

available at [www.sciencedirect.com](http://www.sciencedirect.com)journal homepage: [www.elsevier.com/locate/biocon](http://www.elsevier.com/locate/biocon)

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

David A. Holway<sup>a</sup>, Andrew V. Suarez<sup>b,c,\*</sup>

<sup>a</sup>Section of Ecology, Behavior, and Evolution, Division of Biological Sciences, University of California, San Diego, La Jolla, CA 92093, United States

<sup>b</sup>Department of Entomology, University of Illinois, 320 Morrill Hall, 505 S. Goodwin Avenue, Urbana, IL 61801, United States

<sup>c</sup>Department of Animal Biology, University of Illinois, Urbana, IL 61801, United States

## ARTICLE INFO

### Article history:

Received 16 December 2004

Received in revised form 9 May 2005

Accepted 13 May 2005

Available online 20 October 2005

### Keywords:

Argentine ants

Biological invasions

Biotic homogenization

*Linepithema humile*

Urbanization

## 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.

© 2005 Elsevier Ltd. All rights reserved.

## 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,

\* Corresponding author. Tel.: +1 217 244 6631; fax: +1 217 244 4565.

E-mail addresses: [dholway@ucsd.edu](mailto:dholway@ucsd.edu) (D.A. Holway), [avsuarez@life.uiuc.edu](mailto:avsuarez@life.uiuc.edu) (A.V. Suarez).

0006-3207/\$ - see front matter © 2005 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2005.05.016

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  $\leq 50$  m to the nearest urban development) and within uninvaded interior

sites (those  $\geq 100$  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  $50 \times 50$  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.

At four of the invaded riparian–scrub edges, we conducted pitfall sampling during May in two consecutive years: May 2002 followed a record dry winter with only ca. 75 mm winter precipitation, whereas May 2003 followed a year of average rainfall with ca. 250 mm winter precipitation. In each year of sampling we used identical methods, and traps were placed in exactly the same locations in both years. We used an Aquaterr EC-300 soil moisture meter to quantify moisture 10 cm below the soil surface at the location of every pitfall trap; we took these measurements in May 2004, which followed a winter with ca. 150 mm precipitation (i.e., intermediate between 2002 and 2003). Soil moisture measurements primarily serve to illustrate the large difference between riparian and scrub sites; this disparity would not be expected to vary much from year-to-year (with respect to within-season comparisons).

