

Distance to suburban/wildland border interacts with habitat type for structuring exotic plant communities in a natural area surrounding a metropolitan area in central Chile

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Background: The explosive growth of urbanisation in Mediterranean ecosystems in Chile has favoured the rapid expansion of exotic plant species, yet factors driving these invasion patterns in adjacent natural areas remain poorly assessed.

Aims: To assess how distance to a suburban/wildland border, habitat type, site-scale disturbance and woody plant cover of native species influences the diversity of exotic species in a natural area surrounding the city of Santiago, Chile.

Methods: Three watersheds were chosen, and the diversity of exotic species was assessed in 36 100-m-long transects, equally distributed over two distance categories and three habitats. For each transect, we measured woody plant cover of native species and frequency of rabbit faeces as a measure of competitive exclusion and site-scale disturbance, respectively.

Results: Species diversity decreased as the distance from the suburban/wildland border increased, and it was found to be higher in north-facing habitats compared to south-facing and alluvial habitats. Neither native woody plant cover nor frequency of rabbit faeces had an effect on species diversity.

Conclusions: The current pattern of exotic plant species in this natural area is mainly influenced by the distance to suburban border and habitat type. An adequate management of conditions favouring exotic species in suburban/wildland border may prevent the spread of these into natural areas next to urban settings.

Keywords: Andean piedmont; exotic species; Mediterranean region; propagule source; Santiago de Chile; urbanisation

Introduction

Understanding the patterns and processes of plant invasion is becoming an increasingly important objective in conservation biology (Blackburn and Duncan 2001; Cassey et al. 2004; Pauchard and Shea 2006; Gassó et al. 2009). Owing to its increasing impact on biodiversity, such as alterations in community structure (Vila et al. 2006), modification of disturbance regimes (Mandle et al. 2011), changes in ecosystem dynamics (Evans et al. 2001) and homogenisation of local biota (Qian and Guo 2010; see Vilà et al. 2011 for a review), identifying the factors affecting exotic species distribution at different spatial scales is a necessary step to predict the impact of exotic species on native ecosystems. For plants, the effective establishment of exotic species in a new area is closely related to successful dispersion and habitat suitability (Rejmanek and Richardson 1996; Lonsdale 1999). From the perspective of the recipient site, successful dispersion is determined by the spatial location of propagule sources. Hence, assessment of the spatial distribution of propagule sources is necessary to evaluate the probability of invasion in surrounding areas (MacArthur and Wilson 1967; Hanski et al. 1994; Lockwood et al. 2005). For instance, after accounting for species-specific traits, Gassó et al. (2009) found that distance to the coastline had a negative correlation with the richness of invasive plant species, when

assessing patterns of exotic plant in Spain. Similarly, Rouget and Richardson (2003) found that the relative abundance of most widespread invasive species in the Cape Floristic Region, South Africa, was explained by the distance to the closest invasion source of these species.

However, although propagule distance is an important factor, exotic species will not be homogeneously spread over all habitat types, despite similar distance, and even more so, sometimes may fail to settle and establish. This suggests that exotic species–environment interactions cannot be ignored. Consequently, it was shown that environmental factors, such as habitat structure, level of disturbance and elevation, affect the establishment and expansion of exotic species in new areas at both local and regional scales (Rodgers and Parker 2003; Lake and Leishman 2004; Pauchard and Alaback 2004; Gassó et al. 2009). Thus, interactions between environmental factors and spatial factors must also be considered to better understand the distribution patterns of exotic species (Rouget and Richardson 2003).

Mediterranean ecosystems in south-central Chile have been widely invaded by exotic plant species, favoured by increasing human activities (Matthei 1995; Arroyo et al. 2000). Urban growth in this region (Romero and Ordenes 2004) as well as related agricultural and forestry activities (Pauchard et al. 2006) has caused a reduction in native plant

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communities and, at the same time, favoured the rapid expansion of exotic species. Land-use change may favour the increase of exotic plant species in natural areas, especially those adjacent to urban and suburban areas, leading to biotic homogenisation of the adjacent native ecosystems (McKinney 2006). Local disturbances near to suburban/wildland borders (e.g. roads) and the large concentration of exotic plants within urban parks and suburban gardens might act as dispersal routes and propagule sources of exotic species, respectively (Pauchard and Alaback 2004; Dehnen-Schmutz et al. 2007). For instance, roads were the main routes for the dissemination of exotic species into protected areas in the south of Chile (Pauchard and Alaback 2004; Fuentes et al. 2010). Alston and Richardson (2006) found that distance from putative source populations had a significant effect on exotic plant richness in a suburban area in Cape Town, South Africa, with richness of exotic species decreasing as distance from the suburban border (putative source) increased.

