits). Alien ants were less likely to share baits with any other species compared with native species (alien ant species at same bait 5 times, native ant species at same bait 35 times), and native and alien ants shared a bait only three times.

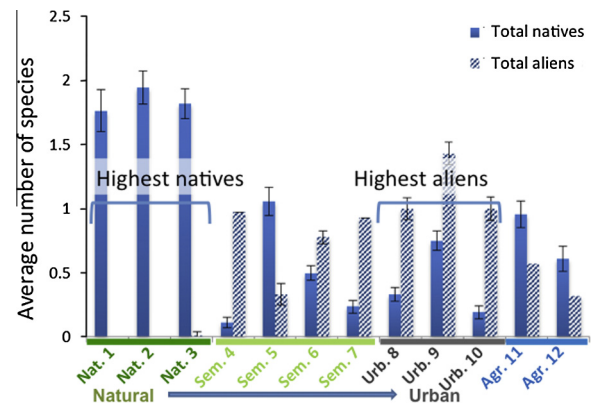


Fig. 3. Average number of occurrences of native and non-native ant species across sites. Error bars represent standard errors of the mean. *L. humile* is the only alien species found in semi-natural sites.

Seven ant species, all native, can be regarded as “urban avoiders”, as they were never found on urban sites; three species, all native, were “urban adaptables”, found in both disturbed and undisturbed sites; and four species, of which 3 non-native were “urban exploiters”, showing preference for human dwellings, (Fig. 7, after Blair, 1996. For analysis of species by site see Fig. B8). *Prenolepis imparis* was found in all habitat types, and *L. humile* was found in all but the natural habitats.

A total of 24,535 individual ants were counted in visual searches, 8841 ants were counted by shaking vegetation, and 19,450 ants were counted on baits (data from all 12 sites). Even though visual search and baiting detected a similar total number of species (15 and 14 respectively), visual search was most effective, detecting ants 625 times (13 species), compared with baiting (400, 12 species) and vegetation shaking (437, 9 species; numbers from 10 sites only, where all three methods were used). Visual search detected all species but two more often than the other methods. The number of species observed by each method was significantly different (One-way ANOVA:  $F = 51.39$ ,  $df = 2$ ,  $P < 0.0001$ ; Tukey,  $df = 1077$ ,  $P < 0.0001$ ).

Distance from buildings was found to be the most important human-related environmental variable to explain species distributions. Environmental variables, the sum of all canonical eigenvalues in the RDA model, explained 27.6% of the variability in ant community composition. The first canonical axis, correlated mainly with distance from buildings and with concrete cover, explained 22.1% of the total variability in the species data. The second canonical axis was correlated with grassland, tree and shrub cover. Forward selection of the environmental variables then showed three significant components: distance from buildings explained 14.4% of the variance ( $F = 23.8$ ,  $P = 0.002$ , Fig. 8. RDA test using Canoco 4.5) and was used to order the 12 sites on the non-linear gradient. Concrete cover and tree and shrub cover also had a significant effect on ant distribution, explaining 6% ( $F = 15.12$ ,  $P = 0.001$ ); and 3.1% ( $F = 9.47$ ,  $P = 0.007$ ) of the variance, respectively.

According to the RDA analysis, alien species were affected mostly by close proximity to buildings and high concrete cover, both of which were highest in urban environments. Most native species, by contrast, were found away from buildings where there was no concrete cover. Two native species, *Liometopum occidentale* (velvety tree ant) and *Prenolepis imparis* (the winter ant) showed a preference for high tree cover, while *Pheidole californica* showed a preference for grasslands. Surprisingly, *Tapinoma sessile*, the odorous house ant, was more likely to occur away from buildings.

Ant abundance was highest in the summer: 47.37% of the ants were sampled or counted during summer, 22.65% during fall, 19.4% during spring, and only 10.58% were sampled during winter

