How Widespread are Nonnative Species? Estimating Habitat Occupancy in an Ecological Reserve within a Megacity

Authors: Ramírez-Cruz, Gonzalo A., Mendoza-Hernández, Pedro E., Solano-Zavaleta, Israel, and Zúñiga-Vega, J. Jaime

Source: Natural Areas Journal, 38(1) : 68-87

Published By: Natural Areas Association

URL: https://doi.org/10.3375/043.038.0108

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Natural-Areas-Journal on 14 Jun 2025
Terms of Use: https://complete.bioone.org/terms-of-use

R E S E A R C H A R T I C L E

•

How Widespread are Nonnative Species? Estimating Habitat Occupancy in an Ecological Reserve within a Megacity

Gonzalo A. Ramírez-Cruz[1]

[1] Posgrado en Ciencias Biológicas
Facultad de Ciencias
Universidad Nacional Autónoma de México
Ciudad Universitaria
C.P. 04510 Ciudad de México, México

Pedro E. Mendoza-Hernández[2]
Israel Solano-Zavaleta[2]
J. Jaime Zúñiga-Vega[2,3]

[2] Departamento de Ecología y Recursos Naturales
Facultad de Ciencias
Universidad Nacional Autónoma de México
Ciudad Universitaria
C.P. 04510 D.F., México

•

ABSTRACT: Exotic species are fairly common within cities. However, urban areas also contain isolated fragments of original ecosystems, which may act as small ecological reserves. Unfortunately, these natural areas that are completely surrounded by urban structures are more vulnerable to human-induced disturbance and to the presence of nonnative species. Given the importance of these remnants of original ecosystems embedded within cities, efforts must be made to know if, once a nonnative species enters an urban reserve, it occupies the majority of the area or becomes restricted to some specific patches. This knowledge is important to determine the invasiveness and success of nonnative species, as well as the level of threat to the native biota. Additionally, it is important to understand which microhabitat conditions promote the presence and establishment of such nonnative species. Here, we used occupancy models to estimate the proportion of the total area that is occupied by exotic species of plants and animals within a natural reserve completely surrounded by urban areas. We also examined which environmental factors are associated with the presence of these exotic plants and animals. Our results revealed that occupancy of nonnative species is relatively high (>40%) within this urban reserve. However, we found an overall preference of nonnatives for specific patches of the reserve where human-made structures are present and where gardening activities take place. Some of the species that we studied deserve special attention because of their potential negative effects on native species.

Index terms: detection probability, Mexico City, nonnative species, occupancy, urban reserves

INTRODUCTION

Species introduction is a global phenomenon that currently affects almost every ecosystem on the planet (Mack et al. 2000; Simberloff et al. 2013). Exotic species may become invasive after establishing in novel environments where they experience a rapid population growth due to high resource availability and lack of competitors and/or predators (Thomsen et al. 2011; Harvey and Fortuna 2012). Nonnative species may affect ecosystem functioning by displacing local species and, in some cases, by altering the nutrient and water cycles of their new habitat (Sousa et al. 2011; Harvey and Fortuna 2012; Lapiedra et al. 2015).

Urban areas constitute heavily modified environments that contain not only species introduced by humans, but also scattered and isolated fragments of original ecosystems (Francis and Chadwick 2013). These remnants of native flora and fauna embedded within cities play a vital role as small ecological reserves, and may also offer a number of ecosystem services (Ehrenfeld 2000; Johnson and Handel 2016). Unfortunately, within confined areas such as urban reserves, native species are more vulnerable to competitive exclusion and local extinction due to their small population sizes and the continual arrival of exotic invaders (Pulliam 1998; With 2002; Strauss et al. 2006).

Despite their value as remnants of original vegetation and suitable habitat for native fauna, reserves within urban areas are still vastly understudied (Francis and Chadwick 2015). Particularly, the degree to which such fragments of native ecosystems are already affected by exotic species is an important topic that deserves attention. This information may serve as the basis to implement control strategies for invasive populations in these urban reserves (Zavaleta et al. 2001). Specifically, ecological studies of exotic species in urban reserves should examine if, once a nonnative species enters a reserve, it occupies the majority of the area or becomes restricted to some specific patches (Xiangzhen et al. 2016; Xiao et al. 2016).

Knowledge about how widespread exotic species are in an area of interest is important to determine the invasiveness/success of such species (Mack et al. 2000). In the particular case of exotic species that occupy only specific parts of confined reserves (such as reserves embedded in urban areas), it is important to understand which microhabitat conditions promote the presence and establishment of such nonnative species (Lee and Carroll 2014). In other words, how do the patches inhabited by exotic species differ from other patches within the same reserve where such species are absent? Monitoring invasive populations and the conditions that promote their presence/absence can lead to effective strategies for their control.

---

[3] Corresponding author: jzuniga@ciencias.unam.mx; (52) 55-5622-4912

Natural Areas Journal 38:68–87

Here, we use occupancy models to estimate the proportion of the total area that is occupied by exotic species of plants and animals within an ecological reserve completely surrounded by urban areas. This robust analytical approach estimates the proportion of occupied area by taking into account that species are detected imperfectly in field surveys (MacKenzie et al. 2002; MacKenzie 2006). In addition, we examined which environmental factors are associated with the presence of these exotic plants and animals. Our results may help to understand the environmental conditions that favor or hinder the establishment of exotic species in an ecological reserve within a megacity. This information may provide the basis to design management strategies for such nonnative species.

METHODS

Study Area and Field Methods

The Reserva Ecológica del Pedregal de San Ángel (REPSA) is an ecological reserve situated within Mexico City (Figure 1), which is among the top ten megacities in the world (Folberth et al. 2015). This city has a total area of 1485 km^2, with a population of 8.8 million people. The average population density is 5920 persons per km^2 (INEGI 2010). The estimated projection of urban growth predicts that most of the conservation grounds that currently surround the city will be urbanized by the year 2020 (Suárez-Lastra 2016). However, the REPSA is the only reserve completely surrounded by the urban area that preserves part of the original ecosystem that was situated in what is now southern Mexico City (Zambrano et al. 2016). This reserve was created in October 1983 to protect the last remnants of a xerophytic scrubland established over the lava field created by the eruption of the Xitle volcano nearly 2000 y ago (Rzedowski 1994; Siebe 2000; Razo-González et al. 2014). Two climatic seasons are clearly discernible: the rainy season from June to October and the dry season from November to May (Rzedowski 1994). This ecosystem is unique in the world due to its particular composition of endemic plants and animals (Lot and Cano-Santana 2009). The REPSA is home to 1849 native and 317 exotic species of plants and animals (REPSA 2017) and is situated within the limits of the main campus of the National Autonomous University of Mexico (Universidad Nacional Autónoma de México, UNAM), which is the institution that currently oversees the care and maintenance of this ecosystem.

This ecological reserve has a total area of 237 ha divided into three core areas and 13 buffer areas, all of them interspersed among buildings and facilities of the University (Figure 1; Peralta-Higuera and Prado-Molina 2009). The core areas correspond to patches of original scrubland with minimal human-induced disturbance and restricted access to people. These core areas were established for conservation purposes. The buffer areas were added to the reserve in 1997 to serve as connectivity corridors interspersed among the core and urban areas (Zambrano et al. 2016). These areas are composed of both original scrubland and exotic vegetation introduced during early attempts of reforestation in the campus around 1950 (Estañol-Tecuatl and Cano-Santana 2017). In these areas, access by people is only partially restricted and, therefore, some of them experience disturbances caused by human activities.

We established 100 observation sites in both core and buffer areas, as well as in some of the urban areas surrounding them (Figure 1). To randomly select the observation sites, we overlapped a grid with 1000 numbered squares on the map of the study area. Then, we used the computer program R 3.3.0 (R Core Team 2016) to generate 100 random numbers that corresponded to 100 particular squares of our grid. In those cases where the selected squares were located in inaccessible areas, we slightly adjusted their location to the nearest accessible sites. The minimum distance between observation sites was 150 m. We visited each site on five occasions during May of 2015 as well as during September of 2015. Some easily accessible sites were visited on one or two additional occasions during these two months. In our analysis, May represents the dry season and September represents the rainy season. All observations were carried out by the same group of previously trained observers. Observations were conducted within a 20-m radius around the center of each observation site. Species of flora and fauna were detected and identified independently by the observers during a 15-min time lapse with the use of binoculars and through direct observation. In the case of plants, we identified seedlings, saplings, and adult individuals based mainly on their leaf morphology. At each visit we recorded whether a species was detected or not and, based on these data, we constructed detection histories for each species and for each observation site. Given the short observation time per visit, some plant species may have been missed. However, our study deals with this potential issue in three ways. First, each site was visited on at least five occasions during each sampling month, which means a total of 75 min of total observation time per site and season. Second, occupancy models were designed to explicitly deal with imperfect detection (see occupancy estimation below). Third, our focal plant species (Table 1) are easily distinguished from the surrounding flora even during their early stages of development due to their particular leaf morphology.

At each site and during both dry and rainy seasons, we quantified the following environmental variables that may influence the presence (or absence) of our focal species: proportion of the substrate that corresponds to exposed rock, percent vegetation cover at herb (<1.5 m in height), shrub (1.5–3 m in height), and tree (>3 m in height) layers, as well as percentage of the area covered by human-associated litter. Additionally, we measured organic soil depth, registered whether the site is frequently subject to gardening activities such as mowing of exotic grasses that grow on the borders of the breaches that run through the core areas, removal of weeds and some exotic trees in the buffer areas, and pruning, weed removal, and watering within the urban areas. Lastly, we measured the distance from the center of the observation site to the nearest human-made structure (e.g., building, road, garden) using Google Earth (Google 2017).

