



Edge effects of an invasive species across a natural ecological boundary

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Abstract

Natural habitats adjacent to human-modified areas often suffer edge effects stemming from physical disturbance, elevated predator densities, or invasive species. Although seldom documented, detrimental edge effects can also occur at natural ecological boundaries. Here I examine the spatial pattern and ecological effects of a biological invasion at well-delineated and abrupt edges between riparian corridors and coastal sage scrub at 10 sites in southwestern California. The invasive Argentine ant *Linepithema humile* thrives in moist riparian corridors but decreases greatly in number with increasing distance into adjacent dry scrub habitats. As *L. humile* numbers decrease, both the number of native ant workers and the number of native ant species captured in pitfall traps increase. Argentine ants appear to suppress native ants within at least 50 m of riparian corridors, but these effects diminish to undetectable levels by 200 m. At comparable uninvaded sites neither the number of native ant workers nor the number of native ant species captured in pitfall traps varies significantly across riparian-scrub edges. Areas subject to this edge effect may be sinks both for native ants and for organisms that depend on them for food or services. In general edge effects occurring at natural boundaries should receive increased attention as they might disrupt ecosystems not greatly altered by human activity.

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1. Introduction

Negative consequences attributable to edge effects are both diverse and well known (Wilcove et al., 1986; Janzen, 1986; Murcia, 1995). Numerous studies, for example, document biotic and abiotic edge effects in primary forest bordering anthropogenically modified habitats (Donavan et al., 1997; McGeoch and Gaston, 2000; Laurance et al., 2002). Such edge effects can physically degrade habitat (Gascon et al., 2000), endanger resident biota (Robinson et al., 1995), and reduce the functional size of nature reserves (Laurance and Yensen, 1991; Laurance, 2000).

A unifying feature of most edge effect studies is a focus on anthropogenic edges. Less often considered are detrimental edge effects at natural ecological boundaries. If such effects occur at natural edges, then it is essential to

assess their scale and importance. Unlike edge effects that result from anthropogenic activity, those occurring at natural edges might compromise the integrity of ecosystems not greatly modified by humans. Moreover, given the many recent studies addressing how natural boundaries affect different ecological and evolutionary processes (Polis and Hurd, 1995; Smith et al., 1997; Fagan et al., 1999; Nakano and Murakami, 2001; Grover and Wilbur, 2002), investigations aimed at uncovering the importance of harmful edge effects in these contexts now seem highly relevant. For example, transfers of energy, nutrients, and resources that often occur at ecological boundaries (Laurance et al., 2001) might be monopolized by invasive species. If so, such cross-boundary subsidies (Janzen, 1986) might result in non-native species disrupting community structure even where they would otherwise fail to persist.

In this study I examine the effects caused by Argentine ants *Linepithema humile* on native ants at natural boundaries. Argentine ants are a widespread and

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abundant invasive species (Holway et al., 2002a). In many parts of the world *L. humile* invades natural environments (Suarez et al., 2001) and displaces native ants (Erickson, 1971; Bond and Slingsby, 1984; Ward, 1987; Human and Gordon, 1996; Cammell et al., 1996; Carpintero et al., 2004). In California mesic riparian woodlands support high densities of Argentine ants and serve as corridors of dispersal (Tremper, 1976; Ward, 1987; Holway, 1998a); Argentine ants almost entirely displace native ants from these habitats (Ward, 1987; Holway, 1998b). Chaparral and coastal sage scrub, in contrast, are usually too dry to support *L. humile*. These habitats become invaded primarily where fragmented and irrigated by urban runoff (Suarez et al., 1998; Holway et al., 2002b) or in coastal areas where summer fog ameliorates the summer drought. At riparian-scrub edges, however, Argentine ants may invade otherwise unsuitable scrub habitat because of its juxtaposition with riparian woodland. Here I examine the spatial scale of this edge effect and its impact on native ants at replicate sites distributed across a large geographic area.

2. Methods

This study included five replicate pairs of riparian – scrub boundaries in southwestern San Diego County, California (Fig. 1). Each pair of sites was located along the same river or creek and included one site invaded by Argentine ants and one otherwise similar site that still supported native ants (Fig. 1). All sites were located away from urban development, situated inside protected federal, state, or county preserves, and connected to large, unfragmented ecosystems. The habitats at each site were natural in the sense that they contained common native perennial plants typical of the region and were not altered much by human activity. Within each watershed I matched sites for habitat, aspect, and slope.