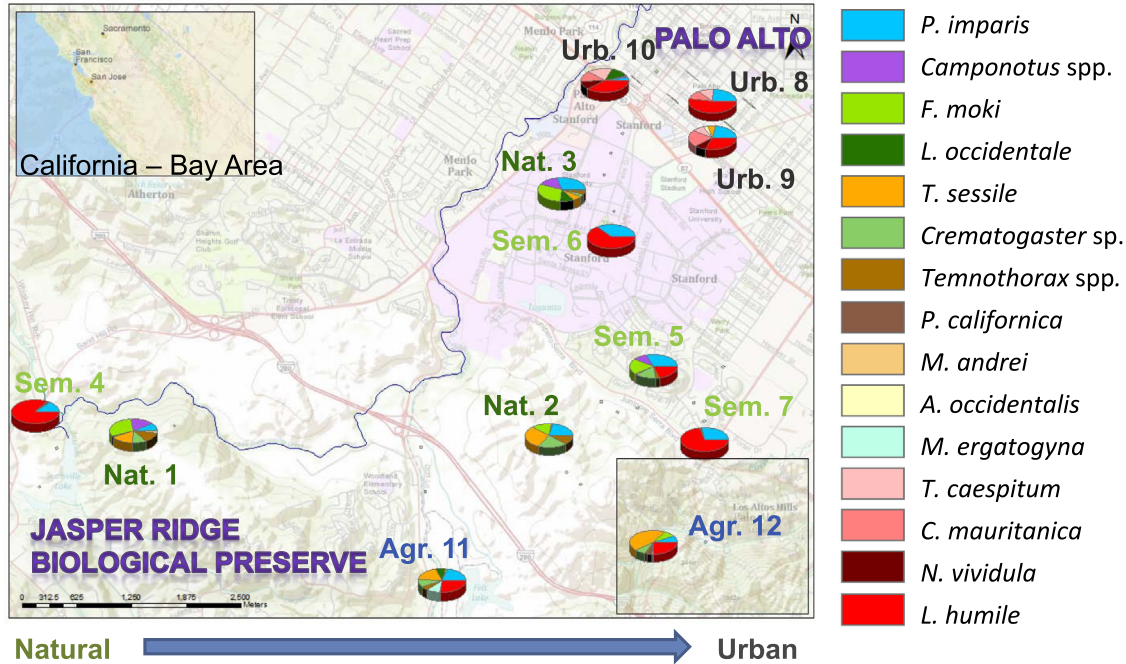


Fig. 4. Ant diversity across the urban–rural gradient: 1–12 research sites (Nat. = natural sites, SemN. = semi-natural sites, Urb. = urban sites, Agr. = agricultural sites). Pie charts represent ant occurrences per site (number of observations per species). Alien species indicated in pink and red.

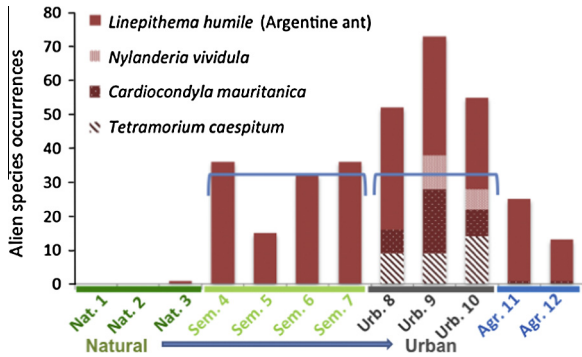


Fig. 5. Occurrences of alien ant species only, by species. Maximum possible value per species per site is 36 (12 months of observations, sum of three replicated plots).

(Main effect ANOVA, with season and land use as factors:  $F = 34.28$ ,  $df = 3$ ,  $P < 0.0001$ ; Tukey,  $df = 1721$ ,  $P < 0.001$ ).

The sites corresponded as expected to the environmental variables we measured. Distance from disturbance was greatest at the natural sites (Fig. 2. Buildings: One-way ANOVA,  $F = 14.8$ ,  $df = 3$ ,  $P < 0.0001$ ; Tukey,  $df = 32$ ,  $P < 0.01$ ; parking lots: One-way ANOVA,  $F = 9.2$ ,  $df = 3$ ,  $P < 0.001$ ; Tukey,  $df = 32$ ,  $P < 0.01$ ; paved roads: One-way ANOVA,  $F = 15.6$ ,  $df = 3$ ,  $P < 0.0001$ ; Tukey,  $df = 32$ ,  $P < 0.001$ ; water source: One-way ANOVA,  $F = 13$ ,  $df = 3$ ,  $P < 0.0001$ ; Tukey,  $df = 32$ ,  $P < 0.001$ ). At the site level, distance from buildings was greatest at the natural sites, and Nat. 1 and Nat. 3 were significantly different from the other sites (One-way ANOVA,  $F = 59.4$ ,  $df = 11$ ,  $P < 0.0001$ ; Tukey,  $df = 24$ ,  $P < 0.001$ ). Sites also differed with regard to distance from parking lots, where Nat. 1, Nat. 3, and SemN. 4 were significantly more distant (One-way ANOVA,  $F = 30.6$ ,  $df = 11$ ,  $P < 0.0001$ ; Tukey,  $df = 24$ ,  $P < 0.05$ ). Nat. 1 and Nat. 3 were significantly different by distance from roads (One-way ANOVA,  $F = 181.9$ ,  $df = 11$ ,  $P < 0.0001$ ; Tukey,  $df = 24$ ,  $P < 0.001$ ), and natural and artificial water sources (One-way ANOVA,  $F = 10.6$ ,  $df = 11$ ,  $P < 0.0001$ ;

Tukey,  $df = 24$ ,  $P < 0.001$ ). Further analysis of environmental variables is discussed in Appendix A, and illustrated in Appendix B.