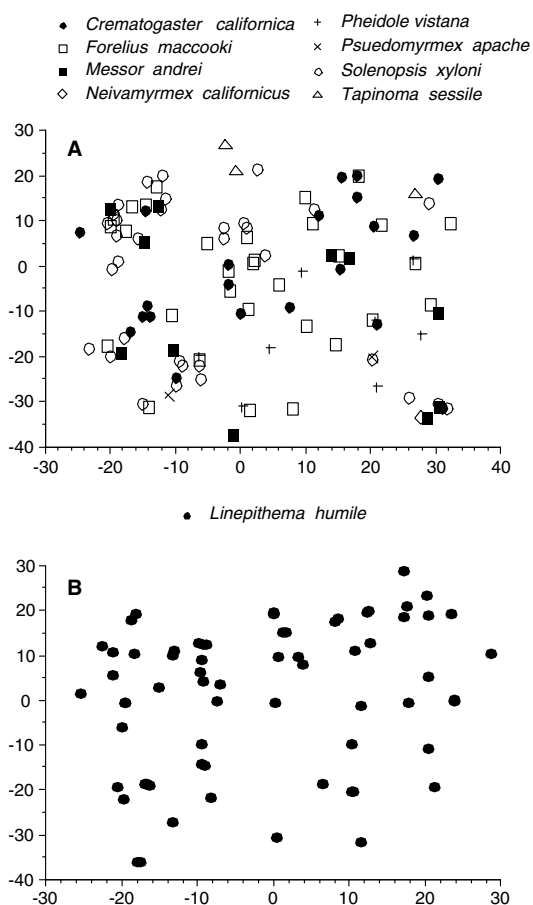
### 3. Results and discussion

#### 3.1. Patterns of homogenization

##### 3.1.1. Invasion by Argentine ants

Native ant displacement by Argentine ants is known from many parts of the world, especially from seasonally dry mediterranean-type ecosystems (Tremper, 1976; Ward, 1987; Bond and Slingsby, 1984; Cammell et al., 1994; Carpintero et al., 2004). The effects of Argentine ants on native ants are perhaps best known for California where numerous studies have found that *L. humile* displaces nearly every species of above ground foraging native ant (reviewed in Holway et al., 2002a). Our fine scale mapping of ant nests at the UC Elliot Chaparral Reserve clearly reveals the extent of this displacement (Fig. 1). We detected 116 nest entrances of 8 species of native ant species in the uninvaded plot but found only Argentine ants (and 69 nest entrances) in the invaded plot. Although the majority of native ants in California succumb to Argentine ants, a few species persist. These exceptions include hypogeics (e.g., species that are leaf litter dwelling or below ground foraging), and the winter active *Prenolepis imparis* (Ward, 1987; Holway, 1998; Suarez et al., 1998; Sanders et al., 2001; see also DiGirolamo and Fox, in press).

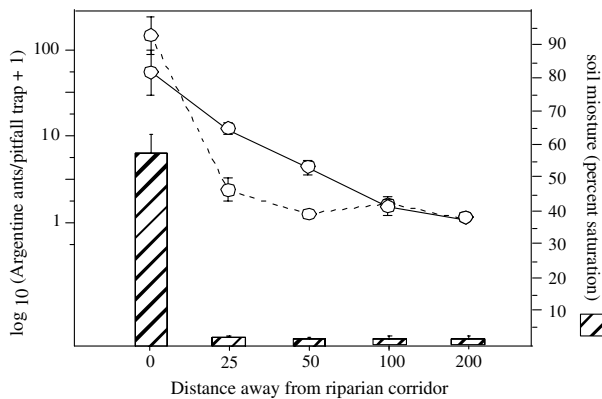
Although areas invaded by *L. humile* suffer reductions in native ant diversity, the effects of this invasion in California remain somewhat localized. Large-scale surveys, for example, document that Argentine ants occur primarily in relatively mesic environments: irrigated urban areas, riparian woodlands, and coastal areas (where the effects of the summer drought may be mitigated by coastal fog) (Tremper, 1976; Ward, 1987). The importance of abiotic suitability manifests itself at smaller spatial scales as well (Human et al., 1998; Holway, 1998; Holway et al., 2002b). At natural edges between riparian woodlands and coastal sage scrub in southern California, for example, Argentine ant abundance is correlated with soil moisture (Fig. 2;  $r = 0.848$ ,  $P < 0.001$ ,  $n = 20$ ). Riparian woodlands and scrub obviously differ in ways other than with respect to soil moisture, but the close association between moist soils and high *L. humile* abundance is nonetheless striking and points to an important role for abiotic factors. Abundance also correlates with inter-annual differences in



**Fig. 1** – Distribution of ant nests in 50 m<sup>2</sup> plots in (A) uninvaded sites and (B) invaded sites at the UC Elliot Chaparral Reserve in San Diego Co., CA. Both plots were sampled over a one-month period in March 1996. Each point represents a separate nest entrance but not necessarily a different colony; some species (e.g., *Linepithema humile*, *Forelius maccooki*) are polydomous. It is also worth noting that *Pseudomyrmex apache* is arboreal and *Neivamyrmex californicus* is nomadic.

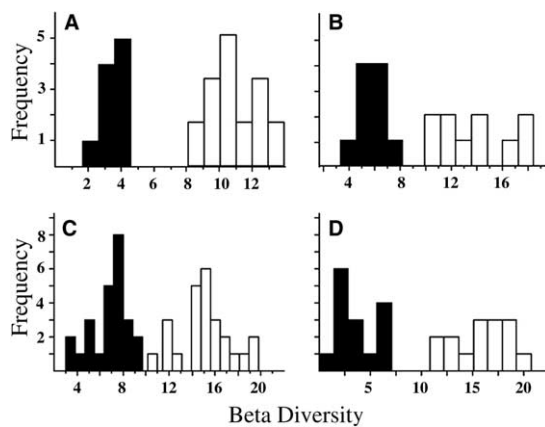
winter precipitation (Fig. 2; see also DiGirolamo and Fox, in press). Argentine ants were more abundant in dry scrub just outside of riparian corridors in 2003, a year of approximately average rainfall, than they were in 2002, a record drought year (Fig. 2; paired t-tests: 25 m,  $t_3 = 7.33$ ,  $P < 0.005$ ; 50 m,  $t_3 = 3.98$ ,  $P < 0.005$ ). Abundance inside corridors, where moisture presumably was not limiting, did not differ between years (paired t-test:  $t_3 = 2.23$ ,  $P > 0.05$ ). Note that although only two years of data are available for this comparison, the between-year differences evident in Fig. 2 result from parallel responses occurring at multiple sites distributed across a large geographic area.