In spite of the prominent role that urbanisation may have on local patterns of exotic species diversity, the effects of urban settlements in Mediterranean ecosystems have rarely been studied (e.g. Pauchard et al. 2006) and the interaction with factors operating at a smaller scale is poorly understood. The Mediterranean ecosystems of south-central Chile are particularly important from a biological conservation perspective because they represent one of the 25 global biodiversity hotspots and their biological endemism is highly threatened by agriculture, mining and urbanisation (Myers et al. 2000).

The objective of this study was to examine the relationship between the diversity of exotic plant species in natural areas adjacent to urban areas, and a set of factors known to affect plant invasions are (1) distance to suburban/wildland border, (2) habitat type, (3) site-scale disturbance and (4) native woody plant species cover. We predicted that the diversity of exotic species would be lower in areas far from the suburban border as the suburban settings might act as a propagule source of exotic species to natural areas (Alston and Richardson 2006). Similarly, as exotic species have shown positive response to increases in light availability (Gurevitch et al. 2008) and the reduction in density of native plants (Lonsdale 1999), we predicted that exotic species diversity would increase as vegetation cover decreased and the site-scale disturbance increased (this later measured as activity of exotic herbivorous). Consequently, we hypothesised that diversity would be larger in north-facing habitats, which are more exposed to sunlight in the southern hemisphere, with sparse woody vegetation.

Material and methods

Study area

The study was conducted in the Mediterranean semi-arid region of the Andean piedmont adjacent to the Metropolitan

Area of Santiago (MAS; 33.434° S, 70.514° W; Di Castri and Hajek 1976). The Andean piedmont consists of a mosaic of Mediterranean shrubland composed of sclerophyllous trees and shrub species. Topography is rugged with multiple watersheds and ravines; elevation ranges from 700 to 1200 m. Variations in solar radiation and moisture modulate the structure of the vegetation at the watershed-scale, with the south-facing slope habitats (moister conditions) containing larger plant biomasses and more woody vegetation cover than the north-facing slopes (drier conditions; Armesto and Martinez 1978). Native woody plants have different levels of dominance in these habitats with the following species being the more dominant in their respective areas: *Colliguaya odorifera* and *Retamilla trinervia* in north-facing habitats, *Lithraea caustica* and *Kageneckia oblonga* in south-facing habitats, and *Quillaja saponaria* in alluvial habitats (Gajardo 1994). Agricultural and forestry lands have been described as main propagule sources of exotic species in south-central Chile (Fuentes et al. 2010; Pauchard and Barbosa 2013). However, our study focused on areas in which land-cover change appears due to urban expansion (Romero and Ordenes 2004).

Sampling design

The study was conducted in austral spring of 2005. Data were collected from 36 100-m-long transects, equally distributed over three watersheds that are located along the piedmont areas: San Ramon, Mahuida and Macul (Figure 1). At each watershed, transects were randomly situated at 150 and 750 m distance from the suburban/wildland border, which we consider as the boundary between permanently man-made urban areas (i.e. built-up areas and roads) and areas with semi-natural vegetation. At each distance category, transects were situated in three main types of habitat: north-facing slope, south-facing slope and alluvial flats. The final design ($n = 36$ transects) included two distance categories with 18 transects each, or alternatively, three habitat types with 12 transects each (Figure 2).