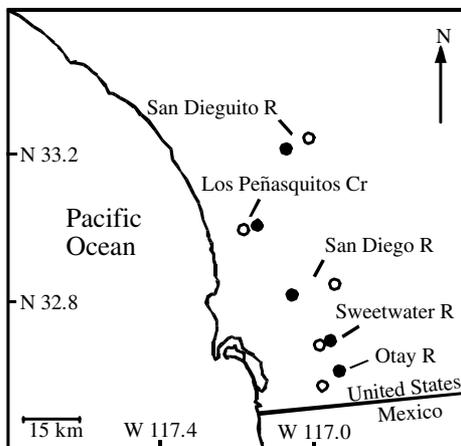


Fig. 1. Map of study sites in southwestern California. Open circles are sites that lack Argentine ants; closed circles are invaded sites.

Invaded and uninvaded sites did not differ, on average, in their proximity to the coast (Invaded: 21 ± 3 km, Uninvaded: 24 ± 6 km (mean (± 1 SE))), elevation (Invaded: 98 ± 18 m, Uninvaded: 103 ± 26 m), or distance to nearest paved road (Invaded: 0.52 ± 0.13 km, Uninvaded: 0.40 ± 0.10 km). Sites within each watershed were on average 8 km apart. Given the geographical scope of the sampling effort, the perennial flora varied somewhat from drainage to drainage, but all sites exhibited the following similarities. Riparian corridors varied in width from 50 to 100 m and were composed of *Salix* spp., *Populus fremontii*, *Platanus racemosa*, and *Quercus agrifolia*. Outside of river corridors, lush riparian vegetation always gave way abruptly (i.e., within a few meters at all 10 sites) to open formations of xeric coastal sage scrub consisting primarily of *Artemisia californica*, *Eriogonum fasciculatum*, *Malosma laurina*, *Salvia mellifera*, and *S. apiana*.

The sites described above can be classified as either invaded or uninvaded (Fig. 1) because Argentine ants exhibit inherently limited powers of dispersal. Unlike ants with winged dispersal of gynes, colonies of *L. humile* appear to reproduce only by budding (Newell and Barber, 1913). This mode of dispersal constrains the rate of spread to around 100 m yr^{-1} in suitable habitat and prevents jump-dispersal of propagules ahead of invasion fronts (Suarez et al., 2001). Because of these limited dispersal capabilities and the vagaries of human introduction, it is common for riparian corridors, such as those included in this study, to contain invaded and uninvaded sections (Tremper, 1976; Ward, 1987; Holway, 1995). Based on the Argentine ant's dispersal limitations and its local distribution in the areas surrounding invaded sites in this study, this species has probably been present for a minimum of several years at each of the five invaded sites (and probably for longer). Several lines of evidence suggest that uninvaded sites are all at risk of being invaded eventually: (1) uninvaded sites are directly connected to invaded sites via continuous riparian vegetation, (2) Argentine ants are advancing along riparian corridors at all five invaded sites, and (3) riparian habitat at uninvaded sites appears to be suitable to Argentine ants.

At each of the 10 sites shown in Fig. 1 I used pitfall traps to sample ants along a transect spanning riparian-scrub edges. Pitfalls are a commonly used and effective method to sample ants (Porter and Savignano, 1990; Suarez et al., 1998; Holway, 1998b; Morrison, 2002; Morrison and Porter, 2003). This is especially true for coastal sage scrub, where techniques such as leaf-litter sampling and dead wood inspection would be of little use given that ants from this habitat seldom nest in the sparse leaf litter or in twigs. At each site I established a linear, 200-m transect originating at and oriented perpendicular to the riparian corridor. On each transect I placed a set of five traps at each of four distances from

the edge of the riparian corridor: 25, 50, 100, and 200 m. I also placed a set of traps inside each riparian corridor; these sets are referred to as 0-m traps. For each distance category, I placed the individual traps within a set approximately 10 m apart in an irregular line parallel to the riparian corridor. Each trap consisted of a 50 ml plastic centrifuge tube buried with the rim flush with the level of the soil. All traps contained 30 ml of a non-toxic dilute saline-detergent solution (Burger et al., 2001). I left traps in the ground for five days during each of three sampling periods (May 2002, July 2002, September 2002). The total sampling effort was 750 pitfalls. About 3% of all traps were dug up by mammals, but trap loss was distributed fairly evenly across site \times distance categories such that each category received an approximately equivalent level of sampling. After I removed traps from the field I sorted ants from non-ants and placed samples in 95% ethanol. I identified ants to species and deposited voucher specimens in the Bohart Museum of Entomology, University of California, Davis (UCDC). In a recent study also conducted in San Diego, Suarez et al. (1998) found that the approximate level of sampling employed here was sufficient to detect a majority of ant species within sites similar in size to those included in this study.