While previous work in California provides unambiguous evidence for the local scale displacement of native ants, much remains to be learned about how ant diversity changes at larger scales (Gotelli and Arnett, 2000; Kaspari et al., 2003). Unlike the case for some groups of organisms, such as fish, for which species-level distributional data are available for a variety of spatial and temporal scales (e.g., Marchetti et al.,



**Fig. 2** – Argentine ant abundance across naturally occurring moisture gradients. Circles show mean ( $\pm 1$  SE) abundance of Argentine ants in pitfall traps across four riparian–scrub edges in San Diego Co., CA. Each site is located in a different watershed. The dashed line represents abundance in May 2002, which followed a record dry winter; the solid line represents abundance in May 2003, which followed a winter of average rainfall. Hatched bars show mean ( $\pm 1$  SE) soil moisture at the exact location of each pitfall trap in May 2004, which followed a winter of intermediate rainfall (e.g., relative to 2002 and 2003).

2001, 2004), analogous information remains scarce to non-existent for most terrestrial arthropods, even for relatively well-studied taxa such as ants. Existing data, however, illustrate the homogenizing potential of *L. humile* invasions. In both northern and southern California, estimates of beta diversity between paired invaded and uninvaded riparian sites exhibit entirely non-overlapping distributions (Fig. 3A



**Fig. 3** – Beta diversity estimates for ants in riparian woodlands (A–C) at paired invaded (closed bars) and uninvaded sites (open bars). (A) Riparian sites from San Diego Co., CA (Holway, 2005), (B) Riparian sites from Yolo and Solano Cos., CA (Holway, 1998), and (C) comparisons between northern (Yolo/Solano) and southern (San Diego) California. (D) Beta diversity estimates for ants in 5 large (> 30 ha) fragments of scrub habitat in urban San Diego. Invaded edge sites (< 50 m to urban edge – closed bars) are compared to uninvaded interior sites (> 100 m from urban edge – open bars) among fragments (data from Suarez et al., 1998).

and B). This disparity holds as well for comparisons between northern and southern California (Fig. 3C), suggesting that, even across large spatial scales and in the absence of urbanization, invasion by Argentine ants leads to increased faunal similarity. For large habitat fragments in urban San Diego, estimates of beta diversity are again lower at invaded sites compared to uninvaded sites (Fig. 3D). However, it is not possible to tease apart the independent impacts of invasion versus urbanization with this example. In all four comparisons depicted in Fig. 3, the native ants detected at invaded sites were nearly all hypogeic species, which do not appear to interact strongly with *L. humile*. If only above ground foraging native ants are included in these comparisons, the disparities in beta diversity between invaded and uninvaded sites become even more striking.