Presence and abundance (number of individuals) of exotic plant species were recorded in 50 1-m² plots along each transect (Figure 2). We registered all herbaceous and woody species, but excluded grasses as they were not identifiable in the absence of inflorescences/fruits. In addition, we measured woody cover of native plants along each transect using the point-intercept method (Jonasson 1988). We used European rabbit (*Oryctolagus cuniculus*) activity as an indirect measure of disturbance level at site scale. The European rabbit is an introduced and abundant herbivorous species in the Mediterranean ecosystem in Chile (Jaksic 1998), having a widespread and detrimental effect on native plant communities (Jaksic and Fuentes 1980; Fuentes et al. 1983), and favouring exotic species by promoting competitive exclusion (Holmgren et al. 2000; Keane and Crawley 2002). Although other disturbance sources may explain the diversity of exotic plant species in south-central Chile at large

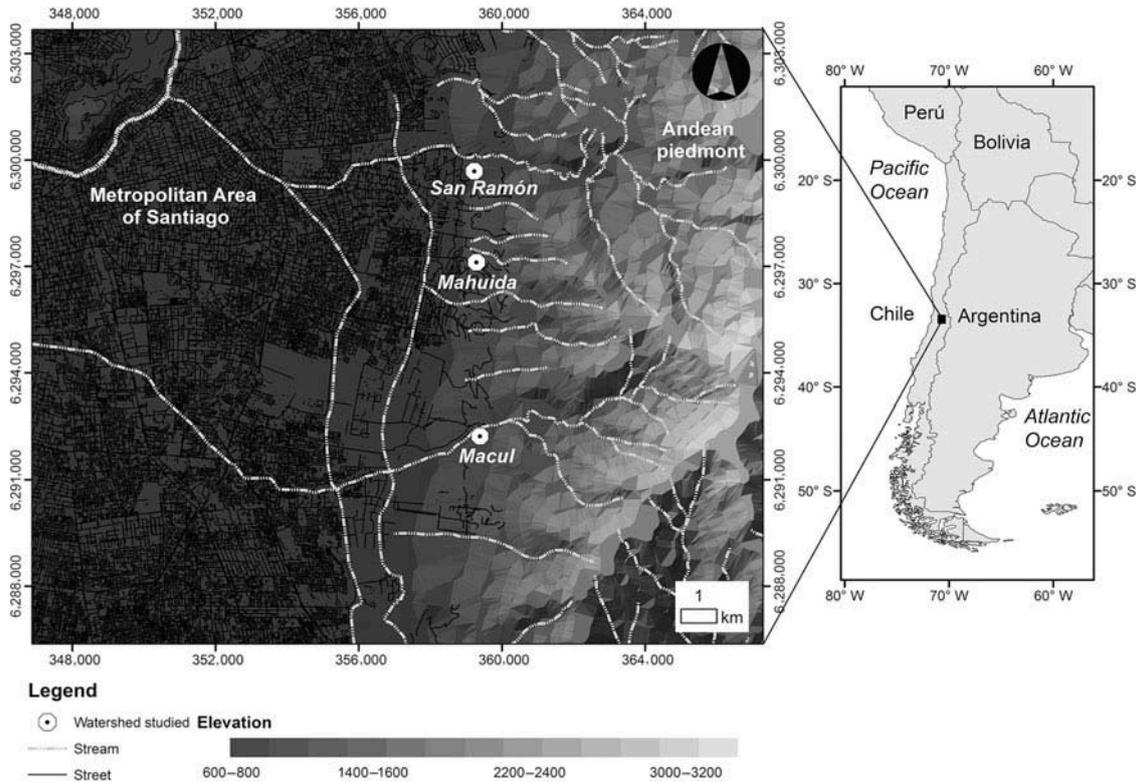


Figure 1. Watersheds used in the study, located in the Andean piedmont, adjacent to the metropolitan area of Santiago, Chile.