I used split-plot analysis of variance (ANOVA) to compare invaded and uninvaded sites with respect to the number of native ant species and the number of native ant workers. There were two main effects in each ANOVA: (1) status (invaded and uninvaded), and (2) distance away from the edge of the riparian corridor (0, 25, 50, 100, and 200 m). Status was a whole-plot effect; distance was a split-plot effect. Blocks of sites were random effects; status and distance were treated as fixed effects. For the ANOVA with the number of native ant species as the dependent variable, I used cumulative species counts for each site \times distance category as data points. In the ANOVA with worker abundance in pitfalls as the dependent variable, for each site \times distance category, I calculated the number of native ant workers captured per trap and averaged these values across the three sampling periods. I used these means (\log_{10} -transformed) as data points. Note that abundance estimates reflect above-ground activity during sampling periods; these estimates may be uncorrelated with colony density. I performed all statistical tests using SYSTAT, Version 5.2.1.

3. Results

Argentine ants were extremely common in pitfalls at all five invaded riparian corridors but decreased sharply in abundance with increasing distance into the coastal sage scrub (Fig. 2(a)). Argentine ants were captured 100 m away from riparian corridors at all five invaded sites

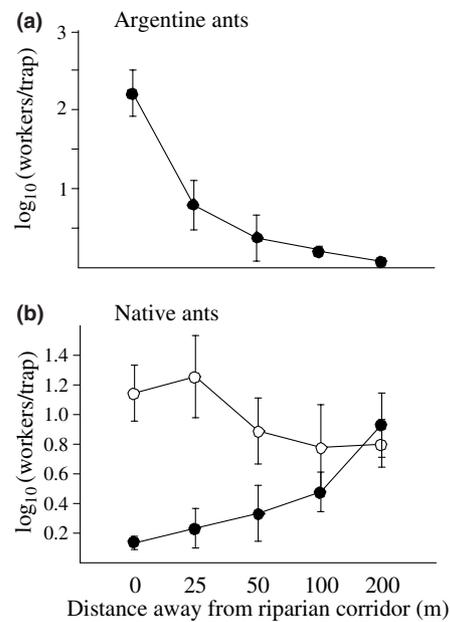


Fig. 2. Mean (± 1 SE) abundance of (a) Argentine ants and (b) native ants captured in pitfalls at 10 riparian-scrub edges. Open circles are sites that lack Argentine ants ($n = 5$); closed circles are invaded sites ($n = 5$).

but reached 200 m at only one site (Table 1). Consistent with the dispersal limitations of this species, no Argentine ants were recorded from uninvaded sites (Table 1). Abundance of native ants in pitfalls across the riparian-scrub edge depended strongly on the presence of Argentine ants (Fig. 2(b); split-plot ANOVA, status \times distance interaction: $F_{4,32} = 4.40$, $p = 0.006$). Native ant abundance in pitfalls increased linearly with distance away from the corridor at invaded sites (Fig. 2(b); linear contrast: $F_{1,32} = 11.81$, $p = 0.002$), whereas no significant relationship existed between distance and abundance in pitfalls at uninvaded sites (Fig. 2(b); linear contrast: $F_{1,32} = 2.142$, $p = 0.153$). Compared to uninvaded sites, invaded sites supported fewer native ants (Fig. 2(b); split-plot ANOVA: $F_{1,4} = 8.58$, $p = 0.041$), but this was due primarily to low abundance in the first three distance categories. By 200 m, the numbers of native ants in pitfalls at invaded sites were similar to those from uninvaded sites (Fig. 2(b)).