4. Discussion

The level of urbanization had a substantial impact on ant communities, affecting ant abundance, species richness, and community composition. Ant species richness showed a bimodal distribution, with one peak at the natural sites, composed of native species only, and a second peak at the urban sites, with up to four alien species and some native species. This was consistent with our prediction that Invasive species abundances increase in response to human waste and suburban gardening (Fig. 1a). The semi-natural sites, on the other hand, had very low species richness, while

Table 2  
Ant species list – species documented during the current study.

Subfamily	Species	Common name
Myrmicinae	<i>Aphaenogaster occidentalis</i>	Gypsy ant
	<i>Crematogaster</i> sp.	Acrobat ant
	* <i>Cardiocondyla mauritanica</i>	
	<i>Temnothorax</i> spp.	
	<i>Messor andrei</i>	Harvester ant
	<i>Monomorium ergatogyna</i>	
	<i>Pheidole californica</i>	Big-headed ant
	<i>Solenopsis molesta</i>	Thief ant
	* <i>Tetramorium cf. caespitum</i>	Pavement ant
	Formicinae	<i>Camponotus</i> spp.
<i>Formica moki</i>		Field ant
* <i>Nylanderia vividula</i>		Crazy ants
<i>Prenolepis imparis</i>		Winter ant
Dolichoderinae	* <i>Linepithema humile</i>	Argentine ant
	<i>Liometopum occidentale</i>	Velvety tree ant
	<i>Tapinoma sessile</i>	Odorous house ant
Ponerinae	<i>Hypoponera</i> sp.	

Invasive species were marked with \*. More details about the species can be found in Ward, 2005.

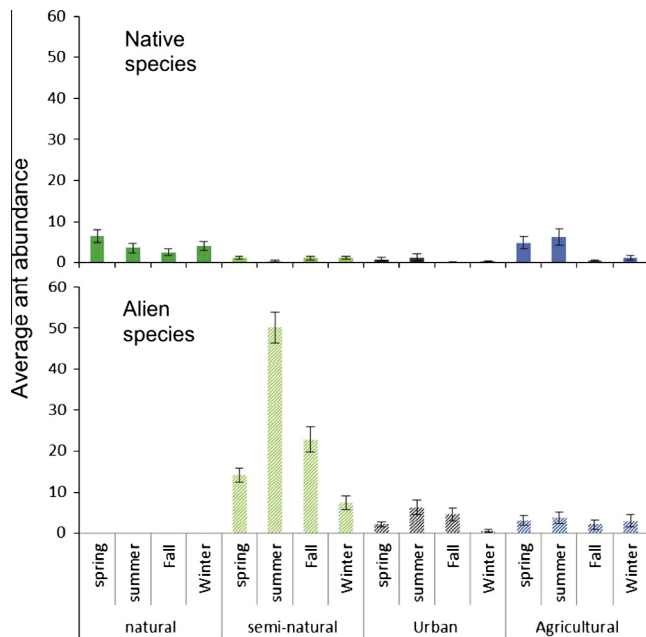


Fig. 6. Native (top) and alien (bottom) ant abundance, based on observations at baits, by land use type and season.

the agricultural sites had high species richness. Human disturbance had the opposite effect on native and alien species richness: while native ants were found more frequently in natural habitats, alien species were less frequent in natural habitats and common in disturbed ones. Remarkably, the highest ant abundance was found in semi-natural habitats, due to very high numbers of Argentine ants (*L. humile*) (Fig. 1b). Urban habitats may serve as an alien species source, promoting biological homogenization in nearby habitats.