### 3.1.2. Urbanization

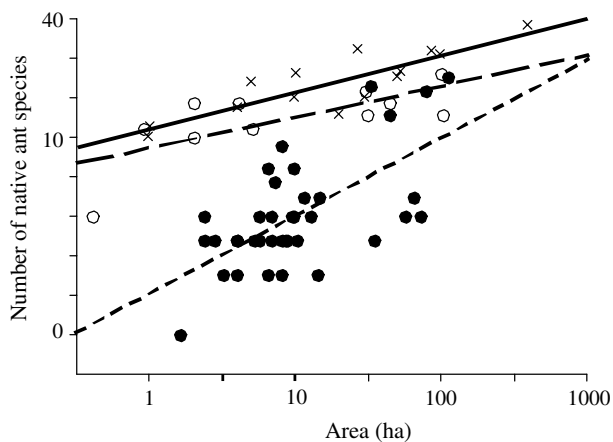
Isolating the effects of urbanization on ants native to mediterranean California is difficult given that Argentine ants now largely dominate urban environments, but direct and indirect effects of urbanization may both be important. Some native ants clearly experience difficulty persisting in urbanized areas even in the absence of Argentine ants. Species with narrow diets (e.g., specialized predators) or specific nesting requirements (e.g., some arboreal taxa, litter nesting species), for example, may often succumb directly to changes brought about by urbanization. For other ants, however, urban areas may be made unsuitable primarily because of the presence of Argentine ants. The above ground foraging and opportunistic native ant genera strongly affected by *L. humile*, for example, (e.g., *Tapinoma*, *Forelius*, *Formica*, and *Solenopsis* (fire ants)) appear to thrive in uninvaded pockets of urban habitat in California and in urban areas in the southwestern United States outside of the Argentine ant's introduced range. Harvester ants (e.g., *Pogonomyrmex*) also persist in some urban areas lacking Argentine ants. The possibility even exists that some of these native ant species may prosper in urban areas lacking *L. humile* to a greater extent, on average, than they do in more natural environments. Although ants in human dominated landscapes have been studied extensively from the perspective of urban entomology, far fewer studies have quantitatively assessed how urbanization affects native ants in the absence of behaviorally dominant invasive species (but see Carpintero et al., 2004).

Although the direct effects of urbanization on native ants remain incompletely studied, the indirect effects stemming from the presence of Argentine ants seem obvious. Urban environments often support high densities of *L. humile*, especially in areas with irrigation. The Argentine ant's general nesting and dietary requirements as well as its remarkable ability to relocate nests in the face of disturbance (Newell and Barber, 1913) may predispose this species for survival in urban environments. Its strong competitive ability (Human and Gordon, 1996; Holway, 1999) and aggressive intolerance of other ants (Erickson, 1971; Hölldobler and Wilson, 1977; Passera, 1994) make heavily invaded urban areas difficult for native ants to colonize. For example, from our sampling of five sites within urban San Diego, Argentine ant workers were one to two orders of magnitude more abundant than all native ants combined and only four species of native ant were



detected: *Solenopsis molesta*, *Temnothorax andrei*, *Prenolepis imparis* and *Dorymyrmex insanus* – the species that persist the longest in invaded natural habitats in San Diego (Suarez et al., 1998).

Native ants occupying habitat fragments surrounded by urban areas are also at risk of being displaced by Argentine ants (Suarez et al., 1998; Bolger et al., 2000). The pattern of Argentine ant abundance observed across anthropogenic moisture gradients (Suarez et al., 1998; Bolger et al., 2000) resembles that documented across natural moisture gradients (Fig. 2; Holway, 2005). At the urban–scrub interface, Argentine ants decrease sharply in abundance with increasing distance away from edges such that by 200 m few remain (Suarez et al., 1998; Bolger et al., 2000). In these situations, native ant diversity correlates inversely with the abundance of *L. humile* (Suarez et al., 1998). The similarity in the spatial patterns of Argentine ant abundance at riparian–scrub edges and urban–scrub edges suggests a key role for soil moisture. Soil moisture may also underlie disparities in the extent of invasion for fragments that differ in topography: Argentine ants invade canyon fragments (which collect run off) to greater extent than mesa fragments (which do not collect run off) (Holway et al., 2002b). Differences in the extent of invasion of these fragments can be used to estimate the impact of Argentine ants independent of habitat loss and disturbance alone. By comparing the species/area relationships of mesic habitat fragments (invaded), xeric habitat fragments (uninvaded), and similarly sized plots within uninvaded tracts of continuous habitat, it becomes apparent that xeric fragments in urban southern California lose relatively few species (~10–20%) compared to mesic fragments where most native ants (up to 95%) are lost within a few years of invasion (Fig. 4) (Suarez et al., 1998; Holway et al., 2002b). Only Argentine ant-free refugia within the largest invaded fragments continue to maintain species rich ant communities.