As with native ant abundance, the number of native ant species captured in pitfalls across the riparian-scrub edge depended strongly on the presence of Argentine ants (Fig. 3; split-plot ANOVA, status \times distance interaction: $F_{4,32} = 7.70$, $p < 0.0005$). The number of native ant species detected increased linearly with distance away from the riparian corridor at invaded sites (Fig. 3; linear contrast: $F_{1,32} = 24.98$, $p < 0.0005$), whereas no significant relationship existed between distance and the number of native ant species in pitfalls at uninvaded sites (Fig. 3; linear contrast: $F_{1,32} = 0.47$, $p = 0.500$). Compared to uninvaded sites, invaded sites

Table 1
Ants recorded at riparian-scrub edges

Status	Invaded					Uninvaded				
	0	25	50	100	200	0	25	50	100	200
Subfamily Ponerinae										
<i>Hypoponera opacior</i>	1	0	0	1	0	1	0	0	0	0
<i>Hypoponera opaciceps</i>	0	0	0	0	0	1	0	0	0	0
Subfamily Dolichoderinae										
<i>Dormyrmex insanus</i>	0	0	0	1	1	1	1	2	0	0
<i>Forelius mccooki</i>	0	0	2	1	5	2	4	4	3	4
<i>Linepithema humile</i>	5	5	5	5	1	0	0	0	0	0
<i>Liometopum occidentale</i>	0	0	0	0	0	3	0	0	0	0
<i>Tapinoma sessile</i>	0	0	0	0	1	5	1	0	0	0
Subfamily Formicinae										
<i>Camponotus dumetorum</i>	0	0	0	1	1	0	0	0	0	0
<i>Camponotus</i> sp. cf. <i>semitestaceus</i>	0	0	0	0	0	3	1	0	0	0
<i>Camponotus vicinus</i>	0	0	0	1	0	0	0	0	0	0
<i>Formica francoeuri</i>	0	0	0	0	0	1	1	1	1	0
<i>Formica moki</i>	0	0	0	1	0	1	0	0	0	1
<i>Myrmecocystus wheeleri</i>	0	0	0	0	0	0	0	0	0	1
<i>Paratrechina</i> sp. cf. <i>terricola</i>	0	0	0	0	0	0	0	0	0	1
<i>Prenolepis imparis</i>	0	0	0	0	0	1	0	0	0	0
Subfamily Myrmicinae										
<i>Cardiocondyla mauritanica</i>	0	1	0	0	0	1	0	0	0	0
<i>Crematogaster californica</i>	0	1	2	2	5	1	2	1	4	5
<i>Crematogaster hespera</i>	0	0	0	0	0	3	1	0	0	0
<i>Cyphomyrmex wheeleri</i>	0	0	0	0	0	0	2	1	2	1
<i>Messor andrei</i>	0	0	0	0	0	0	0	1	0	0
<i>Monomorium ergatogyna</i>	0	0	0	1	1	1	0	0	0	1
<i>Pheidole californica</i>	0	1	0	0	0	0	0	0	0	0
<i>Pheidole cerebrostor</i>	0	2	1	0	0	0	2	2	2	2
<i>Pheidole clementensis</i>	0	2	2	2	1	0	0	1	2	0
<i>Pheidole hyatti</i>	0	0	0	0	0	1	0	0	0	0
<i>Pheidole pilifera</i>	0	0	0	0	0	0	0	0	1	0
<i>Pheidole vistana</i>	0	0	0	4	5	1	4	4	4	5
<i>Pogonomyrmex californicus</i>	0	0	0	0	0	1	2	1	0	0
<i>Pogonomyrmex rugosus</i>	0	0	0	0	0	1	1	1	1	1
<i>Solenopsis amblychila</i>	0	0	0	1	1	1	2	1	0	1
<i>Solenopsis molesta</i>	2	2	0	0	2	2	3	1	1	1
<i>Solenopsis xyloni</i>	0	0	2	2	4	1	5	4	1	1
<i>Stenamma</i> sp. cf. <i>punctatoventre</i>	1	0	0	0	0	0	0	0	0	0
<i>Temnothorax andrei</i>	3	2	2	3	2	1	3	5	2	2
<i>Tetramorium spinosum</i>	0	0	0	1	3	0	1	2	1	2

Table entries refer to number of sites (out of 5) that each species was recorded in each distance category. Distances refer to meters away from riparian corridors. Non-native species are in bold type.

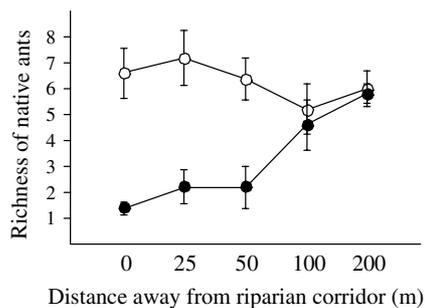


Fig. 3. Mean (\pm 1 SE) number of native ant species captured in pitfalls at 10 riparian-scrub edges. Open circles are sites that lack Argentine ants ($n = 5$); closed circles are invaded sites ($n = 5$).

supported fewer native ant species (Fig. 3; split-plot ANOVA: $F_{1,4} = 10.07$, $p = 0.034$), but this was due to depressed diversity in the first three distance categories. At both 100 and 200 m, the number of native ant species detected at invaded sites had risen to levels similar to those recorded in these same distance categories at uninvaded sites.