Our results correspond with similar plant studies that found higher total (native and alien) species richness in urban habitats (Zipperer et al., 1997; Hope et al., 2003; Angold et al., 2006;

Grove et al., 2006), but in these studies, at least some of the non-native plant species, unlike alien ants, were introduced intentionally. Studies of other animal taxa have shown a very different pattern, with lower species richness and evenness in cities: urban stream flora and fauna (Paul and Meyer, 2001); vertebrates (Sullivan and Flowers, 1998); other organisms (McKinney, 2002); and even ants (Thompson and McLachlan, 2007; Uno et al., 2010). Studies by Blair and colleagues (Blair and Launer, 1997; Blair 1996, 2004) showed that bird and butterfly diversity peaked at intermediate human disturbance along an urban gradient, in the same region as the current study. The pattern observed in these studies could be attributed to higher habitat complexity, resource diversity and availability, and increased primary productivity, and also, as we suggest for ants, to reduced competition with invasive species (Blair, 1996; see also Marzluff, 2005).

We used the number of ant workers counted at baits as an abundance index (Fig. 6). Alien ants (mostly *L. humile*) were most abundant at the baits, and, surprisingly, they were most abundant at the semi-natural sites. We did not find any non-native species at the natural sites. Carpintero (2003) found similar patterns in Doñana National Park, Spain, where *L. humile* reduced species richness in semi-natural sites, displacing dominant and aggressive species. *L. humile* invaded California from South America over 100 years ago, and today its devastating impact on the local arthropod fauna is well documented (e.g., Sanders et al., 2001, 2003; Holway et al., 2002). Urban habitats provide many resources for *L. humile* and other alien species: water from irrigation; food from garbage; honeydew from exploding populations of garden plant pests; and nest sites in gardens and under paving stones. Populations of *L. humile* maybe reduced by competition with other alien species, present only at the urban sites. There may be a competition–colonization trade-off (Yu and Wilson, 2001), if *L. humile*'s queens are worse colonizers than others; species that are better colonizers might have an advantage in the patchy urban habitat while in the more homogenous semi-natural one, poor colonizers such as *L. humile* may be successful.

Alien ants, including *L. humile*, were less likely to share baits with other ant species than native species. Previous studies have also shown that only a few ant species were able to coexist with

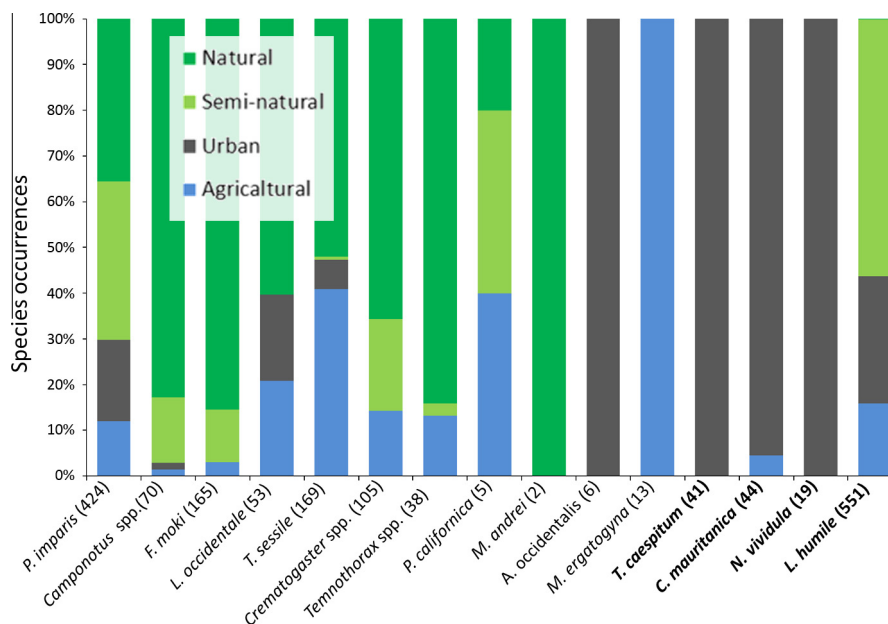
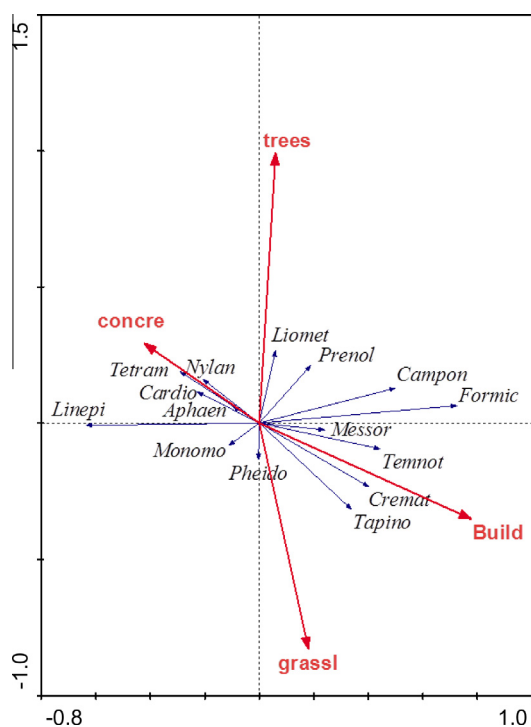