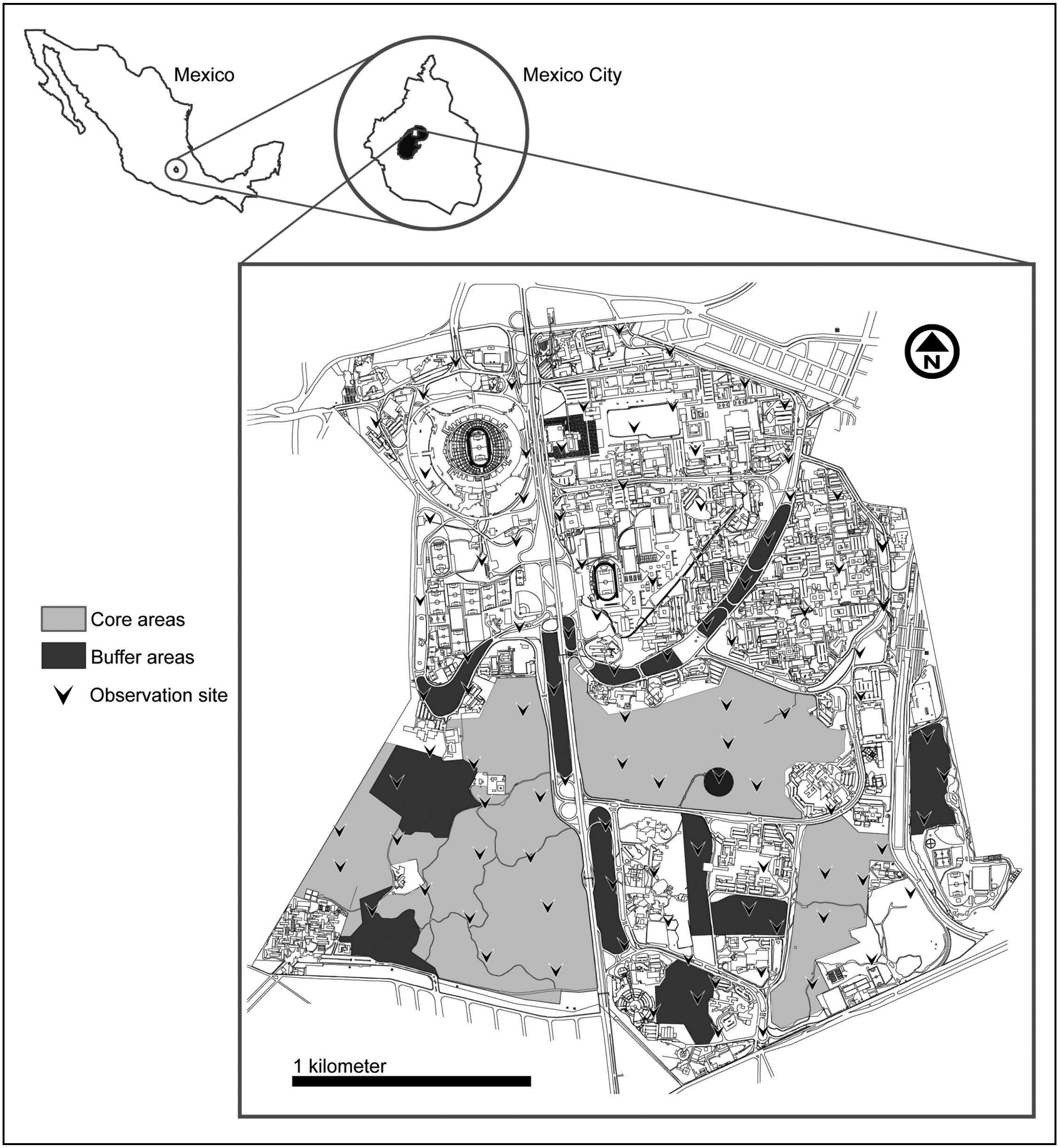


Figure 1. Geographic location of the study area (Reserva Ecológica del Pedregal de San Ángel) within Mexico City. We indicate the location of core (light grey), buffer (dark grey), and urban (non-shaded) areas. Arrows depict observation sites. The dark area within Mexico City indicates the original extent of the native ecosystem.

Table 1. Description of the ten nonnative species that we studied, including notes on their original distribution, ecological requirements, and potential negative effects on the native flora and fauna.

Species (Taxonomic group)	Common name	Original distribution and introduction date	Habitat and ecological requirements	Potential negative effects	References
Animals					
Passer domesticus L. (Aves: Passeriformes)	House sparrow	Native to Europe and North Africa. First introduced into North America in 1852 or 1853.	Affinity for human-modified habitats. Diet includes seeds, insects, fruit, and litter.	Known to act aggressively toward native bird species. Its presence is associated with reduced species richness.	1, 2, 3, 4
Sciurus aureogaster nigrescens Bennett (Mammalia: Rodentia)	Mexican red-bellied squirrel	Atlantic and Pacific coastal plains of Mexico and southwestern Guatemala. First record in REPSA in 1999.	Tropical scrub to temperate cloud forests. Diet consists primarily of oak and pine seeds; occasionally eats small reptiles, arthropods, and bird eggs.	Known to cause skinning of tree bark, which increases the probability of fungal or insect infections.	5, 6, 7, 8, 9, 10
Trees					
Eucalyptus camaldulensis Dehnh (Magnoliopsida: Myrtaceae)	River red gum	Native to Australia. Introduced into urban areas in Mexico City during early twentieth century.	Riparian environments and flood plains. Tolerant to drought as well as to degraded and saline soils.	Allelopathic plant. Fragile wood prone to fall, which may cause damage to adjacent vegetation.	11, 12, 13
Fraxinus uhdei (Wenz) Lingelsh. (Magnoliopsida: Oleaceae)	Tropical ash	Native to Mexico, Guatemala, and Honduras. Introduced into urban areas in Mexico City during early twentieth century.	Temperate forests and riparian vegetation. Secondary vegetation of pine-oak forests. Common in disturbed forests. Tolerant to various soil types, to low water availability, and to intense insolation.	Great invasive potential. Known to alter the three-dimensional structure of native forests. May spread certain plagues.	14, 15, 16, 17, 18
Jacaranda mimosifolia D. Don (Magnoliopsida: Bignoniaceae)	Jacaranda	Native to northeast Argentina and southeast Bolivia, also inhabits tropical and subtropical areas of Brazil. Introduced as an ornamental tree for urban reforestation of Mexico City.	Tropical prairies in its original range of distribution. Naturalized in Wales, Australia, and Spain. Tolerant to insolation and drought.	Adult trees are capable of breaking sidewalks, walls, and pipes in urban areas.	12, 19, 20
Schinus molle L. (Magnoliopsida: Anacardiaceae)	Peruvian pepper	Natural distribution includes Ecuador, Bolivia, Chile, and especially Peru. Introduced to Mexico by Antonio de Mendoza y Pacheco during the sixteenth century.	Areas above 3900 m elevation. Pioneer tree that can be found in disturbed areas with secondary vegetation, roads, and agricultural fields. Well adapted to rocky soils. Resistant to drought.	It is known as a strong competitor for sunlight. Alters the vertical and horizontal structure of the vegetation. No known herbivores or pathogens. Allelopathic effects reported on the establishment and germination of native plants.	15, 21, 22, 23, 24

Continued

Table 1. (*Cont'd*)

Species (Taxonomic group)	Common name	Original distribution and introduction date	Habitat and ecological requirements	Potential negative effects	References
Herbs					
Leonotis nepetifolia (L) R. Br. (Magnoliospida: Lamiaceae)	Klip dagga	Native to South Africa and India. Considered an introduced weed in Mexico and the REPSA since 1990.	Humid and sub-humid tropical regions of Africa. Common in edges of roads, disturbed grasslands, and agricultural fields. May grow on clayey, sandy, and rocky soil.	Highly invasive weed. May serve as a reservoir for plant viruses.	25, 26, 27, 28
Melinis repens (Willd.) (Liliopsida: Poaceae)	Rose natal grass	Tropical perennial annual grass from southern Africa. Widely distributed and naturalized in many subtropical regions. Originally introduced into Florida in 1893. Since 1903 it extended its distribution throughout northern New Mexico and Arizona. First reports in northern Mexico from the late twentieth century. Currently present in all Mexican states and other warm regions of the world.	Inhabits savannas, rocky cliffs, and even edges of creeks and streams. In Mexico it can be found in temperate zones, scrublands, deciduous tropical forest, highway borders, and agricultural fields. Tolerant to poor soil and environmental stress.	Reduces species richness within seasonal environments. Its seeds may maintain a viability of more than 50% for more than a year.	15, 27, 29, 30, 31
Pennisetum clandestinum Hochst. ex Chioy (Liliopsida: Poaceae)	Kikuyu grass	Native to tropical Africa and Ethiopia. Tropical distribution including regions of Africa, Asia, and Oceania. First introduced into California in 1918. Widely distributed throughout Mexico.	Tropical climates and coastal areas. Tolerant to frost.	Known to replace local species due to its rapid growth and propagation through rhizomes and high seed production. Promotes fires due to excessive biomass accumulation during the dry season in southern Mexico City.	15, 26, 27, 31, 32, 33, 34
Ricinus communis L. (Magnoliopsida: Euphorbiaceae)	Castorbean	Native to tropical Africa. Widely distributed in both hemispheres. Considered exotic throughout Mexico.	Tropical and subtropical ecosystems. Resistant to drought.	Dominant weed. Seeds are toxic to animals.	15, 26, 27, 35

References: [1] Gowaty 1984; [2] Anderson 2006; [3] Joshi 2009; [4] MacGregor-Fors et al. 2010; [5] Musser 1968; [6] Ramos-Lara and Cervantes 2007; [7] Hortelano-Moncada et al. 2009; [8] Mora-Ascencio et al. 2010; [9] Ramos-Lara and Cervantes 2011; [10] Palmer et al. 2014; [11] del Moral and Muller 1970; [12] Chacalo et al. 1994; [13] Wen et al. 2009; [14] Ares and Fownes 2001; [15] Calderón and Rzedowski, 2001; [16] Asner et al. 2008; [17] Wallander 2008; [18] Bonfil 2010; [19] Hosking et al. 2003; [20] Gilman and Watson 1993; [21] Ramírez-Albores and Bandano 2013; [22] Jøker et al. 2002; [23] Howard and Minnich 1989; [24] Iponga et al. 2008; [25] Parsons and Cuthbertson 2001; [26] Villaseñor and Espinosa-Garcia 2004; [27] Castillo-Argüero et al. 2009; [28] Imran et al. 2012; [29] Melgoza et al. 2014; [30] Possley and Machinski 2006; [31] Antonio-Garcés et al. 2009; [32] Elmore et al. 1997; [33] Cudney et al. 1993; [34] Muscolo et al. 2003; [35] Pandey 2013.

Study Species

We focused on ten exotic species of plants and animals that inhabit the REPSA (Table 1). These included one bird: house sparrow (*Passer domesticus* L.); one small mammal: Mexican red-bellied squirrel (*Sciurus aureogaster nigrescens* Bennett); four trees: river red gum (*Eucalyptus camaldulensis* Dhenh.), tropical ash (*Fraxinus uhdei* (Wenz) Lingelsh.), jacaranda (*Jacaranda mimosifolia* D. Don), and Peruvian pepper (*Schinus molle* L.); and four herbs: klip dagga (*Leonotis nepetifolia* (L) R. Br.), rose natal grass (*Melinis repens* Willd.), kikuyu grass (*Pennisetum clandestinum* Hochst. ex Chiov.), and castorbean (*Ricinus communis* L.). These species are both easy to see and identify in the field. Some were introduced because of their aesthetic value to parks and gardens, whereas others arrived after expanding their original distributional ranges due to human activities. In the case of herbs and trees, we focused on species that are able to disperse and establish seedlings outside of gardening areas without human intervention.