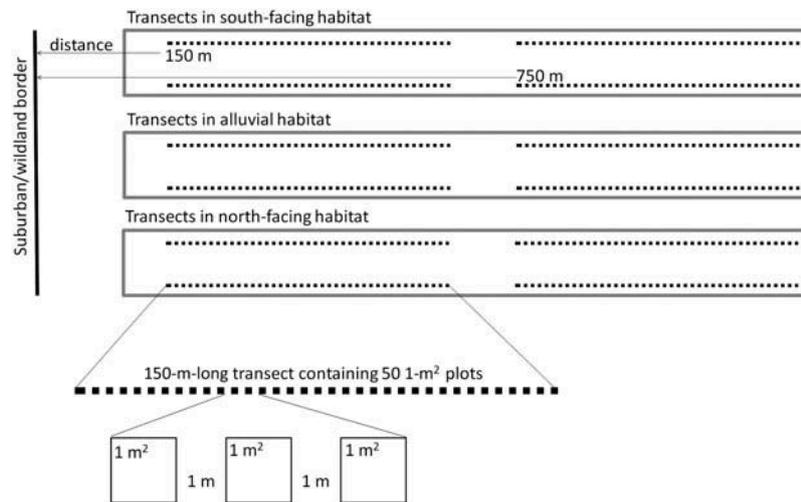


Figure 2. Sampling design used to assess the relationship between exotic plant diversity and spatial and environmental factors. Grey rectangles represent habitat types (i.e. south-facing, alluvial and north-facing habitats). Dotted lines (within each grey rectangle) represent the 100-m transects deployed at 150 and 750 m from the suburban/wildland border ($n = 18$). Solid line squares indicate 1-m² plots where rabbit activity and native woody plant cover were assessed ($n = 50$ per transect).

scale (e.g. land-cover change, Arroyo et al. 2000; Fuentes et al. 2010; Pauchard and Barbosa 2013), we considered rabbit activity to be an adequate index to represent disturbance level at local scale in our area. Rabbit activity at each transect was estimated as the relative frequency of rabbit faeces (number of 1-m² plots with faeces present divided by the total number of plots [50]).

Statistical analyses

The richness of exotic species and their relative abundance were calculated at each transect. With this information, we measured exotic species diversity (as dependent variable) in each category (distance and habitat type) by using the Shannon–Wiener index (H') (Krebs 1989). We used Shannon–Wiener over other indices due to its sensitivity

to changes in rare species, which largely dominated our exotic plant community (Itô 2007; Table S1).

As assumptions of normality and homogenous variance were met for species diversity, we used linear mixed-effect models with the ‘watershed’ as a random factor to assess the relationship between exotic species diversity and distance from the suburban/wildland border, type of habitat, native woody cover and relative frequency of rabbit faeces. This allowed us to analyse all watersheds simultaneously (with an intercept for each one), facilitating the capture of general patterns and reducing type-2 errors owing to a small sample size. We also tested for the interaction between distance and habitat type in order to explore whether habitat type affected exotic plant diversity significantly also for transects set far from the wildland/suburban border. A level of $P < 0.05$ was used in all statistical tests.

Results

A total of 49 exotic plant species from 19 families and 42 genera were recorded in the three watersheds we studied. *Erodium cicutarium*, *Rubus ulmifolius*, *Eschscholzia californica* and *Conium maculatum* were recorded in only few transects, but at high abundance, while *Medicago minima*, *Antirrhinum majus* and *Fumaria parviflora* were found to have low abundance. When studying habitat, *E. cicutarium*, *Centaurea melitensis*, *Poa annua*, *Vulpia myuros* and *Schismus barbatus* were the most abundant species in north-facing habitats; *R. ulmifolius*, *E. californica* and *Eucalyptus globulus* were the most abundant species in alluvial habitats; *C. maculatum*, *Anthriscus caucalis* and *Brassica nigra* were the most abundant species in south-facing habitats. Regarding distance categories, *E. cicutarium*, *R. ulmifolius*, *C. maculatum*, *A. caucalis* and *E. californica* were the most abundant species close to the suburban/wildland border, and *Bellardia trixago*, *Ulmus minor* and *F. parviflora* were the least abundant species (Table S1 in Supplemental data).

The diversity of exotic species (H') was significantly different between distance categories ($n = 36$, $F = 15.34$,

$P < 0.001$) and between habitat types ($n = 36$, $F = 10.93$, $P < 0.001$). A significant interaction between distance and habitat was also detected ($n = 36$, $F = 4.39$, $P = 0.02$). The analysis showed that exotic species diversity decreased with increasing distance from the suburban/wildland border (Table 1). Moreover, diversity was higher in north-facing habitats compared to south-facing habitats, but no significant differences were found between north- or south-facing habitats compared to alluvial habitats. The differences between habitats were not significant for transects far from the suburban/wildland border (at 750 m distance) but only for the transects close to the border (at 150 m distance; Figure 3). Rabbit faeces and native woody plant species cover were only slightly correlated ($r_{\text{pearson}} = -0.4$). The diversity of exotic species was not associated either with the abundance of rabbit faeces or with woody cover.

Discussion

Human-mediated introduction is a frequent mechanism of biological invasion in plants (Mack and Lonsdale 2001). Further factors, such as proximity to propagule sources, frequency of disturbance and habitat structure, may play a fundamental role in successful invasion (Hobbs and Humphries 1995; Lake and Leishman 2004).