Fig. 7. Percentage of species observations by land use, normalized by number of sites per land use. Numbers in parentheses indicate the total number of observations per species. Alien species are indicated in bold.



**Fig. 8.** RDA (redundancy analysis) of ant occurrences, accounting for seasonal differences. Environmental variables are presented as arrows, and species as triangles. The length of the arrow is correlated with the relative importance of the variable. Species arrow points to the direction of the environmental variable affected it most. Ant species in black, human-related environmental variables in red: land cover percentage: concre = concrete cover, trees = tree cover, and grassl = grassland cover; build = distance from buildings (e.g., the species *Crematogaster* is projected close to the arrow “Build”, meaning that it is actually found away from buildings). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

*L. humile*, possibly by avoiding confrontation; these were characterized by small nests and submissive behavior (Carpintero, 2003; Abril and Gómez, 2009; Roura-Pascual et al., 2010). In our study, by contrast, the only ant species other than *L. humile* found in semi-natural habitats more than twice was *P. imparis*, a species that interacts aggressively with *L. humile* (Sorrells et al., 2011).

Our study shows that, unlike other taxa (Blair, 1996), many ant species, native and alien alike, found urban sites attractive. Interestingly, four ant species were “urban exploiters” with a preference for urban habitats. Three of them were alien species. The fourth species was a rather rare native species, *Aphaenogaster occidentalis*, found only in the city in the current study, although known from at least one nearby natural habitat (Sanders et al., 2001). Another uncommon native species, *L. occidentale*, was found to be an “urban adaptable”, found in urban habitats among others. This arboreal species was found in three out of the four habitats, including a nest on a tree in the middle of the business district of Palo Alto. It seems that certain native species can maintain insulated populations even in the most disturbed sites, resulting in overall high species richness. The vast majority of native ant species (7 species) were found to be “urban avoiders”, showing a clear preference for habitats outside urban areas.

The ant communities found in agricultural habitats were quite different from those elsewhere. These were the only sites where native species other than *P. imparis* were often found together with *L. humile*. Surprisingly, most native species did not avoid agricultural sites, and some even showed a strong preference for them; for example, *Monomorium ergatogyna* was found only in agricultural sites.

The native odorous house ant, *T. sessile*, has the widest distribution of all ants in the US, occupying a wide variety of habitats (Fisher and Cover, 2007). We found it in all habitats, although it was very rare in the semi-natural habitat. It was most abundant in the agricultural sites, and in the plant nursery it was frequently found together with *L. humile*, even though these species are strong competitors (Ward, 2005). Both species include homopteran honeydew in their diet (e.g. Ward, 2005; Fisher and Cover, 2007), and may have agricultural impact. *P. imparis* was common in all four land uses, and was the only species found across all sites, regardless of *L. humile* presence. Interestingly, despite their similar ecological requirements, *P. imparis* and *L. humile* are known to be associated (Fitzgerald and Gordon, 2012).

We found buildings to be the most important human-related environmental factor affecting ant distribution. Previous studies have shown this for *L. humile* (Suarez et al., 1998; Holway and Suarez, 2006; Bolger, 2007; Fitzgerald and Gordon, 2012; Fitzgerald et al., 2012). In addition to providing a source of propagules (Fitzgerald et al., 2012), buildings may provide an escape from unfavorable weather conditions in both winter and summer, as ants take shelter in buildings in cold and rainy winter conditions, as well as hot and dry conditions, in the San Francisco Bay Area (Gordon et al., 2001). This may explain why *L. humile*'s distribution was not correlated with soil moisture in this study, in contrast with previous studies (e.g., Holway and Suarez, 2006); although soil moisture was highest at the urban sites, at the semi-natural sites ants could have used water from irrigation or from inside buildings.