According to previous studies in other regions, some of these species have evident negative effects on endemic plants and animals mostly as a result of competitive interactions (Table 1). For instance, the presence of the house sparrow apparently reduces bird species richness (MacGregor-Fors et al. 2010). When highly abundant, the Mexican red-bellied squirrel may promote fungal infections on adult trees by skinning their bark (Mora-Ascencio et al. 2010). Exotic trees such as the Peruvian pepper and the river red gum can modify the general structure of the vegetation or impede the establishment of other native plants (del Moral and Muller 1970; Iponga et al. 2008).

Occupancy Estimation

For each focal species, we estimated occupancy (ψ) and detection (p) probabilities using likelihood-based procedures implemented in program MARK (White and Burnham 1999). We estimated these parameters separately for the dry (May) and rainy (September) seasons implementing single-season occupancy models (MacKenzie et al. 2002; MacKenzie 2006). These models appropriately deal with uneven sampling occasions by modifying the likelihood expression of any particular site. Using the detection histories we generated different linear models incorporating relevant environmental covariates for each species to model the detection probability (p) first, and subsequently, the probability of occupancy (ψ). Table 2 shows the specific covariates that we used for each parameter and for each species. We started with a null model in which both parameters were kept invariant (constant). Then, we modeled p by testing the effect of different covariates, as well as additive effects between pairs of covariates, while maintaining invariant the parameter ψ. We did not consider models with interactive effects between pairs of covariates because in most cases the regression coefficient for the interaction term was poorly estimated. We compared the fit of all these models by means of the Akaike's information criterion adjusted for small samples (AIC_c; Burnham and Anderson 2002).

After selecting the best parameterization for detection probability, we tested the effect of different covariates on ψ as well as two-way additive effects of these covariates. Similarly to what we observed in p, the interaction between pairs of covariates affecting ψ could not be properly estimated and, hence, we did not consider models with interactive effects. Again in this case we used AIC_c to select the environmental covariates with strongest effects on ψ. In addition, we calculated Akaike weights (w) to estimate the relative support (or strength of evidence) for each fitted model (Johnson and Omland 2004). We focused on models with strong support in the data (models that differed in less than 2 units in their AIC_c scores with respect to the top model; $\Delta AIC_c < 2$). In particular, we placed emphasis on those covariates included in these supported models for which the confidence intervals of their regression coefficients did not include zero. Occupancy probabilities for core, buffer, and urban areas were obtained from the models with the lowest ΔAIC_c in which type of area was included as a factor affecting ψ.

Finally, we must note here that changes between seasons in occupancy of trees do not arise from changes in the occurrence of adult individuals. Instead, decreases in the occupancy of tree species reflect the disappearance of nonreproductive individuals (seedlings and saplings) from one season to the following due to natural mortality or deliberate removal of individuals within certain areas. On the other hand, increases in tree occupancy are caused by establishment of seedlings and saplings in previously unoccupied areas.

RESULTS

Occupied Area

Regarding animals, the house sparrow showed preference for the urban area during both seasons (Figures 2a, 2b). Average occupancy across seasons was 62.3% of the buffer area, and 86.2% of the urban area. Occupancy of core areas was 55.1% during the dry season (although the confidence interval for this parameter was quite wide; Figure 2a), whereas during the rainy season this nonnative bird was absent from these core areas (Figure 2b). Occupancy of the Mexican red-bellied squirrel was very similar during both seasons in buffer and urban areas (averages across seasons were 35.9% and 35.5%, respectively; Figures 2c, 2d). The squirrel was also absent from the core areas during the rainy season (Figure 2d) and it occupied an extremely small proportion of these core areas during the dry season (3.6%; Figure 2c).

Regarding trees, the river red gum occupied 53.4% of the core areas during the dry season and decreased its occupancy of these core areas to 18% during the rainy season (Figures 2e, 2f). Its occupancy in buffer and urban areas remained similar between dry and rainy seasons (68.9% and 46.3% on average, respectively). Occupancy of the tropical ash also decreased slightly in the buffer areas during the rainy season (from 52.4% during the dry season to 30.1%), but did not differ considerably between seasons in the urban areas (77.2% on average; Figures 2g, 2h). For neither season were we able to accurately estimate occupancy of this nonnative tree in the core areas.

Table 2. List of covariates used to estimate occupancy (ψ) and detection (p) probabilities.

Species	Type of area	Exposed rock (%)	Herb cover (%)	Shrub cover (%)	Tree cover (%)	Litter (%)	Soil depth (cm)	Gardening activities	Distance to urban structures (m)
Animals									
House sparrow	ψ, p		ψ	ψ, p	p	ψ		ψ, p	ψ, p
Mexican red-bellied squirrel	ψ, p		p	p	ψ, p	ψ		ψ	ψ
Trees									
River red gum	ψ, p	ψ	ψ, p	ψ, p	p		ψ	ψ	ψ
Tropical ash	ψ, p	ψ	ψ, p	ψ, p	p		ψ	ψ	ψ
Jacaranda	ψ, p	ψ	ψ, p	ψ, p	p		ψ	ψ	ψ
Peruvian pepper	ψ, p	ψ	ψ, p	ψ, p	p		ψ	ψ	ψ
Herbs									
Klip dagga	ψ, p	ψ	p	ψ, p	ψ, p		ψ	ψ	ψ
Rose natal grass	ψ, p	ψ	p	ψ, p	ψ, p		ψ	ψ	ψ
Kikuyu grass	ψ, p	ψ	p	ψ, p	ψ, p		ψ	ψ	ψ
Castorbean	ψ, p	ψ	p	ψ, p	ψ, p		ψ	ψ	ψ

Jacaranda occupancy was higher within the core, buffer, and urban areas during dry season (19.5%, 38%, and 74%, respectively) compared to the rainy season (0%, 20.2%, and 43.1%, respectively; Figures 2i, 2j). In both seasons, this species showed its highest occupancy in the urban areas (58.6% on average). Finally, occupancy of the Peruvian pepper showed no changes between seasons, and had higher values within buffer and urban areas (85.7%, and 83.1% on average, respectively) than in the core areas (56.4% on average; Figures 3a, 3b).

In the case of herbs, occupancy of the klip dagga varied between seasons, with higher occupancy in the rainy season compared to the dry season in the core areas (44% and 15%, respectively) and, in contrast, lower occupancy in the rainy season compared to the dry season in the buffer (33% and 51.8%, respectively) and urban areas (20% and 41%, respectively; Figures 3c, 3d). Occupancy of the rose natal grass did not vary among areas, but was highest during the dry season (95.3% on average; notice that during this dry season this grass was present in all urban areas; Figure 3e) compared to the rainy season (54.7% on average; Figure 3f). The kikuyu grass was present in virtually all buffer and urban areas during both seasons (94.7% and 98.7% on average, respectively), occupying slightly less of the core areas (65% on average; Figures 3g, 3h). Castorbean maintained a low homogeneous occupancy among areas and seasons averaging 8.5% of the core areas, 28.7% of the buffer areas, and 33.6% of the urban areas (Figures 3i, 3j).

Factors Affecting Occupancy

According to the best-supported model (Table 3), occupancy of the house sparrow was positively affected by gardening activities during both seasons (Figures 4a, 4c). However, large amounts of litter, abundant shrub cover, and larger distances to urban structures decreased its occupancy during the dry (Figure 4b) and rainy (Figures 4d, 4e) seasons. With respect to the Mexican red-bellied squirrel, only the tree cover had a positive correlation with occupancy during the dry season (Figure 4f). During

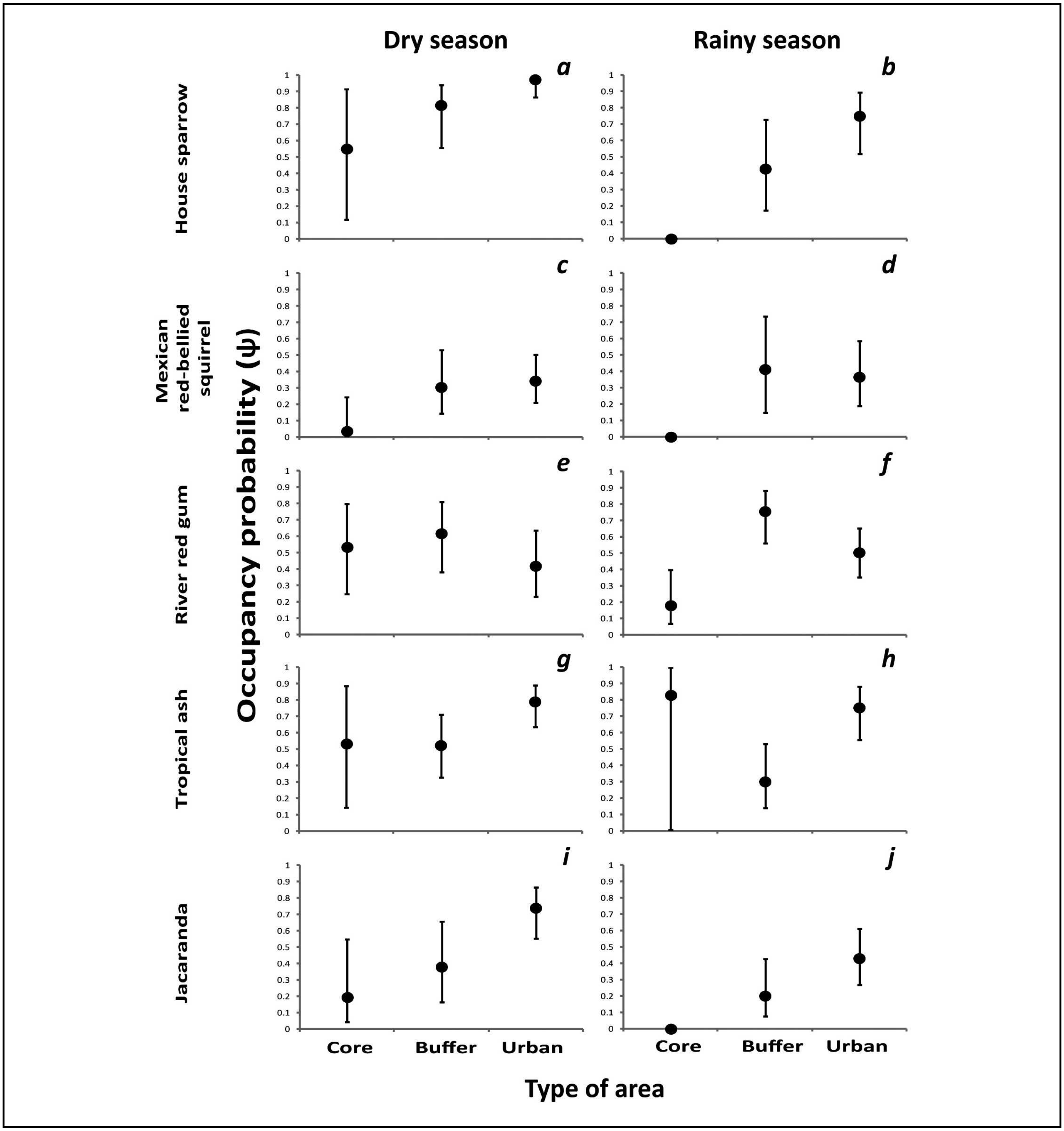


Figure 2. Estimated occupancy probabilities (ψ) of house sparrow (a, b), Mexican red-bellied squirrel (c, d), river red gum (e, f), tropical ash (g, h), and jacaranda (i, j) within core, buffer, and urban areas during dry and rainy seasons. Error bars represent 95% confidence intervals.

the rainy season four different models had strong support in the data. However, in all these models the confidence intervals for all regression coefficients included zero (Table 3).

