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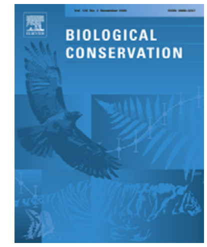

Spatial and temporal variation in the Argentine ant edge effect: Implications for the mechanism of edge limitation

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ABSTRACT

One consequence of human land-use is the exposure of native communities to invasive human commensal species along edges. Argentine ants (*Linepithema humile*) invade a variety of habitats in California with consequent dramatic declines in native ants. In coastal southern California, USA Argentine ants appear to be an edge effect in small habitat fragments [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]. They invade fragments from the urban edge, but only penetrate coastal sage scrub (CSS) habitat to a distance of approximately 200 m. Using pitfall sampling in edge (<250 m from the urban edge) and interior (>600 m from the edge) habitat I tested whether there is also an Argentine ant edge effect in the largest blocks of habitat in the landscape and investigated patterns of spatial and temporal variation in native and Argentine ants. Argentine ants were common in coastal sage scrub habitat within 250 m of urban edges, but rare in interior areas. Correspondingly, native ants were significantly less abundant and diverse in edge areas as compared to interior. Over the period 1997–2000 Argentine ants did not become more abundant in interior habitat suggesting it will remain a refuge for native ants. Argentine ant abundance in edge plots varied greatly among years and sites. Annual variation in abundance was positively related to annual rainfall. Increased soil moisture near edges due to urban runoff has often been suggested as the mechanism that allows the invasion of edge but not interior habitat. This hypothesis predicts that edge habitat downslope of the urban edge should support invasions of higher abundance and greater spatial penetration than habitat upslope. However, I found that edge slope did not predict the extent of invasion, whereas, soil type did. Coarse, well-drained soils supported an Argentine ant invasion of lower abundance and lesser spatial penetration than soils that should retain more moisture. These patterns of spatial and annual variation are more consistent with a biotic flow mechanism where ants move from urban habitat into CSS sites that are temporarily favorable, rather than an abiotic flow where urban runoff causes a physical change to CSS habitat near edges. This invasion affects a substantial area of habitat, however, the inability of Argentine ants to invade interior habitat suggests that refugia for native ants will persist if large unfragmented blocks of habitat are maintained.

1. Introduction

Habitat fragmentation and the creation of edge that accompanies it are widely perceived to be among the greatest threats to global biodiversity (Wilcove et al., 1986; Ries et al., 2004). One consequence of habitat fragmentation and the creation of edge between natural habitat and human land-uses is the increased exposure of native species

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to human commensal species. A number of studies have documented increased abundance of invasive, non-native arthropod species in fragments or along fragment edges (Suarez et al., 1998; Hobbs, 2001; Ness, 2004). The invasion of these non-natives represents one class of edge effects.

Edge effects have been studied most closely in forest fragments in agricultural landscapes in eastern and midwestern North America and in tropical regions (Murcia, 1995; Robinson et al., 1995). As the world becomes more urban (Berry, 1990; Roodman, 1996) edge between urban development and natural habitat increases as does the importance of understanding the ecological changes that occur at these interfaces (Babbitt, 1999). Urban-natural edges may be more ecologically active than agricultural-natural edges due to the bio-physical intensity of urban land-use (Pickett et al., 2001). The inputs of materials, water, energy, nutrients and human commensal species to urban land-uses can be extreme and can spillover to adjacent natural habitat.

In coastal southern California urban residential development is typically the land-use that fragments coastal sage scrub habitat. Coastal sage scrub is a drought-deciduous shrub habitat notable for its restricted range within the US and high diversity of endemic plants and animals (Atwood and Noss, 1994). Approximately 85% of this habitat has been converted to human land-uses and what remains is fragmented and exposed to urban edge to varying degrees (Atwood and Noss, 1994). This land-use pattern has biotic effects, for example, many species of the coastal sage scrub avifauna exhibit fragmentation and edge sensitivity (Bolger et al., 1997; Bolger, 2002; Crooks et al., 2001). There is an ongoing conservation planning effort for this region (Feldman and Jonas, 2000) and the reserve system that results will by necessity be set within an urban matrix. Understanding urban edge and fragmentation effects will be vital to the success of this conservation effort.

