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Homogenization of ant communities in mediterranean California: The effects of urbanization and invasion

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ABSTRACT

In coastal California, the invasive Argentine ant (*Linepithema humile*) displaces nearly all above ground foraging native ant species. The loss of native ants following invasion by Argentine ants homogenizes these faunas; natural habitats invaded by *L. humile* have lower beta diversity compared to comparable uninvaded areas. Argentine ant abundance in the seasonally dry mediterranean environments of this region correlates strongly and positively with soil moisture. For this reason, the displacement of native ants across natural and artificial moisture gradients often resembles an edge effect, the magnitude of which is inversely proportional to the suitability of the physical environment from the perspective of *L. humile*. The direct effects of Argentine ant invasions in natural environments are therefore amplified by inputs of urban and agricultural run off. Indirect ecological effects of these invasions arise from the loss of large-bodied ants, arid adapted ants, and behavioral repertoires unique to particular native ant species. Further research is needed to quantify how these aspects of functional homogenization affect invaded communities. The close association between *L. humile* and moist soils suggests that, at least in arid regions, control strategies might be aimed at reducing urban run off in order to maintain functionally diverse communities of native ants.

1. Introduction

Biotic homogenization is the pattern of increasing similarity among areas in terms of species identity. This process primarily results from two mechanisms: the loss of unique species and the widespread introduction of a few successful species (McKinney and Lockwood, 1999; Lockwood and Mckinney, 2001). Although invasive species are often implicated in the process of homogenization, the mechanisms underlying native displacement are often incompletely known. In some cases, introduced species may not directly displace natives, but instead may colonize sites after native taxa have declined as a result of habitat alteration (Diamond and Case, 1986). In other cases, however, invasive species may be the primary cause of homogenization, with disturbance playing a secondary role. Determining whether anthropogenic modifications to the environment directly imperil native species or affect them indirectly, by creating opportunities for invasive species, remains an important focus of research on biotic homogenization (Marchetti et al., 2001, 2004; Rahel, 2002).

Patterns of biotic homogenization have been well described for some groups of organisms, especially plants (McKinney,

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2004), birds (Lockwood et al., 2000), and freshwater fish (Rahel, 2002), but much needs to be learned about the ecological consequences of homogenization (Olden et al., 2004). In cases where invasive species resemble native species with respect to key ecological attributes (e.g., body size, resource requirements, environmental tolerances, or life-history characteristics), the community-level effects of homogenization may be relatively minor. This expectation seems unlikely to be met, however, when invasive species differ markedly from native species, when one or a few invasive species displace entire assemblages of native species, or when invasive species are present at much higher densities compared to native species.

Here, we address how ant invasions contribute to biotic homogenization. Invasive ants represent appropriate candidates for studies of biotic homogenization because of their local abundance, tendency to displace native ants, and ability to disrupt ecological communities (reviewed in Holway et al., 2002a). In this study, we focus on ant invasions into scrub and riparian habitats in mediterranean California. Unlike most other documented cases of homogenization, which involve multiple introduced species, the homogenization of ant communities in southern California primarily involves a single invasive species, the Argentine ant (*Linepithema humile*). In this study, we re-analyze previous work and provide new data to examine patterns of native ant displacement, the manner in which urbanization and invasion interact to imperil native ants, and the ecological effects of reduced native ant diversity. Given that Argentine ant invasions are now fairly well studied in California, this system offers an interesting comparison to cases of homogenization where whole suites of invasive species are involved.

2. Methods

2.1. Sampling of ant communities in scrub habitats

To estimate the impact of urbanization and invasion on native ant communities, we sampled ants in 50 scrub fragments (between 0.5 and 100 ha) within urban southern California, and in plots within two much larger, unfragmented areas (the University of California Elliot Chaparral Reserve and the Sweetwater River section of the San Diego National Wildlife Refuge). At each site we placed arrays of five pitfall traps every 100 m along transects from the edge to interior of the site. We also placed sample arrays at five urban sites near the locations of habitat fragments (for detailed methods see Suarez et al., 1998 and Holway et al., 2002b). We separated fragments into two categories ("xeric sites" and "mesic sites") based on their topography (e.g., mesa tops versus canyons), which presumably influences the amount of water run off fragments receive from adjacent urban areas (Holway et al., 2002b).

We chose six of the largest scrub fragments (between 30 and 100 ha) surveyed by Suarez et al. (1998) and estimated beta diversity for the invaded and uninvaded portions of each fragment. Large fragments contain heavily invaded edges as well as core areas where Argentine ants have not yet penetrated and native ants persist. For each fragment, we pooled samples from within invaded edge sites (those $\leqslant$50 m to the nearest urban development) and within uninvaded interior sites (those $\geqslant$100 m from the nearest urban development) to develop two species lists for each fragment. We then estimated beta diversity for invaded and uninvaded sites to assess the degree to which Argentine ants homogenize ant faunas in scrub fragments at the scale of San Diego. Following Magurran (1988), we estimated beta diversity as $(a + b)(1 - S)$, where a = number of species detected at site A, b = number of species detected at site B, and $S = j/(a + b - j)$, where j = species found at both sites. This estimate is weighted by species number (Magurran, 1988).

Previous estimates of the impacts of Argentine ants on native ant communities have relied primarily on pitfall trapping and visual surveys. To examine the effects of Argentine ants on the density of ant nests, we located nest entrances for all above ground foraging ants in two 50×50 m plots at the University of California Elliot Chaparral Reserve, one in an area invaded by Argentine ants and a second in an uninvaded area. These data serve to illustrate the drastic change in ant community structure resulting from the displacement of native ants by this invader.

To further examine potential ecological consequences of losing native ant species, we determined head width distributions for native ants at both the University of California Elliot Chaparral Reserve and the Sweetwater River. We measured head widths for 5–10 individuals of each species and used the mean value as a surrogate for the species' body size (see Kaspari and Weiser, 1999). For dimorphic and polymorphic genera (e.g. *Pheidole* and *Camponotus*), we measured at least 2 majors (or largest individuals available) for each species.

2.2. Sampling of ant communities in riparian woodlands

To illustrate the association between ant abundance and soil moisture in natural environments, we sampled ants at five pairs of naturally occurring moisture gradients. Sites within each pair included one invaded site and one uninvaded site. Pairs were separated from one another by at least 10 km, and each was located in a different watershed in San Diego Co., CA: San Dieguito R., Los Peñasquitos Cr., San Diego R., Sweetwater R., and Otay R. Each site consisted of an abrupt natural edge between riparian woodlands and coastal sage scrub. All sites were located away from urban development, situated inside protected federal, state, or county preserves, dominated by common native perennial plants, and connected to large, unfragmented tracts of coastal sage scrub and chaparral. See Holway (2005) for additional information about the study areas. At all sites, we used pitfall traps to sample ants at each of four distances away from the riparian corridor: 25, 50, 100, and 200 m. We also placed a set of traps inside the riparian corridor; these are referred to as 0 m traps. Because of the sharp boundary between riparian and scrub habitats, all traps other than those in the 0 m category were located in scrub. For each distance category we placed a set of 5 traps approximately 10 m apart in an irregular line parallel to the riparian corridor. As with the scrub fragments, we compared beta diversity among paired invaded and uninvaded riparian sites to examine the extent to which Argentine ants are homogenizing ant communities in riparian woodlands.