In the case of trees, occupancy of the river red gum was negatively affected by the distance to urban area and positively affected by herb cover during both seasons (Figures 5a–d). Occupancy of the tropical ash was negatively affected by both percentage of exposed rock and shrub cover during both seasons (Figures 5e–h). Jacaranda occupancy was highest in areas with gardening activities during both seasons (Figures 5i, 5k). However, during the dry season its occupancy was also positively affected by soil depth (Figure 5j) and negatively affected by shrub cover (Figure 5l). Lastly, several models had strong support in the data of the Peruvian pepper during the dry season (Table 3). However, only soil depth had an evident negative effect on its occupancy during this season (Figure 5m). During the rainy season, occupancy of the Peruvian pepper was only affected

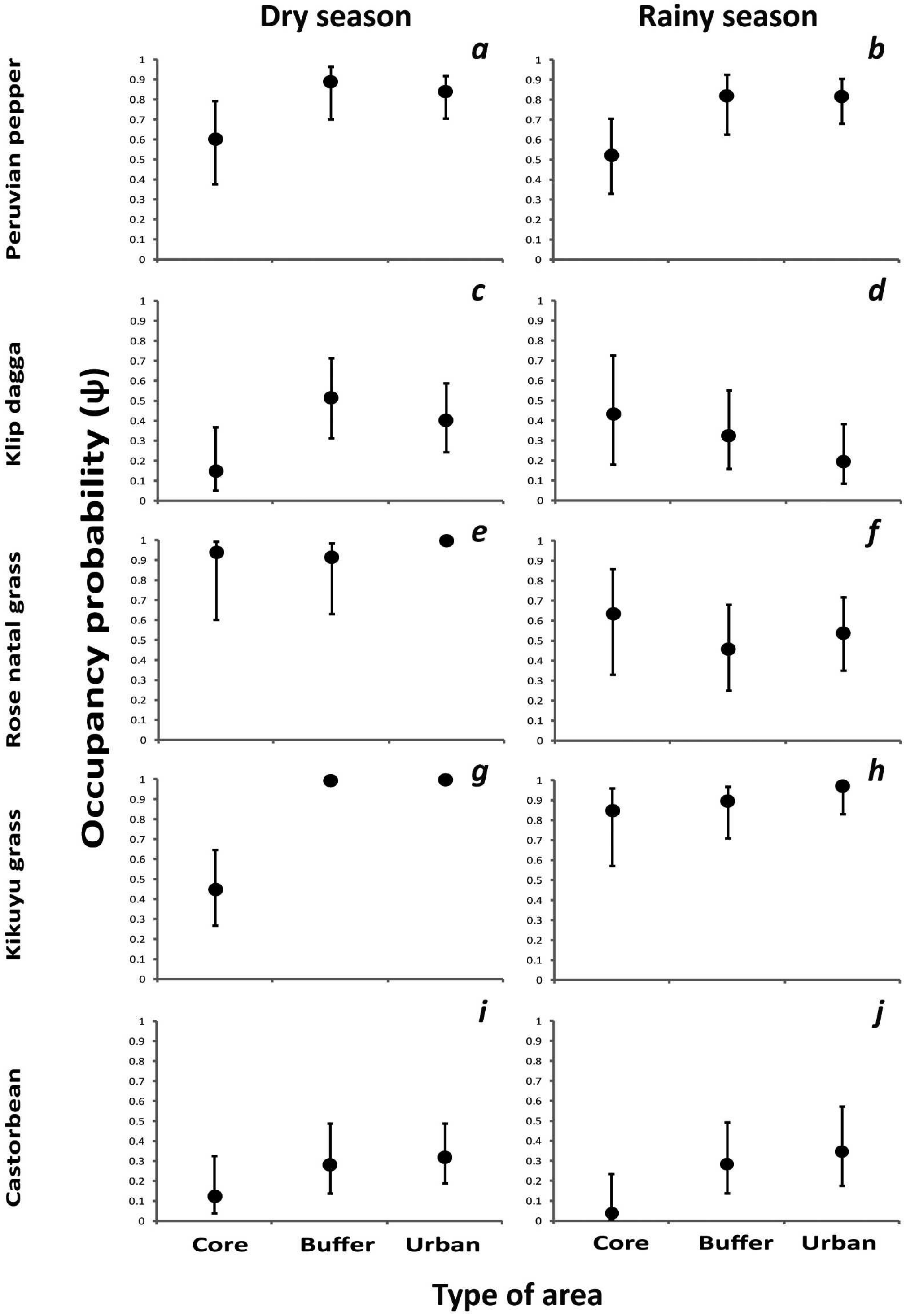


Figure 3. Estimated occupancy probabilities (ψ) of Peruvian pepper (a, b), klip dagga (c, d), rose natal grass (e, f), kikuyu grass (g, h), and castorbean (i, j) within core, buffer, and urban areas during dry and rainy seasons. Error bars represent 95% confidence intervals.

Table 3. Model selection results for occupancy (ψ) and detection (p) probabilities of ten nonnative species during both dry and rainy seasons. For each species and for each season we show models with ΔAICc < 2, as well as the first model with ΔAICc > 2. We also show the relative support for each model in the data (w). We highlight in bold the covariates with regression coefficients that were statistically different than zero (i.e., their confidence intervals did not include zero).

Species	Season	Model	AICc	ΔAICc	*w*
House sparrow	Dry	ψ (**Gardening** + **Litter**) p (Shrub cover + Distance to urban structure)	523.11	0.00	0.554
		ψ (Gardening) p (Shrub cover +Distance to urban structure)	526.68	3.56	0.093
	Rainy	ψ (**Shrub cover** + **Distance to urban structure**) p (Gardening + Distance to urban structure)	388.49	0.00	0.287
		ψ (**Shrub cover** + **Gardening**) p (Gardening + Distance to urban structure)	388.54	0.04	0.280
		ψ (**Shrub cover** + Type of area) p (Gardening + Distance to urban structure)	388.91	0.41	0.233
		ψ (Shrub cover) p (Gardening + Distance to urban structure)	391.45	2.95	0.065
Mexican red-bellied squirrel	Dry	ψ (**Tree cover**+ Distance to urban structure) p (Type of area)	306.93	0.00	0.452
		ψ (**Tree cover**) p (Type of area)	308.77	1.84	0.180
		ψ (**Tree cover** + **Type of area**) p (Type of area)	308.81	1.89	0.176
		ψ (Tree cover + Litter) p (Type of area)	310.70	3.77	0.069
	Rainy	ψ (Distance to urban structure + Litter) p (Tree cover + Herb cover)	194.26	0.00	0.220
		ψ (Distance to urban structure + Type of area) p (Tree cover + Herb cover)	194.33	0.06	0.213
		ψ (Distance to urban structure) p (Tree cover + Herb cover)	194.77	0.51	0.171
		ψ (Tree cover + Type of area) p (Tree cover + Herb cover)	195.03	0.77	0.150
		ψ (Gardening + Distance to urban structure) p (Tree cover + Herb cover)	196.91	2.64	0.059
River red gum	Dry	ψ (**Distance to urban structure** + **Herb cover**) p (Herb cover + Type of area)	510.87	0.00	0.463
		ψ (Distance to urban structure) p (Herb cover + Type of area)	513.11	2.24	0.151
	Rainy	ψ (**Herb cover** + **Distance to urban structure**) p (Tree cover + Shrub cover)	399.46	0.00	0.416
		ψ (**Herb cover** + **Type of area**) p (Tree cover + Shrub cover)	400.40	0.94	0.261
		ψ (Tree cover + Distance to urban structure) p (Tree cover + Shrub cover)	403.47	4.01	0.056
Tropical ash	Dry	ψ (**Exposed rock** + **Shrub cover**) p (Shrub cover + Type of area)	508.20	0.00	0.277
		ψ (Exposed rock + Type of area) p (Shrub cover + Type of area)	511.54	3.35	0.052
	Rainy	ψ (**Exposed rock** + **Shrub cover**) p (Shrub cover + Type of area)	451.51	0.00	0.589
		ψ (**Exposed rock** + **Type of area**) p (Shrub cover + Type of area)	453.26	1.75	0.245
		ψ (Exposed rock + Gardening) p (Shrub cover + Type of area)	455.47	3.96	0.081
Jacaranda	Dry	ψ (**Soil depth** + **Gardening**) p (Herb cover + Shrub cover)	407.55	0.00	0.197
		ψ (**Soil depth** + **Type of area**) p (Herb cover + Shrub cover)	408.08	0.53	0.151
		ψ (Distance to urban structure + **Gardening**) p (Herb cover + Shrub cover)	408.78	1.24	0.106
		ψ (Distance to urban structure + **Shrub cover**) p (Herb cover + Shrub cover)	409.21	1.66	0.086
		ψ (Distance to urban structure + Tree cover) p (Herb cover + Shrub cover)	409.63	2.08	0.069
	Rainy	ψ (**Gardening** + Exposed rock) p (Shrub cover)	300.26	0.00	0.375
		ψ (**Gardening**) p (Shrub cover)	301.58	1.32	0.194
		ψ (Gardening + Shrub cover) p (Shrub cover)	302.68	2.41	0.112
Peruvian pepper	Dry	ψ (Soil depth + Herb cover) p (Tree cover + Type of area)	658.62	0.00	0.109
		ψ (**Soil depth** + Type of area) p (Tree cover + Type of area)	659.57	0.95	0.068

Continued

Table 3. (*Cont'd*)