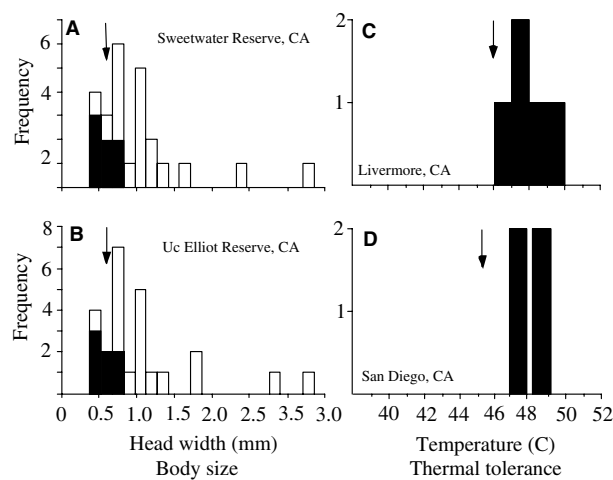
**Fig. 4 – Species/area relationships for native ants in plots within continuous habitat (x, solid line), largely uninvaded xeric fragments (open circles, large dashed line), and heavily invaded mesic fragments (closed circles, small dashed line). Figure modified from Holway et al., 2002b; printed with permission from the Ecological Society of America.**

### 3.2. Functional homogenization of a consumer community

Because ant communities shift from supporting multiple native species prior to invasion by *L. humile* to supporting primarily Argentine ants following invasion, invaded and uninvaded areas may differ profoundly with respect to a variety of community characteristics. In certain respects, Argentine ant invasions may lead to the functional homogenization (Olden et al., 2004) of an ecologically significant assemblage of consumers. Below we summarize three potentially important dimensions of this process and discuss the consequences for invaded communities.

#### 3.2.1. Shifts in mean worker size

Argentine ants are smaller than many of the native ant species they displace in California (Fig. 5A and B). Large-bodied native ants include harvester ants, such as *Pogonomyrmex* and *Messor*, which can form large, long-lived colonies (MacMahon et al., 2000; Johnson, 2001) that can locally influence plant composition (Brown and Human, 1997; Peters et al., 2005). The loss of large native ants can negatively affect species that rely on them for food or services. For example, the coastal horned lizard, a specialist ant predator, suffers because Argentine ants eliminate suitable prey (e.g., ants



**Fig. 5 – Distributions of (A–B) head widths and (C–D) thermal tolerance for common species of native ants from different parts of California. Arrows indicate where Argentine ants fall in each distribution. Data in (A–B) are unpublished data from sampling conducted in Suarez et al. (1998) and Holway et al. (2002b). Data in (C) are from Tremper (1976) and illustrate the mean critical thermal maxima for *Formica moki*, *Tapinoma sessile*, *Liometopum occidentale*, *Messor andrei*, *Crematogaster coarctata* and *Pogonomyrmex brevispinosus*. Data from (D) are reanalyzed from Holway et al. (2002b) and show estimated 50% mortality after 60 min of exposure to different temperatures. Native ants in (D) include *Solenopsis xyloni*, *Dorymyrmex insanus*, *Crematogaster californica*, *Pogonomyrmex subnitidus*, and *Forelius mccooki*. Argentine ants displace all native ant species included in this figure except for those represented by black bars in (A) and (B). These are primarily hypogeic species that do not appear to interact strongly with Argentine ants (Ward, 1987).**

larger than *L. humile*) (Suarez et al., 2000; Suarez and Case, 2002). The loss of large-bodied native ants can also affect mutualistic associations. As in South Africa (Bond and Slingby, 1984; Christian, 2001), the disappearance of large-bodied ants in California may negatively affect plants, such as the tree poppy (*Dendromecon rigidum*), that rely on ants to disperse their seeds. Tree poppy seeds are too large to be dispersed by Argentine ants (Carney et al., 2003). Similar disruptions of ant-mediated seed dispersal mutualisms by small-bodied invasive ants occur worldwide (Ness et al., 2004).