Not all natural habitats are low-quality habitats for *L. humile* populations. Both Bolger (2007) and Fitzgerald and Gordon (2012) described *L. humile* populations near suburban edges as sink populations, where ants migrate from a high-quality habitat, the suburban habitat, to the lower-quality natural habitat. However, we show here that natural habitats differ depending on distance to buildings. Comparing natural habitats, far from buildings; and semi-natural habitats, similar in most characteristics, such as flora and fauna, and soil, but in close proximity to buildings, we found a strong difference in ant abundance, species richness, and community composition between the natural and the semi-natural habitats.

We suggest that in semi-natural habitats, lack of interspecific competition with other alien species, in combination with high resource availability from oaks, while staying close to buildings, creates the most suitable habitat for *L. humile*. These conditions promote large sizes of *L. humile* colonies, allowing them to outcompete and displace most native ant species. In urban habitats, high resource availability promotes high ant species richness, while interspecific competition controls their population sizes. In nearby semi-natural habitats, resource availability is lower, excluding most of the alien species that depend on garbage and other human-derived products in the urban habitat. *L. humile*, on the other hand, utilizes honeydew from aphids and other homopterans in live oak trees (Tillberg et al., 2007) that are very abundant in the semi-natural habitats. Trails of thousands of workers forage on these trees, especially during the summer. In the urban sites, alien species, other than *L. humile*, were never observed foraging in the oak trees.

We found that although some natural habitats in the midst of highly developed areas seem to be in relatively good condition, they are threatened by invasive species due to their close proximity to disturbance. These semi-natural habitats may support vulnerable flora and fauna, but they also may support a limited number of invasive species that compete with native ones, providing the invasive species with easy access to nearby natural habitats. The size of the natural or semi-natural habitat might be important, as larger areas might be less vulnerable to edge effects

(Fitzgerald et al., 2012). The accelerated expansion of urbanized area makes it crucial for conservation to learn which factors promote alien species in urban and semi-natural habitats (Koh and Gardner, 2010).

## Acknowledgements

We would like to thank C. Mendenhall, A. Dosmann, and two anonymous referees for their useful comments on the manuscript. We would like to thank the following field and lab assistants: I. Smith, S. Beder, J. Hubert, M. Ruan, J. Hickman, R. Atwal, S. Seshadri, B. Huang, R. Knight, N. Bortoli, and D. Smith. We would like to thank P.S. Cohen, N. Chiariello, T. Hebert, and the rest of JRBP crew, and A.E. Launer, Stanford's Conservation Program Manager for all their help and support. We would like to thank D. Turner and G. Li for their help in EM-1 lab. We would like to thank Hidden Villa and Boething Treeland for letting us use their property to conduct our field study. This research was funded by Vaadia-BARD Postdoctoral Fellowship Award No. FI-425-2009 from BARD, The United States-Israel Binational Agricultural Research and Development Fund.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.03.024>. These data include Google maps of the most important areas described in this article.