Species	Season	Model	AICc	ΔAICc	*w*
Peruvian pepper (*Cont'd*)	Dry	ψ (Constant) *p* (Tree cover + Type of area)	659.85	1.22	0.059
		ψ (Soil depth) *p* (Tree cover + Type of area)	660.11	1.49	0.052
		ψ (Soil depth + Exposed rock) *p* (Tree cover + Type of area)	660.12	1.50	0.051
		ψ (Soil depth + Distance to urban structure) *p* (Tree cover + Type of area)	660.80	2.18	0.037
		ψ (**Type of area**) *p* (Constant)	642.34	0.00	0.147
	Rainy	ψ (**Type of area** + Herb cover) *p* (Constant)	643.32	0.98	0.090
		ψ (Distance to urban structure) *p* (Constant)	644.02	1.68	0.063
		ψ (**Type of area** + Soil depth) *p* (Constant)	644.14	1.80	0.060
		ψ (Type of area + Tree cover) *p* (Constant)	644.51	2.17	0.050
		ψ (**Shrub cover** + **Distance to urban structure**) *p* (Tree cover + Shrub cover)	395.72	0.00	0.560
Klip dagga	Dry	ψ (Shrub cover + Type of area) *p* (Tree cover + Shrub cover)	400.04	4.32	0.065
		ψ (**Shrub cover** + **Distance to urban structure**) *p* (Tree cover + Type of area)	353.25	0.00	0.826
	Rainy	ψ (Gardening + Distance to urban structure) *p* (Tree cover + Type of area)	357.79	4.55	0.085
		ψ (Constant) *p* (Tree cover + Shrub cover)	721.40	0.00	0.198
Rose natal grass	Dry	ψ (Shrub cover) *p* (Tree cover + Shrub cover)	722.51	1.11	0.114
		ψ (Shrub cover + Tree cover) *p* (Tree cover + Shrub cover)	723.12	1.72	0.084
		ψ (Herb cover) *p* (Tree cover + Shrub cover)	723.54	2.14	0.068
		ψ (**Shrub cover** + Tree cover) *p* (Tree cover)	447.30	0.00	0.380
	Rainy	ψ (**Shrub cover**) *p* (Tree cover)	448.72	1.42	0.187
		ψ (Shrub cover + Herb cover) *p* (Tree cover)	449.84	2.54	0.107
		ψ (**Shrub cover** + **Tree cover**) *p* (Shrub cover)	699.02	0.00	0.923
Kikuyu grass	Dry	ψ (Shrub cover + Distance to urban structure) *p* (Shrub cover)	705.52	6.51	0.036
		ψ (**Shrub cover** + **Exposed rock**) *p* (Shrub cover + Type of area)	400.26	0.00	0.466
	Rainy	ψ (Shrub cover) *p* (Shrub cover + Type of area)	402.84	2.58	0.128
		ψ (Constant) *p* (Herb cover + Shrub cover)	280.46	0.00	0.089
Castorbean	Dry	ψ (Shrub cover) *p* (Herb cover + Shrub cover)	280.46	0.00	0.089
		ψ (Distance to urban structure) *p* (Herb cover + Shrub cover)	281.46	1.00	0.054
		ψ (Gardening) *p* (Herb cover + Shrub cover)	281.63	1.17	0.050
		ψ (Type of area) *p* (Herb cover + Shrub cover)	281.67	1.21	0.049
		ψ (Herb cover) *p* (Herb cover + Shrub cover)	282.01	1.55	0.041
		ψ (Shrub cover + Distance to urban structure) *p* (Herb cover + Shrub cover)	282.39	1.92	0.034
		ψ (Tree cover) *p* (Herb cover + Shrub cover)	282.44	1.98	0.033
		ψ (Shrub cover + Soil depth) *p* (Herb cover + Shrub cover)	282.51	2.05	0.032
		ψ (**Distance to urban structure**) *p* (Shrub cover)	254.59	0.00	0.194
	Rainy	ψ (**Distance to urban structure** + Shrub cover) *p* (Shrub cover)	255.82	1.24	0.104
		ψ (Distance to urban structure + Tree cover) *p* (Shrub cover)	256.38	1.79	0.079

Continued

Table 3. (*Cont'd*)

Species	Season	Model	AICc	ΔAICc	*w*
Castorbean (*Cont'd*)	Rainy	ψ (**Distance to urban structure** + Exposed rock) *p* (Shrub cover)	256.56	1.97	0.072
		ψ (**Distance to urban structure** + Soil depth) *p* (Shrub cover)	256.58	2.00	0.071
		ψ (Type of area) *p* (Shrub cover)	256.62	2.04	0.070

by the type of area (Table 3, Figure 3b).

Regarding herbs, occupancy of the klip dagga was positively affected by shrub cover (Figures 6a, 6c) and negatively affected by the distance to urban area (Figures 6b, 6d) in both seasons. Occupancy of the rose natal grass was not clearly affected by any covariate during the dry season (Table 3), but it was positively affected by shrub cover during the rainy season (Figure 6e). Occupancy of the kikuyu grass was negatively affected by tree and shrub covers during the dry season (Figures 6f, 6g), and by shrub cover and exposed rock during the rainy season (Figures 6h, 6i). Castorbean occupancy was not clearly affected by any covariate during the dry season (Table 3), but was negatively affected by distance to urban area during the rainy season (Figure 6j).

Detection Probability

In general, detection probability was similar between seasons (Appendixes 1 and 2). The two exceptions were the rose natal grass and the kikuyu grass. Detection of the rose natal grass increased during the rainy season in all areas, whereas detection of the kikuyu grass also increased during the rainy season but only in buffer and urban areas. In fact, in urban areas detectability of this latter herb species was quite close to 1 (Appendix 2).

For most species, detectability was lowest in the core areas. However, klip dagga and castorbean showed similar detection probabilities in all areas. In addition, detection of the rose natal grass during the dry season was highest in the core areas (Appendix 2). In contrast, some species were highly detectable in the urban areas, such as the house sparrow, river red gum, tropical ash, Peruvian pepper, and kikuyu grass (in all these species p was higher than 0.58). It is noteworthy that for all plant species detection was <1 (Appendixes 1 and 2), presumably because both grasses and seedlings of trees are less conspicuous when surrounded by other vegetation.

DISCUSSION

The species that we studied here are a small sample of the nonnative plant and animal species that inhabit this last remnant of the original ecosystem of southern Mexico City (Zambrano et al. 2016). With the exception of the Mexican red-bellied squirrel and the castorbean, these nonnative species occupied 40% or more of some areas (at least during one of the two climatic seasons). This means that, although the REPSA seems to have some resilience to these species (particularly the protected core areas), nonnative plants and animals are relatively widespread within its boundaries. Overall, nonnative species seem to share a high affinity for buffer and urban areas. These two types of areas are subject to gardening activities, which involve removal of weeds, pruning of trees, and frequent watering. In the urban areas the tropical ash and the jacaranda are commonly planted and maintained for ornamental purposes, whereas species like the river red gum and the klip dagga have been the target of control efforts (Zambrano et al. 2016; Estañol-Tecuatl and Cano-Santana 2017). Shrub cover is usually very scarce or nonexistent in these patches, and the soil reaches its greatest depth because the original exposed volcanic rock has been artificially covered and filled with soil. Human access to these areas is not restricted, and in most cases this has led to high levels of disturbance through noise pollution and litter.

In the case of animals, the house sparrow showed a clear affinity for urban areas likely because of the abundance of anthropogenic food sources, but also because of its preference for buildings as nesting sites, such as has been documented in previous studies (Chamberlain et al. 2007; Magudu and Downs 2015). Although occupancy of the Mexican red-bellied squirrel in buffer and urban areas was not particularly high, it reached its lowest in the core areas. Studies carried out in forest areas of Mexico found that Mexican red-bellied squirrels prefer tall trees to build their nests (Ramos-Lara and Cervantes 2007); within the study area, tall trees like the river red gum and the tropical ash (both nonnative species) are more commonly available in the buffer and urban areas because, in the recent past, people commonly planted them in urban parks and gardens (Chacalo et al. 1994).

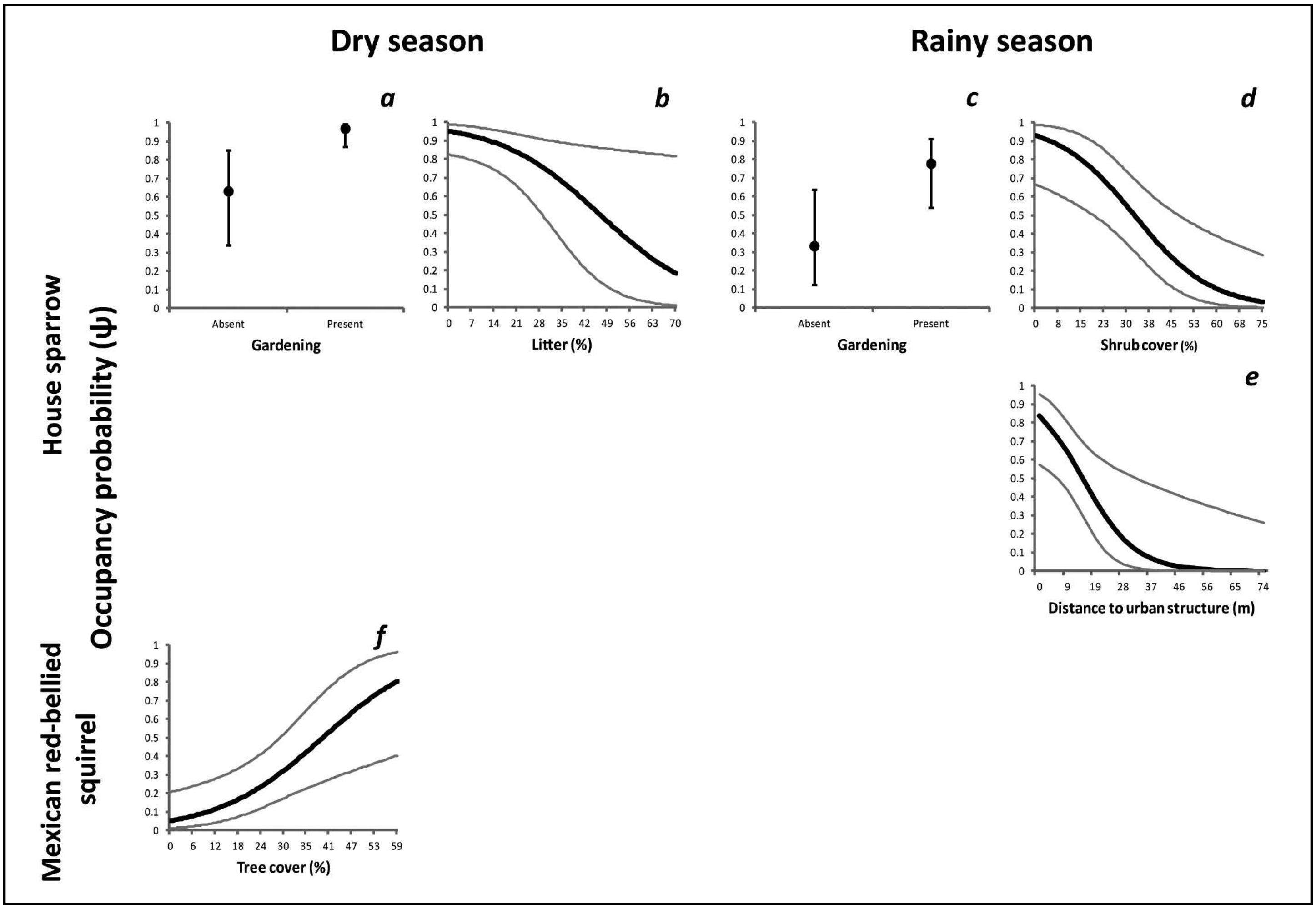


Figure 4. Predicted effects of different environmental factors on occupancy probabilities (ψ) of animal species: house sparrow (a–e), and Mexican red-bellied squirrel (f) during dry and rainy seasons. The regression coefficients for all these environmental variables were derived from models with strong support in the data (see Table 3) and were statistically different than zero. Error bars and gray lines represent 95% confidence intervals.