Our results show that, although exotic species are widely present within our selected watersheds, species are not homogeneously distributed within them. Our analyses indicated that distance from a suburban/wildland border and habitat type are important factors that determine the structure of exotic species communities in the Andean piedmont area. Exotic species diversity decreased significantly with distance from the suburban/wildland border and was higher in open north-facing habitats than in south-facing or alluvial habitats.

The varying degree of diversity in exotic species with respect to distance to the suburban/wildland border may be explained as follows: first, significant disturbance events are commonly found on suburban/wildland borders, favoured for example by the presence of roads, trails and

Table 1. Results of the linear mixed model describing the relationship between exotic plant species diversity and habitat type (north-facing, alluvial and south-facing), woody plant species cover, the relative abundance of rabbit faeces and distance to suburban/wildland border in the Andean piedmont in central Chile.

	Coefficient (β)	SE (β)	DF	t-Value	P-value
Intercept	3.552	0.330	26	10.769	0.000
Faeces relative frequency	-0.001	0.004	26	-0.212	0.834
Woody plant species cover	0.006	0.004	26	1.406	0.172
Distance from suburban/wildland border	-0.777	0.183	26	-4.242	0.000
Alluvial habitat	-0.445	0.382	26	-1.165	0.255
South-facing habitat	-1.691	0.432	26	-3.916	0.001
Distance \times Alluvial habitat	0.005	0.245	26	0.019	0.985
Distance \times South-facing habitat	0.701	0.270	26	2.596	0.015

Note: β , regression coefficient; SE (β), standard error of beta. The diversity in the north-facing habitat is set at zero and its significance is measured against the alluvial and south-facing habitats.

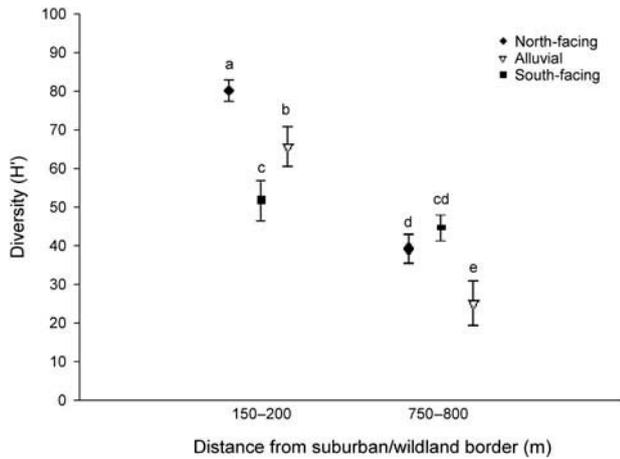


Figure 3. Exotic plant diversity (average ± 2 SE) found at two points located at different distances from the suburban/wildland border (150 and 750 m) and in different habitats (north-facing, alluvial and south-facing) in the piedmont area adjacent to the metropolitan area of Santiago, Chile. Identical letters indicate no statistically significant differences between the samples, $P < 0.05$.

abandoned lands. Anthropogenic disturbance is known to favour invasion in a variety of ecosystems. Rodgers and Parker (2003) found that the abundance of alien species on the Georgia Sea Islands (USA) was strongly related to the degree of disturbance. Sites that experienced changes in the level of available light and soil disruption were highly dominated by exotic species. Similarly, Pauchard and Alaback (2004) found that the frequency of exotic species was higher along roads compared to areas within forest habitats across an elevation gradient in central-south Chile. Roads and trails in the Andean piedmont may fragment native communities and create suitable conditions that facilitate invasion by providing competitive advantages for exotic species. In addition, the presence of suburban gardens close to the wildland/suburban border may potentially facilitate the spread of exotic species into natural areas. Horticultural plants of suburban gardens may escape and establish in surrounding habitats in the Andean piedmont (Dehnen-Schmutz et al. 2007). Although Alston and Richardson (2006) found that the richness of exotic species decreased with distance from the suburbs in Cape Town (South Africa), there was little evidence that gardens located in these suburban areas were the putative source of exotic species. We were unable to assess the composition and abundance of plant species from gardens located at the suburban/wildland borders of each watershed; however, information about species composition within the Metropolitan Area of Santiago de Chile provided by De la Barrera et al. (2010) suggests that exotic plant species distributed within this urban setting may become a putative source of exotic species for wildland areas.