## References

- Abril, S., Gómez, C., 2009. Ascertaining key factors behind the coexistence of the native ant species *plagiopsis pygmaea* with the invasive Argentine ant *Linepithema humile* (Hymenoptera: Formicidae). *Sociobiology* 53, 559–568.
- Angold, P.G., Sadler, J.P., Hill, M.O., Pullin, A., Rushton, S., Austin, K., Small, E., Wood, B., Wadsworth, R., Sanderson, R., Thompson, K., 2006. Biodiversity in urban habitat patches. *Sci. Total Environ.* 360, 196–204.
- Blair, R.B., 1996. Land use and avian species diversity along an urban gradient. *Ecol. Appl.* 6, 506–519.
- Blair, R., 2004. The effects of urban sprawl on birds at multiple levels of biological organization. *Ecol. Soc.* 9, 2.
- Blair, R.B., Launer, A.E., 1997. Butterfly diversity and human land use: species assemblages along an urban gradient. *Biol. Conserv.* 80, 113–125.
- Bolger, D.T., 2007. Spatial and temporal variation in the Argentine ant edge effect: Implications for the mechanism of edge limitation. *Biol. Conserv.* 136, 295–305.
- Carpintero, S., 2003. Distribution of the invasive Argentine ant (*Linepithema humile*) in Doñana National Park (Spain) and displacement of native ant species. *Ecol. Mediterranea* 29, 250–250.
- Ehrendorf, D.W., 1970. *Biological Conservation*. Holt, Rinehart and Winston, New York.
- Fedriani, J.M., Fuller, T.K., Sauvajot, R.M., 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography* 24, 325–331.
- Fisher, B.L., Cover, S.P., 2007. *Ants of North America: A Guide to the Genera*. University of California Press, Berkeley, Los Angeles, London.
- Fitzgerald, K., Gordon, D.M., 2012. Effects of vegetation cover, presence of a native ant species, and human disturbance on colonization by Argentine Ants. *Conserv. Biol.* 26, 525–538.
- Fitzgerald, K., Heller, N., Gordon, D.M., 2012. Modeling the spread of the Argentine ant into natural areas: habitat suitability and spread from neighboring sites. *Ecol. Model.* 247, 262–272.
- Frazier, G.W., Canham, C.D., Lertzman, K.P., 1999. *Imaging Software to Extract Canopy Structure and Gap Light Transmission Indices from True-Colour Fisheye Photographs*, Users Manual and Program Documentation: Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.
- Godron, M., Forman, R.T.T., 1983. Landscape modification and changing ecological characteristics. In: Mooney, H.A., Godron, M. (Eds.), *Disturbance and Ecosystems: Components of Response*. Springer, Berlin, pp. 12–28.
- Gordon, D.M., Heller, N.E., 2013. The invasive Argentine ant *Linepithema humile* (Hymenoptera: Formicidae) in Northern California reserves: from foraging behavior to local spread. *Myrmecol. News* 19, 103–110.
- Gordon, D.M., Moses, L., Falkovitz-Halpern, M., Wong, E.H., 2001. Effect of weather on infestation of buildings by the invasive Argentine ant, *Linepithema humile* (Hymenoptera: Formicidae). *Am. Midl. Nat.* 146, 321–328.
- Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., Briggs, J.M., 2008. Global change and the ecology of cities. *Science* 319, 756–760.
- Grove, J.M., Troy, A.R., O'Neil-Dunne, J.P.M., Burch, W.R., Cadenasso, M.L., Pickett, S.T.A., 2006. Characterization of households and its implications for the vegetation of urban ecosystems. *Ecosystems* 9, 578–597.
- Holway, D.A., 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology* 80, 238–251.
- Holway, D.A., Suarez, A.V., 2006. Homogenization of ant communities in Mediterranean California: the effects of urbanization and invasion. *Biol. Conserv.* 127, 319–326.
- Holway, D.A., Lach, L., Suarez, A.V., Tsutsui, N.D., Case, T.J., 2002. The causes and consequences of ant invasions. *Annu. Rev. Ecol. Syst.* 33, 181–234.
- Hope, D., Gries, C., Zhu, W.X., Fagan, W.F., Redman, C.L., Grimm, N.B., Nelson, A.L., Martin, C., Kinzig, A., 2003. Socioeconomics drive urban plant diversity. *Proc. Natl. Acad. Sci. U.S.A.* 100, 8788–8792.
- Human, K.G., Gordon, D.M., 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia* 105, 405–412.
- Human, K.G., Gordon, D.M., 1997. Effects of Argentine ants on invertebrate biodiversity in Northern California. *Conserv. Biol.* 11, 1242–1248.
- IUCN, 2000. *Guidelines for the Prevention of Biodiversity Loss Caused by Alien Invasive Species*. Prepared by the SSC Invasive Species Specialist Group. Gland, Switzerland.
- Jennings, S., Brown, N., Sheil, D., 1999. Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. *Forestry* 72, 59–74.
- Jones, J.C., Reynolds, J.D., Raffaelli, D., 2006. Environmental variables. In: Sutherland, B. (Ed.), *Ecological Census Techniques*. Cambridge University Press, Cambridge, pp. 370–407.
- Koh, L.P., Gardner, T.A., 2010. Conservation in human-modified landscapes. In: Sodhi, N.S., Ehrlich, P.R. (Eds.), *Conservation Biology for All*. Oxford University Press, Oxford, UK, pp. 236–261.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*. (Developments in Environmental Modelling). Elsevier Science BV, Amsterdam, Netherlands, p. 853.
- Lepš, J., Šmilauer, P., 2003. *Multivariate Analysis of Ecological Data Using Canoco*. Cambridge University Press, Cambridge, UK.
- Lepš, J., Šmilauer, P. (Eds.), 1999. *Multivariate Analysis of Ecological Data*. Faculty of Biological Sciences, University of South Bohemia, Ceske Bodejovice, Czech Republic.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10, 689–710.
- Marzluff, J.M., 2005. Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. *Urban Ecosyst.* 8, 157–177.
- Marzluff, J.M., Ewing, K., 2001. Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. *Restor. Ecol.* 9, 280–292.
- McDonnell, M.J., Hahs, A.K., 2013. The future of urban biodiversity research: moving beyond the 'low-hanging fruit'. *Urban Ecosyst.* 16, 397–409. <http://dx.doi.org/10.1007/s11252-013-0315-2>.
- McDonnell, M.J., Pickett, S.T.A., 1990. Ecosystem structure and function along urban rural gradients – an unexploited opportunity for ecology. *Ecology* 71, 1232–1237.
- McDonnell, M.J., Pickett, S.T.A., Groffman, P., Bohlen, P., Pouyat, R.V., Zipperer, W.C., Parmelee, R.W., Carreiro, M.M., Medley, K., 2008. Ecosystem processes along an urban-to-rural gradient. In: Marzluff, J.M., Shulenberger, E., Endlicher, W., Alberti, M., Bradley, G., Ryan, C., Simon, U., ZumBrunnen, C. (Eds.), *Urban Ecology*. Springer, US, pp. 299–313.
- McKinney, M.L., 2002. Urbanization, biodiversity, and conservation. *Bioscience* 52, 883–890.
- McKinney, M.L., 2006. Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* 127, 247–260.
- Newell, W., Barber, T.C., 1913. The Argentine ant. *USDA Bureau Entomol. Bull.* 122, 1–98.
- Paul, M.J., Meyer, J.L., 2001. Streams in the urban landscape. *Annu. Rev. Ecol. Syst.* 32, 333–365.
- Philpott, S.N., Perfecto, I., Armbrrecht, I., Parr, C.L., 2010. Disturbance and habitat transformation. In: Lach, L., Parr, C.L., Abbott, K.L. (Eds.), *Ant Ecology*. Oxford University Press, New York, pp. 137–156.
- Rebele, F., 1994. Urban ecology and special features of urban ecosystems. *Global Ecol. Biogeography Lett.* 4, 173–187.
- Roura-Pascual, N., Bas, J., Hui, C., 2010. The spread of the Argentine ant: environmental determinants and impacts on native ant communities. *Biol. Invasions* 12, 2399–2412.
- Sanders, N.J., Barton, K.E., Gordon, D.M., 2001. Long-term dynamics of the distribution of the invasive Argentine ant, *Linepithema humile*, and native ant taxa in northern California. *Oecologia* 127, 123–130.
- Sanders, N.J., Gotelli, N.J., Heller, N.E., Gordon, D.M., 2003. Community disassembly by an invasive species. *Proc. Natl. Acad. Sci. U.S.A.* 100, 2474–2477.
- Sorrells, T.R., Kuritzky, L.Y., Kauhane, P.G., Fitzgerald, K., Sturgis, S.J., Chen, J., Djiamco, C.A., Basurto, K.N., Gordon, D.M., 2011. Chemical defense by the native winter ant (*Prenolepis imparis*) against the invasive Argentine ant (*Linepithema humile*). *PLoS ONE* 6, e18717.