Other arboreal squirrels like the grey squirrel (*Sciurus carolinensis* Gmelin) show a similar affinity for urban or suburban areas where they seem to forage more intensely than in environments where humans are absent (Bowers and Breland 1996).

Our results also revealed that overall occupancy of nonnative trees tend to be higher in the buffer and urban areas. Nonetheless, the river red gum maintained a similar occupancy probability in all core, buffer, and urban areas during the dry season. The ability of this tree to colonize a large proportion of the core areas during this season might be explained by its potentially high dispersal capacity. Closely related species, like *Eucalyptus globulus* Labill., are able to disperse their seeds over long distances (up to 80 m; Calviño-Cancela and Ribido-Bará 2013). Furthermore, the river red gum produces large quantities of organic litter that contains water-soluble toxins that affect growth of surrounding herbs (del Moral and Muller 1970; Tererai et al. 2015). We also found that occupancy of the jacaranda decreased during the rainy season in all core, buffer, and urban areas. Similarly, occupancy of the river red gum and the tropical ash decreased during the rainy season in the core and buffer areas, respectively. These observed reductions in the occupied area possibly mean that, although nonnative tree species are capable of establishing seedlings within the core and buffer areas, they might be outcompeted by the local flora during the rainy season. Finally, the Peruvian pepper was the tree species with highest occupancies in all areas, without reductions during the rainy season. This tree is well adapted to shrubland environments and is able to establish and grow on rocky substrates (Howard and Minnich 1989). Given its early introduction into central Mexico during the sixteenth century, the Peruvian pepper is now considered a naturalized species (Ramírez-Albores and Badano 2013). However, increases in its abundance may lead to drastic changes in the vegetation structure; thus, some researchers consider this nonnative tree a potential threat to the native flora (Iponga et al. 2008).

Occupancy of nonnative herbs was also relatively higher in buffer and urban areas. The only exception was the klip dagga, which showed a slightly lower occupancy probability within the urban areas during the rainy season. This reduction during the

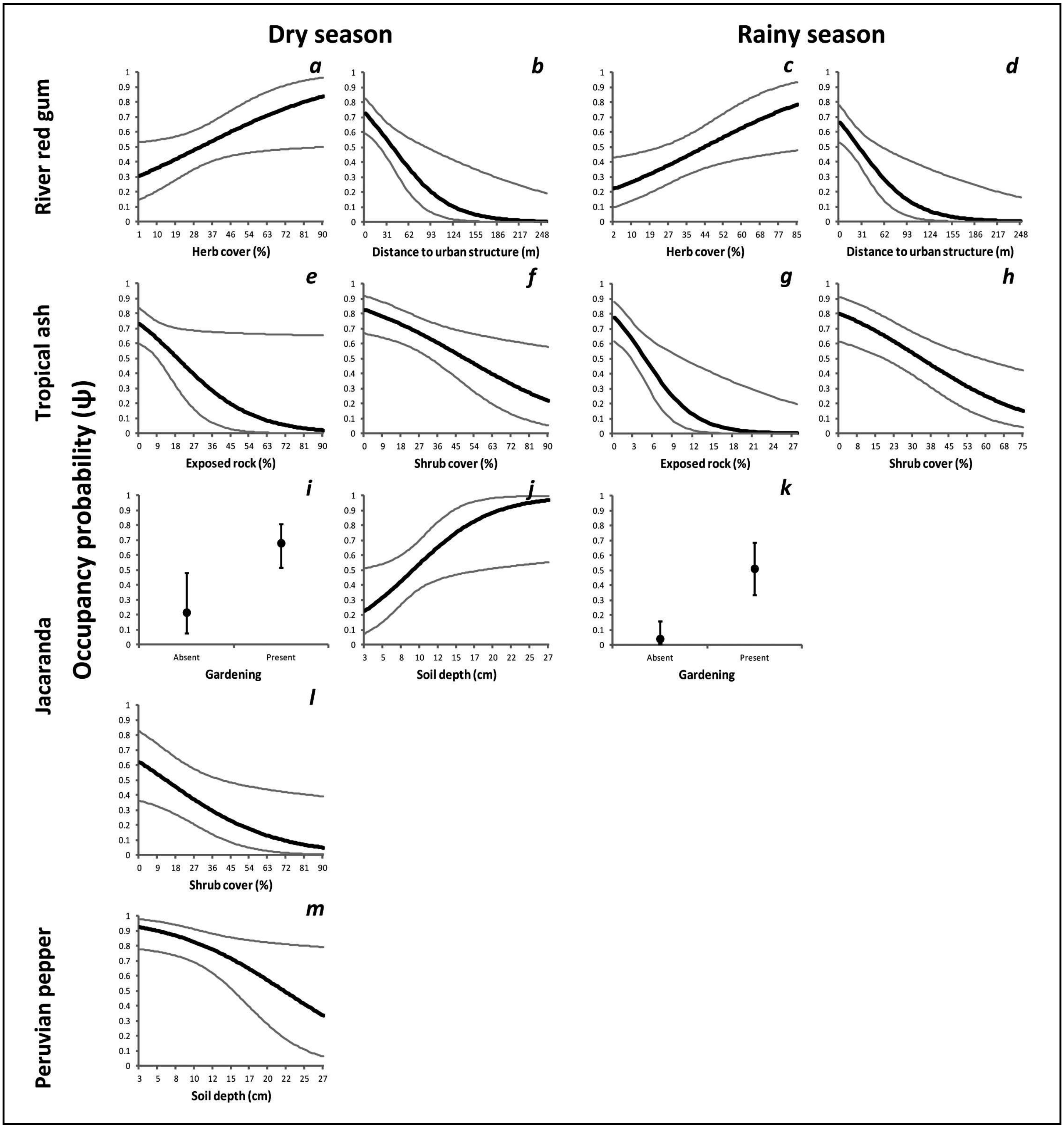


Figure 5. Predicted effects of different environmental factors on occupancy probabilities (ψ) of tree species: river red gum (a–d), tropical ash (e–h), jacaranda (i–l), and Peruvian pepper (m) during dry and rainy seasons. The regression coefficients for all these environmental variables were derived from models with strong support in the data (see Table 3) and were statistically different than zero. Error bars and gray lines represent 95% confidence intervals.

rainy season might stem from the deliberate removal of this species in some buffer and urban patches during active nonnative plant control efforts. In the case of the rose natal grass, its occupancy decreased in all three areas during the rainy season (similar to what we observed in some nonnative trees). Nonetheless, occupancy probability of the rose natal grass was remarkably high (almost 100%) in all three areas during the dry season. Finally, the kikuyu grass was outstanding because of its consistently

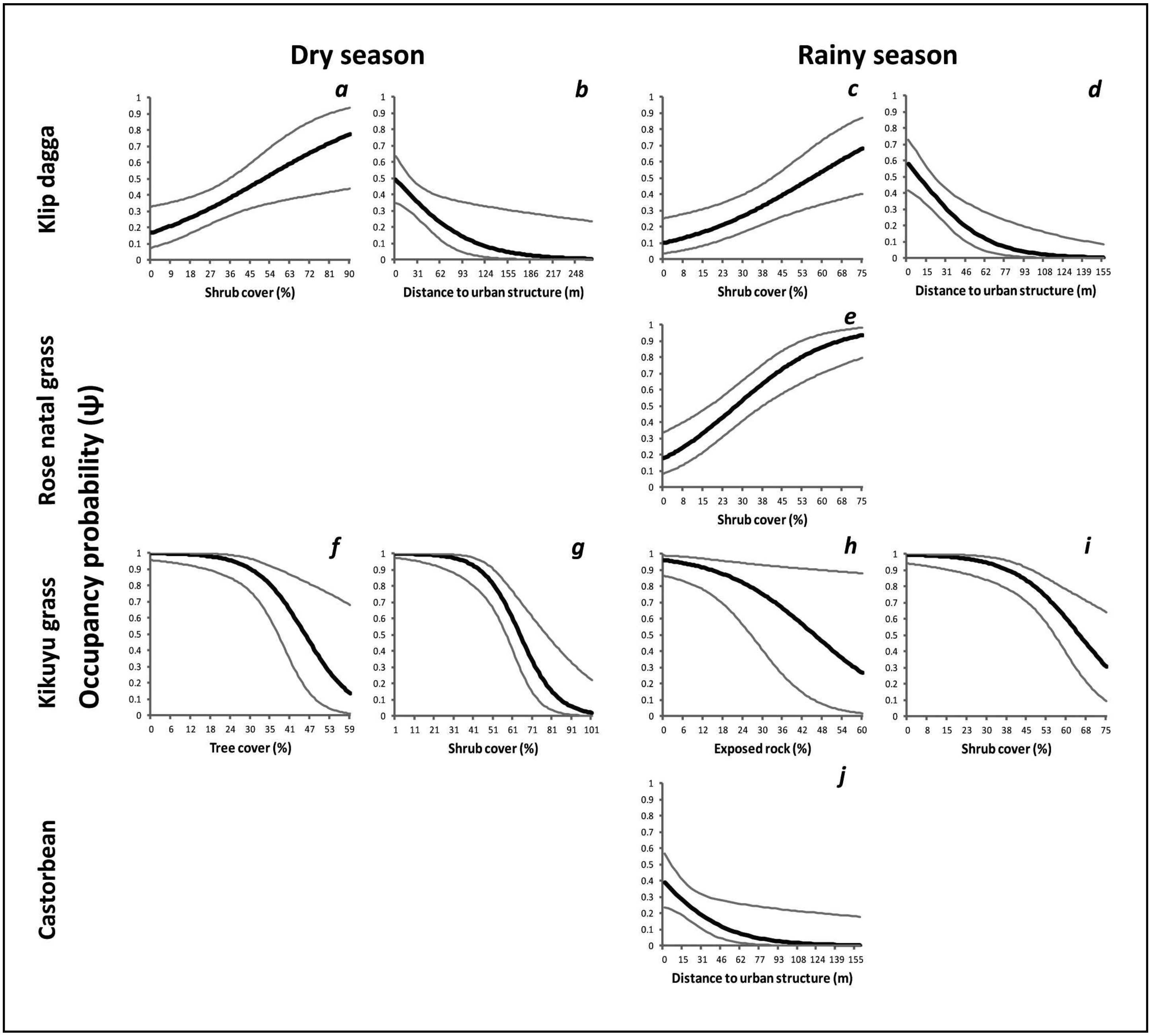


Figure 6. Predicted effects of different environmental factors on occupancy probabilities (ψ) of herb species: klip dagga (a–d), rose natal grass (e), kikuyu grass (f–i), and castorbean (j) during dry and rainy seasons. The regression coefficients for all these environmental variables were derived from models with strong support in the data (see Table 3) and were statistically different than zero. Error bars and gray lines represent 95% confidence intervals.