Above-ground foraging native ants were most affected by Argentine ants. Inside invaded riparian corridors the only native ants detected were litter-dwelling and below-ground foraging species: *Temnothorax andrei*, *Solenopsis molesta*, *Hypoponera opacior*, and *Stenamma* sp. cf. *punctatoventre* (Table 1). Above-

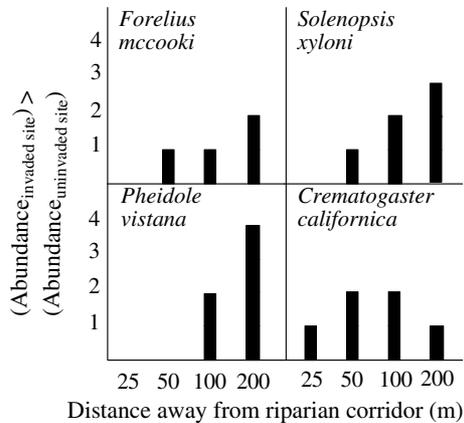


Fig. 4. Relative susceptibility of native ants to displacement by Argentine ants. Height of each bar corresponds to the number of cases (out of 5) that the abundance of a native ant species at an invaded site exceeded its abundance at a paired, uninvaded site. Sites are paired with respect to watershed and distance category. The four native ants included were the most common and widespread omnivorous and above-ground foraging species detected in scrub habitats.

ground foraging species, such as *Liometopum occidentale*, *Camponotus* sp. cf. *semitestaceus*, *Tapinoma sessile*, and *Crematogaster hespera*, were common in uninvaded riparian corridors but were entirely absent from invaded ones. Outside of invaded riparian corridors, in the scrub areas most affected by Argentine ants (e.g., 25 and 50 m distance categories), above-ground foraging native ants were largely absent, even though they were common beyond 100 m at invaded sites and at all distance categories at uninvaded sites (Table 1). Notable among these absences were ecologically important harvester ants (e.g., *Pogonomyrmex* spp.). Of the four most common and widespread omnivorous native ants detected in scrub habitats, *Solenopsis xyloni*, *Forelius mccooki*, and *Pheidole vistana* all appeared highly susceptible to displacement by Argentine ants, whereas no clear pattern was evident for *Crematogaster californica* (Fig. 4 and Table 1).

4. Discussion

This study provides an empirical example of an edge effect produced by an invasive species at a natural ecological boundary. At multiple sites spread across a large area (Fig. 1), invaded riparian corridors appeared to promote the local spread of Argentine ants into coastal sage scrub, a habitat type usually unsuitable to *L. humile* (Suarez et al., 1998; Holway et al., 2002b). Argentine ants attained maximum abundance inside riparian corridors, and native ants were almost entirely absent from these sites (Figs. 2,3 and Table 1). With increasing distance away from invaded corridors, *L. humile* numbers declined dramatically and monotonically (Fig. 2(a)), while the number of native ant workers (Fig. 2(b)) and

the number of native ant species (Fig. 3) captured in pitfalls increased steadily. The decline of Argentine ants with increasing distance from invaded riparian corridors (Fig. 2(a)) qualitatively matches that reported for anthropogenic moisture gradients found at edges between well-watered urban areas and dry scrub habitats elsewhere in southern California (Suarez et al., 1998; Bolger et al., 2000; Holway et al., 2002b). Unlike those previous studies, however, the pattern shown in Fig. 2(a) seems unlikely to have resulted from a gradient in anthropogenic disturbance. All sites were located away from urban development, situated inside protected areas, and embedded in large, unfragmented tracts of coastal sage scrub and chaparral. Evidence that invaded and uninvaded sites were well matched (in respects other than the presence or absence of Argentine ants) comes from Figs. 2 and 3. Both the number of native ant workers (Fig. 2(b)) and the number of native ant species (Fig. 3) captured in pitfalls were strikingly similar between invaded and uninvaded sites in the 200 m distance category.