- StatSoft, Inc., 2011. STATISTICA (data analysis software system), version 10. <[www.statsoft.com](http://www.statsoft.com)>.
- Suarez, A.V., Bolger, D.T., Case, T.J., 1998. Effects of fragmentation and invasion on native ant communities in coastal Southern California. *Ecology* 79, 2041–2056.
- Sullivan, B.K., Flowers, M.A., 1998. Large iguanid lizards of urban mountain preserves in northern Phoenix, Arizona. *Herpetol. Nat. History* 6, 13–22.
- ter Braak, C.J.F., Šmilauer, P. (Eds.), 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, New York, USA.
- Thompson, B., McLachlan, S., 2007. The effects of urbanization on ant communities and myrmecochory in Manitoba, Canada. *Urban Ecosyst.* 10, 43–52.
- Tillberg, C.V., Holway, D.A., LeBrun, E.G., Suarez, A.V., 2007. Trophic ecology of invasive Argentine ants in their native and introduced ranges. *Proc. Natl. Acad. Sci. U.S.A.* 104, 20856–20861.
- Uno, S., Cotton, J., Philpott, S.M., 2010. Diversity, abundance, and species composition of ants in urban green spaces. *Urban Ecosyst.* 13, 425–441.
- Ward, P.S., 2005. A synoptic review of the ants of California (Hymenoptera: Formicidae). *Zootaxa* 936, 1–68.
- Yu, D.W., Wilson, H.B., 2001. The competition–colonization trade-off is dead; long live the competition–colonization trade-off. *Am. Naturalist* 158, 49–63.
- Zipperer, W., Foresman, T., Sisinni, S., Pouyat, R., 1997. Urban tree cover: an ecological perspective. *Urban Ecosyst.* 1, 229–246.