A potentially strong urban edge effect in coastal southern California is exposure to the exotic Argentine ant (*Linepithema humile*). Argentine ants have become established in Mediterranean climates worldwide (Passera, 1994; Majer, 1994) and have been implicated in the decline of native ants (Erickson, 1971; Ward, 1987; Majer, 1994; Holway, 1995; Cammell et al., 1996; Human and Gordon, 1996) and other invertebrates (Cole et al., 1992; Human and Gordon, 1997; Bolger et al., 2000). Argentine ants are the common house ant in coastal San Diego County and occur at high abundance in urban areas (Holway et al., 2002). Suarez et al. (1998) have documented that they invade small urban habitat fragments (1–100 ha) and appear to contribute to the decline of most native ants in those fragments. Argentine ants possess interference and exploitative competitive advantages over native California ants (Human and Gordon, 1996; Holway, 1999).

Work in several systems suggests that Argentine ants may be an urban edge effect in coastal California. Suarez et al. (1998) found that larger fragments (ca. 100 ha) had lower Argentine ant abundance and higher native ant abundance in the fragment center suggesting that large fragments had Argentine ant free refugia at greater distances from the fragment edge. In the 482 ha Jasper Ridge Reserve in Palo Alto, CA, set in an urban and agricultural matrix, Argentine ants were concentrated along the reserve edge and native ants were associated with the reserve interior (Human et al., 1998). Edge effects are generally defined as edge-oriented gradients in biotic or abiotic variables (Murcia, 1995). Thus, there are potentially two edge effects associated with Argentine ants, their increased abundance near edges and the resulting decreased abundance and diversity of native ants. The main focus of this paper is the former.

If Argentine ants are an edge effect, what factors allow them to invade habitat near edges but also limits them to edge areas? Little attention has been paid to the mechanism responsible for the Argentine ant limitation to edge habitat. A variety of mechanisms have been proposed to explain both the penetration of edge species as well as to explain what limits these species to edge and restricts them from interior habitat (Fagan et al., 1999; Ries et al., 2004). An invasion across a habitat edge can result from one or both of two types of cross-boundary flows: abiotic or biotic. Abiotic flows are the movement of matter and energy across the edge (e.g. from urban to CSS habitat), and biotic flow is the movement of organisms. In the case of abiotic flow the effect on patterns of abundance is indirect – these flows change the edge environment to favor the invading species. Abiotic flows are similar to "allochthanous inputs" (Polis and Hurd, 1996). Biotic flows are analogous to Janzen's (1986) "cross-boundary subsidies" and their effect on abundance is direct and demographic. Fagan et al. (1999) point out the similarity between biotic flows and source-sink dynamics; the density in edge habitat can be subsidized by the flow of individuals from the neighboring source habitat and this can affect interspecific interactions in the edge habitat. Practically, it is important to differentiate among these mechanisms because the implications for control may be very different.

Features of Argentine ant population biology and the urban:CSS interface in San Diego provide support for both mechanisms. In terms of abiotic factors, it is clear that Argentine ants are limited by moisture in this and other arid regions. They have been shown to have less resistance to dessication than native ants in arid regions of California (Tremper, 1976; Holway et al., 2002) and Australia (Walters and Mackay, 2003). Schilman et al. (2005) demonstrated higher rates of water loss and greater cuticular permeability in Argentine ants than in native California ants. In the Central Valley of California, Argentine ants invade riparian areas (if they have year-round water flow; Holway, 1998) but do not invade adjacent, drier, upland habitat (Ward, 1987). Menke and Holway (2006) have demonstrated experimentally that irrigation of coastal sage scrub habitat leads to an increase in Argentine ant abundance and spatial spread. These observations have led a number of authors to hypothesize that Argentine ants can invade habitat near urban edges because urban runoff increases moisture availability there (Suarez et al., 1998; Menke and Holway, 2006).

Argentine ants are also a candidate for a biotic flow mechanism because they have a flexible social structure that allows for a particularly dynamic use of space. They are unicolonial with multiple queens per nest, and queens, workers and brood all move facultatively between ephemeral, shallow nests. Unlike most other ant species, Argentine ant queens disperse by crawling rather than flying (Holway, 1998). Colonies expand by budding by non-flying queens (Ingram and Gordon, 2003), perhaps in density-dependent