high occupancy in all three areas during both seasons. Our results suggest that these nonnative herbs may thrive in both seasons, as opposed to some of the nonnative trees, which decreased their presence during the rainy season. This is especially worrying considering that klip dagga has been known to affect the growth of other species when it is highly abundant (Chau et al. 2013), and both the rose natal grass and kikuyu grass seem to be associated with reductions in species diversity (Possley and Maschinski 2006; Estañol-Tecuatl and Cano-Santana 2017). Thus, we suggest that these three species need constant monitoring to prevent them from causing further disturbances within the core areas of the reserve.

Interestingly, all plant species were imperfectly detected during our field surveys. Occupancy models address this issue by simultaneously estimating both detection and occupancy probabilities (MacKenzie et al. 2002; MacKenzie 2006). This means that changes in detectability among areas or seasons do not affect the precise estimation of occupancy probabilities. Hence, these models provided us with unbiased estimates of the proportion of the total area that is occupied by these nonnative plants. For example, detectability of the rose natal grass increased substantially during the rainy season compared to the dry season

(Appendix 2). However, its occupancy was lower during the rainy season (Figures 3e, 3f). This indicates that the probability of detecting plants does not depend on their relative abundance but rather on their visibility. Specifically, during the rainy season the rose natal grass grows in height and its spikes turn bright pink.

Regarding factors that affect occupancy, distance to urban structure was associated with the occupancy of four species: house sparrow, river red gum, klip dagga, and castorbean. Specifically, closeness to buildings and gardens promotes the presence of these species. Likely, humans and human-made structures provide them with some resources such as food, refuges, and appropriate soil. Shrub cover had two different effects on occupancy probability. On the one hand, abundant shrub cover seemed to promote the presence of klip dagga and the rose natal grass, presumably due to nurse plant effects on their seeds. On the other hand, shrub cover had a negative impact on two tree species (tropical ash and jacaranda) and one herb (kikuyu grass). This suggests that for these species shrub cover might hinder germination of their seeds by blocking access to light or by means of strong competition for soil nutrients and water. Exposed rock in the area had a negative effect on the tropical ash and the kikuyu grass, which are almost absent in areas where rock is abundant, likely because these plants need deeper soil for their growth. Lastly, gardening activities clearly increased occupancy of the house sparrow and the jacaranda. In the case of the former species, this positive effect might be related to the closeness of these areas to buildings, whereas in the case of the latter species it seems to be related to the common use of the jacaranda as an ornamental tree.

Our results point toward the need to conduct additional studies on nonnative species inhabiting urban reserves. Physiological needs of potential invaders deserve further studies to discern the particular mechanisms by which nonnative species affect the native biota. In addition, potential negative interactions between nonnatives and local species should be analyzed experimentally or through spatial models (i.e., MacKenzie et al. 2004) to broaden our understanding of ecological processes taking place within such remnants of original vegetation.

ACKNOWLEDGMENTS

The present work is submitted as a partial fulfillment of the requisites for G.A. Ramírez-Cruz to obtain the PhD degree in the Posgrado en Ciencias Biológicas of the Universidad Nacional Autónoma de México. G.A. Ramírez-Cruz would like to thank the Posgrado en Ciencias Biológicas, UNAM, for support, and the Consejo Nacional de Ciencia y Tecnología (CONACyT) for financial support through a scholarship (440952). Funding for this project was provided by the Dirección General de Asuntos del Personal Académico-UNAM through the project PAPIIT IV200117. The authors would like to thank L. Zambrano, F. Martínez, G. Gil, M. Pérez, and M. Fabila for their continued support and advice during field work in the reserve, and S. Rodríguez for his help with preparation of Figure 1. Lastly, we would like to thank the following people who provided technical assistance: M. Vilchis, D. Tovar, E. Serrano, L. Santiago, M. Méndez-Janovitz, M. Suárez-Rodríguez, R. Ortega-Álvarez, N. Neri, N. Saleh, V. Argaez, E. García, and M. Barajas.

Gonzalo Ángel Ramírez-Cruz is a PhD student at Universidad Nacional Autónoma de México (UNAM), School of Sciences. His current interests include urban ecology and zoology. When he is not working on science, he is a semiprofessional illustrator, an avid reader, and an aspiring fiction writer.

Pedro Eloy Mendoza-Hernández has a PhD in biological sciences. He is an academic technician at Universidad Nacional Autónoma de México (UNAM), School of Sciences. His areas of interest include ecophysiology and population and community ecology with an emphasis on ecological restoration of plant communities.

Israel Solano-Zavaleta is an academic technician at Universidad Nacional Autónoma de México (UNAM), School of Sciences. He is interested in systematics, ecology, natural history, geographic distribution, and conservation mainly of amphibians and reptiles in Mexico and Latin America.

J. Jaime Zúñiga-Vega is currently a full professor at Universidad Nacional Autónoma de México (UNAM), School of Sciences. He obtained his PhD degree from this same University and was a postdoctoral fellow at Brigham Young University and at the Biology Institute from UNAM. He has published 45 scientific papers in international journals and is coauthor of a textbook in Spanish about analytical techniques in animal demography. He is Associate Editor for Western North American Naturalist and was the recipient of the National University Award for Young Academics in 2014.

LITERATURE CITED

Anderson, T.R. 2006. Biology of the Ubiquitous House Sparrow: From Genes to Populations. Oxford University Press, New York.

Antonio-Garcés, J.I., M. Peña, Z. Cano-Santana, A. Orozco-Segovia, and M. Villeda. 2009. Cambios en la estructura de la vegetación derivados de acciones de restauración ecológica en las Zonas de Amortiguamiento Biológicas y Vivero Alto. Biodiversidad del Ecosistema del Pedregal de San Ángel. México: Universidad Nacional Autónoma de México 465-481.

Ares, A., and J.H. Fownes. 2001. Productivity, resource use, and competitive interactions of *Fraxinus uhdei* in Hawaii uplands. Canadian Journal of Forest Research 31:132-142.

Asner, G.P., R.F. Hughes, P.M. Vitousek, D.E. Knapp, T. Kennedy-Bowdoin, J. Boardman, R.E. Martin, M. Eastwood, and R.O. Green. 2008. Invasive plants transform the three-dimensional structure of rain forests. Proceedings of the National Academy of Sciences 105:4519-4523.

Bonfil, C. 2010. Present state, use, and perspectives of the genus *Fraxinus* in Mexico. P. 2 *in* C.H. Michler and M.D. Ginzel, eds., Proceedings of Symposium on Ash in North America. USDA Forest Service GTR-NRS-P-72, Newtown Square, PA.

Bowers, M.A., and B. Breland. 1996. Foraging of gray squirrels on an urban–rural gradient: Use of the GUD to assess anthropogenic impact. Ecological Applications 6:1135-1142.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: A

Practical Information-Theoretic Approach. Springer-Verlag, New York.

Calderón, G., and J. Rzedowski, J. 2001. Flora fanerogámica del Valle de México. Comisión Nacional para el Estudio de la Biodiversidad e Instituto de Ecología, AC. México.

Calviño-Cancela, M., and M. Rubido-Bará. 2013. Invasive potential of *Eucalyptus globulus*: Seed dispersal, seedling recruitment and survival in habitats surrounding plantations. Forest Ecology and Management 305:129-137.

Castillo-Argüero, S., Y. Martínez-Orea, J.A. Meave, M. Hernández-Apolinar, O. Nuñez-Castillo, G. Santibañez-Andrade, and P. Guadarrama-Chávez. 2009. Flora: Susceptibilidad de la comunidad a la invasión de malezas nativas y exóticas. Pp. 107-133 *in* A. Lot and Z. Cano-Santana, eds., Biodiversidad del ecosistema del Pedregal de San Ángel. Universidad Nacional Autónoma de México, México DF.

Chacalo, A., A. Aldama, and J. Grabinsky. 1994. Street tree inventory in Mexico City. Journal of Arboriculture 20:222-226.

Chamberlain, D.E., M.P. Toms, R. Cleary-McHarg, and A.N. Banks. 2007. House sparrow (*Passer domesticus*) habitat use in urbanized landscapes. Journal of Ornithology 148:453-462.

Chau, M.M., W.R. Reyes, and T.A. Ranker. 2013. Ecological factors influencing growth of the endangered Hawaiian fern *Marsilea villosa* (Marsileaceae) and implications for conservation management. American Journal of Botany 100:1532-1543.

Cudney, D.W., J.A. Downer, V.A. Gibeault, J.M. Henry, and J.S. Reints. 1993. Kikuyugrass (*Pennisetum clandestinum*) management in turf. Weed Technology 7:180-184.

del Moral, R., and C.H. Muller. 1970. The allelopathic effects of *Eucalyptus camaldulensis*. American Midland Naturalist 83:254-282.

Ehrenfeld, J.G. 2000. Evaluating wetlands within an urban context. Ecological Engineering 15:253-265.

Elmore, C.L., V.A. Gibeault, and D.W. Cudney. 1997. Invasion resistance of tall fescue (*Festuca arundinaceae*) and perennial ryegrass (*Lolium perenne*) to kikuyugrass (*Pennisetum clandestinum*). Weed Technology 11:24-29.