### 3.2.2. Shifts in mean thermal tolerance

Invasion by Argentine ants also eliminates native ant species with a greater capacity to withstand stressful abiotic conditions (Fig. 5C–D). The loss of arid-adapted species may lead to situations in which areas that are seasonally invaded by Argentine ants support fewer ants compared to uninvaded areas. Along moisture gradients, for example, dry areas adjacent to sources of water may lose native ants as a result of Argentine ant occupation during winter and spring when abiotic conditions are suitable. With the onset of the summer drought, however, Argentine ants may recede into contiguous mesic areas, leaving neighboring dry areas with few, if any, ants (Fig. 6A; see also Markin, 1970). Empirical support for such an occurrence comes from patterns of ant abundance across riparian–scrub edges in southern California. Fig. 6B illustrates mean differences in the number of ant workers captured in pitfall traps at five pairs of uninvaded and invaded edges as a function of increasing distance away from riparian corridors. This difference is strongly positive inside riparian corridors because Argentine ants attain extremely high densities in these habitats. Outside of riparian corridors, however, more ants were detected at uninvaded sites than at invaded sites. The magnitude of this deficit decreases with decreasing Argentine ant abundance such that by 100 m (where Argentine ants are rare), invaded and uninvaded sites had approximately equal numbers of ants – nearly all of them native. The ecological implications of the phenomenon illus-

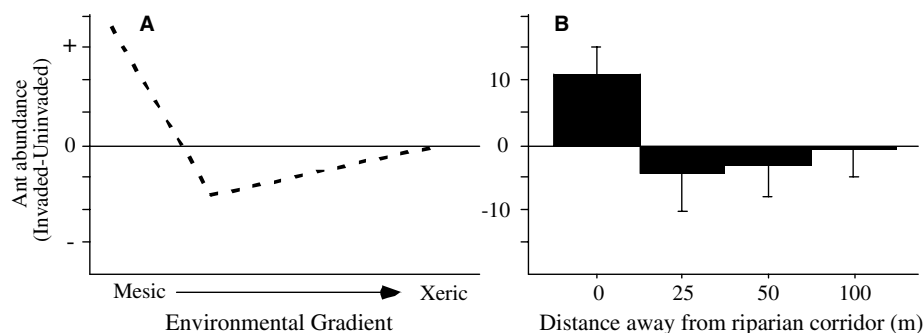
trated in Fig. 6 are little explored, but the seasonal absence of ants from dry habitats will perturb food webs in proportion to the importance of ants in these ecosystems.

### 3.2.3. Loss of unique behavioral repertoires

A final form of functional homogenization could involve reductions in behavioral diversity as native ants disappear from invaded areas. Communities of native ants, for example, exhibit a diversity of nesting habits, dispersal strategies, and foraging behaviors that are not fully represented in the behavioral repertoire of *L. humile*. Changes in behavioral diversity may be enhanced by the somewhat anomalous behaviors of *L. humile*. Unlike many of the native ants they displace, for example, Argentine ants are semi-nomadic, invest little in nest infrastructure, have queens that are not known to participate in mating flights, and form expansive supercolonies in their introduced range (Newell and Barber, 1913; Hölldobler and Wilson, 1977; Tsutsui et al., 2000). Of any of these behavioral differences, disparities in nest architecture may be the most ecologically important. Harvester ants, for example, excavate deep, long-lived soil nests that differ greatly from the ephemeral, usually shallow nests opportunistically occupied by Argentine ants. The ecological ramifications of behavioral homogenization deserve further study.

### 3.3. Management of Argentine ant invasions at the urban– natural interface

Large-scale eradication of invasive social insects has never been achieved. Although elimination should always be the goal in the case of newly detected infestations, local management may be the only realistic option for established populations. With respect to Argentine ant invasions in Mediterranean California, an obvious management strategy could involve sensible water use practices. A good deal of circumstantial evidence suggests that urban irrigation contributes to the success of Argentine ants not only inside the urban matrix but also in surrounding natural areas that receive



**Fig. 6 – (A) Hypothesis for how differences in ant abundance between paired invaded and uninvaded sites change across a moisture gradient. In mesic areas, Argentine ants at invaded sites may commonly outnumber native ants at otherwise comparable uninvaded sites. In dry areas adjacent to mesic areas, Argentine ants may displace native ants when abiotic conditions permit (winter and early spring) only to abandon these areas as environmental conditions deteriorate (summer and early fall). In such situations invaded sites may support fewer ants compared to otherwise similar uninvaded sites. The magnitude of this disparity is expected to decrease with increasing distance away from mesic sites as Argentine ants become progressively less common. (B) Differences in ant abundance in pitfalls across 5 paired, invaded and uninvaded riparian–scrub edges. The empirical pattern appears consistent with (A). Sampling for (B) took place from May to Sep. 2002. Each pair of sites is located in a different watershed.**