Heterogeneous spatial distributions of exotic plant species presumably reflect their dispersal abilities and their ecological response to differences in site conditions, such as light availability and biotic interactions (Lake and

Leishman 2004). In our case, the Mediterranean ecosystem in central Chile shows contrasting biotic conditions between north-facing and south-facing habitats (Armesto and Martinez 1978). Both habitats experience differences in vegetation structure and density of native shrubs and trees. In particular, the presence of a dense shrub stratum may limit the success of invasion by reducing the germination rate and survival of exotic plant seedlings (Cabin et al. 2002; Kolb et al. 2002; Schramm and Ehrenfeld 2010), therefore modulating the distribution of these species in Mediterranean ecosystems (Figueroa et al. 2004).

Despite our hypothesis that certain environmental conditions may negatively affect the diversity of exotic plants in south-facing habitats, we failed to detect a significant effect of native woody plant species cover and relative frequency of rabbit faeces on species diversity at local scale. It is known that the spatial distribution of exotic plant species in Mediterranean shrub is positively related to the presence of grazing species (e.g. rabbit and cattle), where native plant species are also less abundant (Holmgren 2002). The lack of such association in our study may illustrate the fact that biological invasion patterns and processes are often driven by subtle mechanisms operating at different scales not easily detected in natural experiments (Pauchard and Shea 2006). As pointed out by Figueroa et al. (2004), the effects of herbivory and canopy cover on exotic plants cannot be generalised in Mediterranean ecosystems in Chile. Other factors, such as nutrient availability and soil pH, may also influence distribution patterns of exotic species.

As has been noted for other natural-urban regions (Kowarik 2011), the presence of exotic plants may have important consequences for native Andean piedmont ecosystems. For example, native and invasive plants compete directly for resources and are differently exposed to pressure from herbivores (Blossey and Notzold 1995). Consequently, changes in the structure of the plant community may alter the provision of ecosystem services (e.g. pollination from native species and rainwater infiltration), the frequency of ecosystem disturbances or even trigger events that had not occurred naturally, such as wildfires (Brooks et al. 2004; Pauchard et al. 2008; Contreras et al. 2011; Pauchard and Barbosa 2013). For instance, exotic species can affect fire regimes, acting as ladder-fuel and thereby increasing the spatial extent and intensity of fires (e.g. Pauchard et al. 2008). In turn, fires can favour exotic species by increasing their germination rate (García et al. 2010; Mandle et al. 2011), generating a positive feedback that could potentially modify the vegetation structure (Franklin 2010). To our knowledge, these phenomena have not been reported for our study area, even though they have been described in central-south Chile (e.g. García et al. 2010).

Exotic species may also affect ecosystem dynamics by altering resource supply. Exotic plant species significantly alter nutrient cycling by modifying the phosphorus, nitrogen and carbon availability and pools (e.g. Evans et al. 2001; Vila et al. 2006; see Liao et al. 2008 for a review).

All these alterations induce ecological changes that may have significant bottom-up impacts that affect ecosystem stability and function. Changes in ecosystem functions can be particularly important in natural areas surrounding urban settlements, because they provide supporting and regulating ecosystem services (e.g. water provision, microclimate regulation and prevention of landslides) that significantly impact on human well-being in cities (McDonnell et al. 1997; Pejchar and Mooney 2009; Vilà et al. 2010; De la Barrera and Moreira 2013).

Conclusions

We found the distribution of exotic plant species in Andean piedmont of MAS is shaped by the simultaneous effect of habitat type and distance to wildland/suburban border. These factors also interact with each other in space, becoming environmental filters restricting the establishment of these species in the area. On the contrary, site-scale factors seem to not strongly modulate these distribution patterns, which contrast with other previous studies conducted in the Mediterranean scrubland. Our results provide a clear warning that urban areas may have important impacts on plant communities by facilitating the spread of exotic species into them throughout an increment of disturbance or even acting as potential propagule sources of exotic species. Being aware of these factors and their interactions has important implications in anticipating the ecosystem effect of urban sprawl on surrounding natural areas in ecosystems highly susceptible to biological invasions.

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Supplemental data

Supplemental data for this article can be accessed [here](#).

Notes on contributors

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