Invaded riparian corridors might be subsidizing the invasion of Argentine ants into drier scrub habitats, which would otherwise not support colonies of this species. Both abiotic and biotic factors could contribute to this effect. Soil moisture, for example, appears to govern the distribution (Tremper, 1976; Ward, 1987), abundance (Holway et al., 2002b), and rate of spread (Holway, 1998a) of Argentine ants in the seasonally dry habitats of California. Compared to ants native to interior and southern California, Argentine ants more readily succumb to aridity and thermal stress (Tremper, 1976; Holway et al., 2002b). Because of these physiological constraints and because Argentine ants do not nest very deeply underground, they remain largely confined to areas with adequate levels of superficial soil moisture. For this reason, mesic riparian woodlands in California represent excellent habitat. Riparian corridors may also provide important food resources. For Argentine ants, a key resource may be honeydew-excreting insects, such as aphids and scales (Newell and Barber, 1913). Riparian corridors support large aggregations of these insects (personal observation), which may enable *L. humile* to persist at high densities, as has been found for other ant species that exploit honeydew-excreting insects (Davidson et al., 2003).

Coastal sage scrub sites in this study became invaded only when in close proximity to invaded riparian corridors. Opportunistic and somewhat nomadic in its nesting behavior (Newell and Barber, 1913), *L. humile* forage and nest in near-corridor scrub areas under suitable abiotic conditions (e.g., at night or in winter and early spring when soils remain moist from winter rains), but mostly desert these areas when conditions become unfavorable (personal observation). Seasonal relocation along a moisture gradient was noted by

Markin (1970) who observed Argentine ants in southern California nesting on a scrub covered hillside adjacent to a citrus orchard during winter only to abandon it in favor of the shadier orchard during summer. An alternative hypothesis for the Argentine ant's limited ability to penetrate scrub (Fig. 2(a); see also Holway et al., 2002b) could involve biotic resistance in the form of interspecific competition from native ants. However, at the uninvaded sites in this study neither the number of native ant workers nor the number of native ant species captured in pitfalls varied significantly across riparian-scrub edges (Figs. 2(b) and 3). Assuming invaded sites exhibited a similar pattern prior to invasion, riparian and scrub habitats at these sites might have offered comparable levels of biotic resistance.

Although this study is the first to demonstrate statistically the effects of Argentine ant invasions at natural boundaries, previous studies have commented on analogous phenomena. At a site in central California, for example, Kennedy (1998) found that Argentine ants were common in a riparian corridor and in adjacent coastal sage scrub (growing on one side of a creek) but were absent from adjacent chaparral (growing on the opposite side of the creek). Because Kennedy (1998) conducted his study at the leading edge of a single invasion front, however, it is difficult to know whether this pattern reflects static distributional limits or whether Argentine ants simply had not yet invaded unoccupied areas. In southern Portugal Way et al. (1997) found Argentine ants in areas with sand and clay loam soils but not in areas with sandy loam soils associated with metamorphic rocks. The mechanism underlying this association is not known (Way et al., 1997). The strong signal of soil moisture observed in the present study may be a result of San Diego's more arid climate, which averages only ≈ 250 mm annual rainfall.

The edge effect documented in this study may well transform riparian-scrub edges into sinks not only for native ants but also for organisms that depend on them for food or services. Argentine ants apparently eliminated or greatly reduced nearly all ant species within 50 m of riparian corridors. It seems likely that the replacement of this native ant community by a single, non-native species will give rise to a variety of direct and indirect ecological effects. The loss of large bodied harvester ants (e.g., *Pogonomyrmex* and *Messor*), for example, may well ramify throughout the community to affect plants that depend on these ants to disperse their seeds (Carney et al., 2003) and vertebrates that rely on them for food (Suarez and Case, 2002). These results imply that riparian reserves may be susceptible to species loss both inside and outside of the riparian corridor unless they are bordered by a sufficient buffer zone of upland habitat.

The importance of edge effects caused by invasive species at natural ecological boundaries generally de-

serves further scrutiny, perhaps especially in cases that involve resource subsidies. In such situations strongly competitive invasive species may not only dominate native species in source habitats but also in habitats that are unsuitable for the invader in the absence of the subsidy (see also Maurer and Zedler, 2002). Such spatially subsidized exclusion of native species could lead to important and unforeseen ecological effects outside of the main areas of invasion. A subsidized invader, for example, might disrupt ecological communities in sink habitats where it is present only intermittently.

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