urban run off. To the extent that water conservation and run off containment would decrease the abundance of *L. humile*, such strategies would encourage colonization and recruitment by native ants and would have the added benefit of conserving water, curbing the spread of other mesic adapted invasive species, and enhancing fire protection (through reductions in plant biomass). This approach exploits not only the physiological limitation of the Argentine ant, but also the dispersal limitations of this species. Because of its inherently poor dispersal abilities, *L. humile* will be unable to colonize isolated mesic areas without being introduced by humans. Although of limited use in more mesic environments (e.g., the southeastern United States, coastal northern California, parts of Hawaii), water conservation measures could discourage Argentine ants in seasonally dry environments throughout the world.

## Acknowledgments

We thank I. Kay for permission to work at the University of California Elliot Chaparral Reserve and J. Richmond for help mapping ant nests. T.J. Case provided intellectual support and lab space throughout the course of this project. The paper was improved by comments from N.J. Sanders and an anonymous reviewer. This research was made possible through grants from the USDA (NRIGCP award 99-35302-8675 to D.A.H.) and NSF (INT-0305660 to D.A.H. and A.V.S.).

## REFERENCES

- Bolger, D.T., Suarez, A.V., Crooks, K.R., Morrison, S.A., Case, T.J., 2000. Arthropods in urban habitat fragments in southern California: area, age and edge effects. *Ecological Applications* 10, 1230–1248.
- Bond, W., Slingsby, P., 1984. Collapse of an ant-plant mutualism – the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. *Ecology* 65, 1031–1037.
- Brown, M.J.F., Human, K.G., 1997. Effects of harvester ants on plant species distribution and abundance in a serpentine grassland. *Oecologia* 112, 237–243.
- Cammell, M.E., Way, M.J., Paiva, M.R., 1994. Diversity and structure of ant communities associated with oak, pine, eucalyptus and arable habitats in Portugal. *Insectes Sociaux* 43, 37–46.
- Carney, S.E., Byerley, M.B., Holway, D.A., 2003. Invasive Argentine ants (*Linepithema humile*) do not replace native ants as seed dispersers of *Dendromecon rigida* (Papaveraceae) in California, USA. *Oecologia* 135, 576–582.
- Carpintero, S., Reyes-Lopez, J., Arias de Reyna, L., 2004. Impact of human dwellings on the distribution of the exotic Argentine ant in the Doñana National Park, Spain. *Biological Conservation* 115, 279–289.
- Christian, C.E., 2001. Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature* 413, 635–639.
- Diamond, J., Case, T.J., 1986. Overview: introductions, extinctions, exterminations, and invasions. In: Diamond, J., Case, T.J. (Eds.), *Community Ecology*. Harper and Row, New York, pp. 65–79.
- DiGirolamo, L.A., Fox, L.R., The influence of abiotic factors and temporal variation on local invasion patterns of the Argentine ant (*Linepithema humile*). *Biological Invasions*, in press.
- Erickson, J.M., 1971. The displacement of native ant species by the introduced Argentine ant *Iridomyrmex humilis* Mayr. *Psyche* 78, 257–266.
- Gotelli, N., Arnett, A.E., 2000. Biogeographic effects of red fire ant invasion. *Ecology Letters* 3, 257–261.
- Hölldobler, B., Wilson, E.O., 1977. The number of queens: an important trait in ant evolution. *Naturwissenschaften* 64, 8–15.
- Holway, D.A., 1998. Factors controlling rate of invasion: a natural experiment using Argentine ants. *Oecologia* 115, 206–212.
- Holway, D.A., 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology* 80, 238–251.
- Holway, D.A., 2005. Edge effects of an invasive species across a natural ecological boundary. *Biological Conservation* 121, 561–567.
- Holway, D.A., Lach, L., Suarez, A.V., Tsutsui, N.D., Case, T.J., 2002a. The causes and consequences of ant invasions. *Annual Review of Ecology & Systematics* 33, 181–233.
- Holway, D.A., Suarez, A.V., Case, T.J., 2002b. Role of abiotic factors in governing susceptibility to invasion: a test with Argentine ants. *Ecology* 83, 1610–1619.
- 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., Weiss, S., Sandler, B., Gordon, D.M., 1998. Effects of abiotic factors on the distribution and activity of the invasive Argentine ant (Hymenoptera: Formicidae). *Environmental Entomology* 27, 822–833.
- Johnson, R.A., 2001. Biogeography and community structure of North American seed-harvester ants. *Annual Review of Entomology* 46, 1–29.
- Kaspari, M., Weiser, M.D., 1999. The size-grain hypothesis and interspecific scaling in ants. *Functional Ecology* 13, 530–538.
- Kaspari, M., Yuan, M., Alonso, L., 2003. Spatial grain and the causes of regional diversity gradients in ants. *American Naturalist* 161, 459–477.
- Lockwood, J.L., Brooks, T.M., Mckinney, M.L., 2000. Taxonomic homogenization of the global avifauna. *Animal Conservation* 3, 27–35.
- Lockwood, J.L., Mckinney, M.L. (Eds.), 2001. *Biotic Homogenization*. Kluwer Academic, New York.
- MacMahon, J.A., Mull, J.F., Crist, T.O., 2000. Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. *Annual Review of Ecology and Systematics* 31, 265–291.
- Magurran, A.E., 1988. *Ecological Diversity and its Measurement*. Princeton University Press, New Jersey.
- Marchetti, M.P., Light, T., Feliciano, J., Armstrong, T., Hogan, Z., Viers, J., Moyle, P., 2001. Homogenization of California's fish fauna through abiotic change. In: Lockwood, J.L., Mckinney, M.L. (Eds.), *Biotic Homogenization*. Kluwer Academic, New York, pp. 259–278.
- Marchetti, M.P., Light, T., Moyle, P., 2004. Fish invasions in California watersheds: testing hypotheses using landscape patterns. *Ecological Applications* 14, 1507–1525.
- Markin, G.P., 1970. Seasonal life cycle of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* 63, 1238–1242.
- McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* 14, 450–453.
- McKinney, M.L., 2004. Measuring floristic homogenization by non-native plants in North America. *Global Ecology and Biogeography* 13, 47–53.
- Ness, J.H., Bronstein, J.L., Andersen, A.N., Sogard, S.M., 2004. Ant body size predicts dispersal distance of ant-adapted seeds: implications of small-ant invasions. *Ecology* 85, 1244–1251.
- Newell, W., Barber, T.C., 1913. The Argentine ant. *USDA Bureau of Entomology Bulletin* (Washington, DC) 122, 1–98.

- Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E., Fausch, K.D., 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* 19, 18–24.
- Passera, L., 1994. Characteristics of tramp species. In: Williams, D.F. (Ed.), *Exotic Ants: Impact and Control of Introduced Species*. Westview Press, Boulder, CO, pp. 23–43.
- Peters, H.A., Chiariello, N.R., Mooney, H.A., Levin, S.A., Hartley, A.E., 2005. Native harvester ants threatened with widespread displacement exert localized effects on serpentine grassland plant community composition. *Oikos* 109, 351–359.
- Rahel, F.J., 2002. Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics* 33, 291–315.
- 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.
- 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.
- Suarez, A.V., Case, T.J., 2002. Bottom-up effects on persistence of a specialist predator: ant invasions and horned lizards. *Ecological Applications* 12, 291–298.
- Suarez, A.V., Richmond, J.Q., Case, T.J., 2000. Prey selection in horned lizards following the invasion of Argentine ants in southern California. *Ecological Applications* 10, 711–725.
- Tremper, B.S., 1976. Distribution of the Argentine ant, *Iridomyrmex humilis* Mayr, in relation to certain native ants of California: ecological, physiological, and behavioral aspects. Ph.D. Thesis, University of California at Berkeley.
- Tsutsui, N.D., Suarez, A.V., Holway, D.A., Case, T.J., 2000. Reduced genetic variation in the success of an invasive species. *Proceedings of the National Academy of Sciences* 97, 5948–5953.
- Ward, P.S., 1987. Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the lower Sacramento River Valley and its effects on the indigenous ant fauna. *Hilgardia* 55 (2), 1–16.