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Intermediate disturbance promotes invasive ant abundance

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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.

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 (Ehrenfeld, 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

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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).

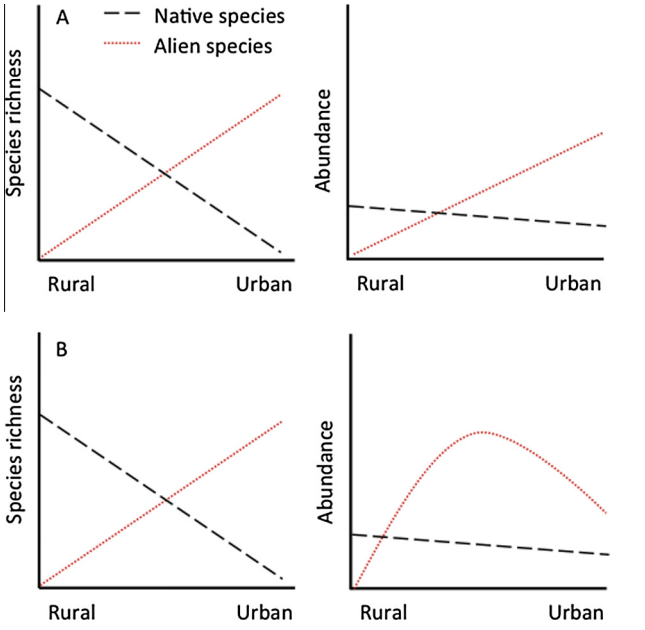

Fig. 1. Hypotheses for ant abundance along urban-natural gradients: (A) alien species abundances peak at urban sites and (B) alien species abundances peak at semi-natural sites.

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 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.