Estañol-Tecuatl, F., and Z. Cano-Santana. 2017. Recovery of basalt substrate for xeric scrub restoration in a lava field in Mexico City. Ecological Restoration 35:41-51.

Folberth, G.A., T.M. Butler, W.J. Collins, and S.T. Rumbold. 2015. Megacities and climate change – A brief overview. Environmental Pollution 203:235-242.

Francis, R.A., and M.A. Chadwick. 2013. Urban Ecosystems: Understanding the Human Environment. Routledge, Abingdon, UK.

Francis, R.A., and M.A. Chadwick. 2015. Urban invasions: Non-native and invasive species in cities. Geography 100:144-151.

Gilman, E.F., and D.G. Watson. 1993. *Jacaranda mimosifolia*. Fact Sheet ST-317, Environmental Horticulture Department, Florida Cooperative Extension Service, University of Florida, Gainesville. <http://www.ci.milpitas.ca.gov/_pdfs/council/2016/021616/item_04.pdf>.

Google. 2017. Google Earth. Mountain View, CA. <https://www.google.com/earth/>.

Gowaty, P.A. 1984. House sparrows kill eastern bluebirds. Journal of Field Ornithology 55:378-380.

Harvey, J.A., and T.M. Fortuna. 2012. Chemical and structural effects of invasive plants on herbivore–parasitoid/predator interactions in native communities. Entomologia Experimentalis et Applicata 144:14-26.

Hortelano-Moncada, Y., F.A. Cervantes, and A. Trejo. 2009. Mamíferos silvestres. Pp. 277-293 *in* A. Lot and Z. Cano-Santana, eds., Biodiversidad del ecosistema del Pedregal de San Ángel. Universidad Nacional Autónoma de México, México DF.

Hosking, J.R., B.J. Conn, and B.J. Lepschi. 2003. Plant species first recognised as naturalised for New South Wales over the period 2000–2001. Cunninghamia 8(2):175-187.

Howard, L.F., and R.A. Minnich. 1989. The introduction and naturalization of *Schinus molle* (pepper tree) in Riverside, California. Landscape and Urban Planning 18:77-95.

Imran, S., S.S. Suradkar, and D.K. Koche. 2012. Phytochemical analysis of *Leonotis nepetifolia* (L) R. BR. A wild medicinal plant of Lamiaceae. Bioscience Discovery 3:197-196.

[INEGI] Instituto Nacional de Estadística y Geografía. 2010. XIV Censo General de Población y Vivienda de 2010. Resumen D.F. <http://cuentame.inegi.org.mx/monografias/informacion/df/default.aspx?tema=me&e=09>.

Iponga, D.M., S.J. Milton, and D.M. Richardson. 2008. Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South African savanna. Journal of Arid Environments 72:612-623.

Johnson, J.B., and K.S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology & Evolution 19:101-108.

Johnson, L.R., and S.N. Handel. 2016. Restoration treatments in urban park forests drive long-term changes in vegetation trajectories. Ecological Applications 26:940-956.

Jøker, D., N.T. Cruz, M.U. Morales, and E. Rojas. 2002. *Schinus molle* L. Danida Forest Seed Centre, Seed Leaflet 57:1-2.

Joshi, D.K. 2009. House sparrow (*Passer domesticus*): The endangered bird. Orissa Review 2009:53-55.

Lapiedra, O., D. Sol, A. Traveset, and M. Vilà. 2015. Random processes and phylogenetic loss caused by plant invasions. Global Ecology and Biogeography 24:774-785.

Lee, M.B., and J.P. Carroll. 2014. Relative importance of local and landscape variables on site occupancy by avian species in a pine forest, urban, and agriculture matrix. Forest Ecology and Management 320:161-170.

Lot, A., and Z. Cano-Santana. 2009. Biodiversidad del ecosistema del Pedregal de San Ángel. Universidad Nacional Autónoma de México, México, DF.

MacGregor-Fors, I., L. Morales-Pérez, J. Quesada, and J.E. Schondube. 2010. Relationship between the presence of house sparrows (*Passer domesticus*) and Neotropical bird community structure and diversity. Biological Invasions 12:87-96.

Mack, R.N., D. Simberloff, W.M. Lonsdale, H. Evans, M. Clout, and F.A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications 10:689-710.

MacKenzie, D.I. 2006. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Academic Press, Burlington, MA.

MacKenzie, D.I., L.L. Bailey, and J. Nichols. 2004. Investigating species co-occurrence patterns when species are detected imperfectly. Journal of Animal Ecology 73:546-555.

MacKenzie, D.I., J.D. Nichols, G.B. Lachman, S. Droege, J.A. Royle, and C.A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.

Magudu, K., and C.T. Downs. 2015. The relative abundance of invasive house sparrows (*Passer domesticus*) in an urban environment in South Africa is determined by land use. South African Journal of Wildlife Research 45:354-359.

Melgoza Castillo, A., M.I. Balandrán Valladares, R. Mata-González, and C. Pinedo Álvarez. 2014. Biología del pasto rosado *Melinis repens* (Willd.) e implicaciones para su aprovechamiento o control: Revisión. Revista Mexicana de Ciencias Pecuarias 5:429-442.

Mora-Ascencio, P., A. Mendoza-Durán, and C. Chávez. 2010. Densidad poblacional y daños ocasionados por la ardilla *Sciurus aureogaster*: Implicaciones para la conservación de los viveros de Coyoacán, México. Revista Mexicana de Mastozoología (Nueva Época) 14:7-22.

Muscolo, A., M.R. Panuccio, and M. Sidari. 2003. Effects of salinity on growth, carbohydrate metabolism and nutritive properties of kikuyu grass (*Pennisetum clandestinum* Hochst). Plant Science 164:1103-1110.

Musser, G.G. 1968. A systematic study of the Mexican and Guatemalan gray squirrel, *Sciurus aureogaster* F. Cuvier (Rodentia: Sciuridae). Miscellaneous Publications of the Museum of Zoology, University of Michigan, Ann Arbor 137:1–112.

Palmer, G.H., J.L. Koprowski, and A.J. Pernas. 2014. Distribution and spread of an introduced insular population of red-bellied squirrels (*Sciurus aureogaster*) in Florida. Mammalia 78:67-73.

Pandey, V.C. 2013. Suitability of *Ricinus communis* L. cultivation for phytoremediation of fly ash disposal sites. Ecological Engineering 57:336-341.

Parsons, W.T., and E.G. Cuthbertson. 2001. Noxious Weeds of Australia. CSIRO Publishing, Collingwood, Victoria, Australia.

Peralta-Higuera, A., and J. Prado-Molina. 2009. Los límites y la cartografía. Pp. 27-42 *in* A. Lot and Z. Cano-Santana, eds., Biodiversidad del ecosistema del Pedregal de San Ángel. Universidad Nacional Autónoma de México, México DF.

Possley, J., and J. Maschinski. 2006. Competitive effects of the invasive grass *Rhynchelytrum repens* (Willd.) CE Hubb. on pine rockland vegetation. Natural Areas Journal 26:391-395.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652-661.

Ramírez-Albores, J.E., and E.I. Badano. 2013. Perspectiva histórica, sociocultural y ecológica de una invasión biológica: El caso del pirul (*Schinus molle* L., Anacardiaceae) en México. Boletín de la Red Latinoamericana para el Estudio de Especies Invasoras 3:4-15.

Ramos-Lara, N., and F.A. Cervantes. 2007. Nest-site selection by the Mexican red-bellied squirrel (*Sciurus aureogaster*) in Michoacán, Mexico. Journal of Mammalogy 88:495-501.

Ramos-Lara, N., and F.A. Cervantes. 2011. Ecology of the Mexican red-bellied squirrel (*Sciurus aureogaster*) in Michoacán, Mexico. The Southwestern Naturalist 56:400-403.

Razo-González, M., G. Castano-Meneses, A. Callejas-Chavero, D. Pérez-Velázquez, and J.G. Palacios-Vargas. 2014. Temporal variations of soil arthropods community structure in El Pedregal de San Ángel Ecological Reserve, Mexico City, Mexico. Applied Soil Ecology 83:88-94.

R Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

[REPSA] Reserva Ecológica del Pedregal de San Ángel. 2017. Listado de especies de la Reserva Ecológica del Pedregal de San Ángel. Accessed 21 March 2017 from <http://www.repsa.unam.mx/index.php/objetivos/caracteristicas/biodiversidad/listado-de-especies>.

Rzedowski, J. 1994. Geographical affinities of the riparian trees of Mexico. Mémoires Societé de Biogéographie, 3a. serie 4:37-44.

Siebe, C. 2000. Age and archaeological implications of Xitle volcano, southwestern Basin of Mexico-City. Journal of Volcanology and Geothermal Research 104:45-64.

Simberloff, D., J.L. Martin, P. Genovesi, V. Maris, D.A. Wardle, J. Aronson, F. Courchamp, B. Galil, E. García-Berthou, M. Pascal, et al. 2013. Impacts of biological invasions: What's what and the way forward. Trends in Ecology & Evolution 28:58-66.

Sousa, R., P. Morais, E. Dias, and C. Antunes. 2011. Biological invasions and ecosystem functioning: Time to merge. Biological Invasions 13:1055-1058.

Strauss, S.Y., J.A. Lau, and S.P. Carroll. 2006. Evolutionary responses of natives to introduced species: What do introductions tell us about natural communities? Ecology Letters 9:357-374.

Suárez-Lastra, M. 2016. Expansión urbana y reemplazo del hábitat natural. Pp. 119-126 *in* Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), and Secretaría del Medio Ambiente del Distrito Federal (SEDEMA), La biodiversidad en la Ciudad de México. CONABIO/SEDEMA. México.

Tererai, F., M. Gaertner, S.M. Jacobs, and D.M. Richardson. 2015. *Eucalyptus camaldulensis* invasion in riparian zones reveals few significant effects on soil physico-chemical properties. River Research and Applications 31:590-601.

Thomsen, M.S., J.D. Olden, T. Wernberg, J.N. Griffin, and B.R. Silliman. 2011. A broad framework to organize and compare ecological invasion impacts. Environmental Research 111:899-908.

Villaseñor, J.L., and F.J. Espinosa-Garcia. 2004. The alien flowering plants of Mexico. Diversity and Distributions 10:113-123.

Wallander, E. 2008. Systematics of *Fraxinus* (Oleaceae) and evolution of dioecy. Plant Systematics and Evolution 273:25-49.

Wen, L., J. Ling, N. Saintilan, and K. Rogers. 2009. An investigation of the hydrological requirements of River Red Gum (*Eucalyptus camaldulensis*) Forest, using Classification and Regression Tree modelling. Ecohydrology 2:143-155.

White, G.C., and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46:S120-S138.

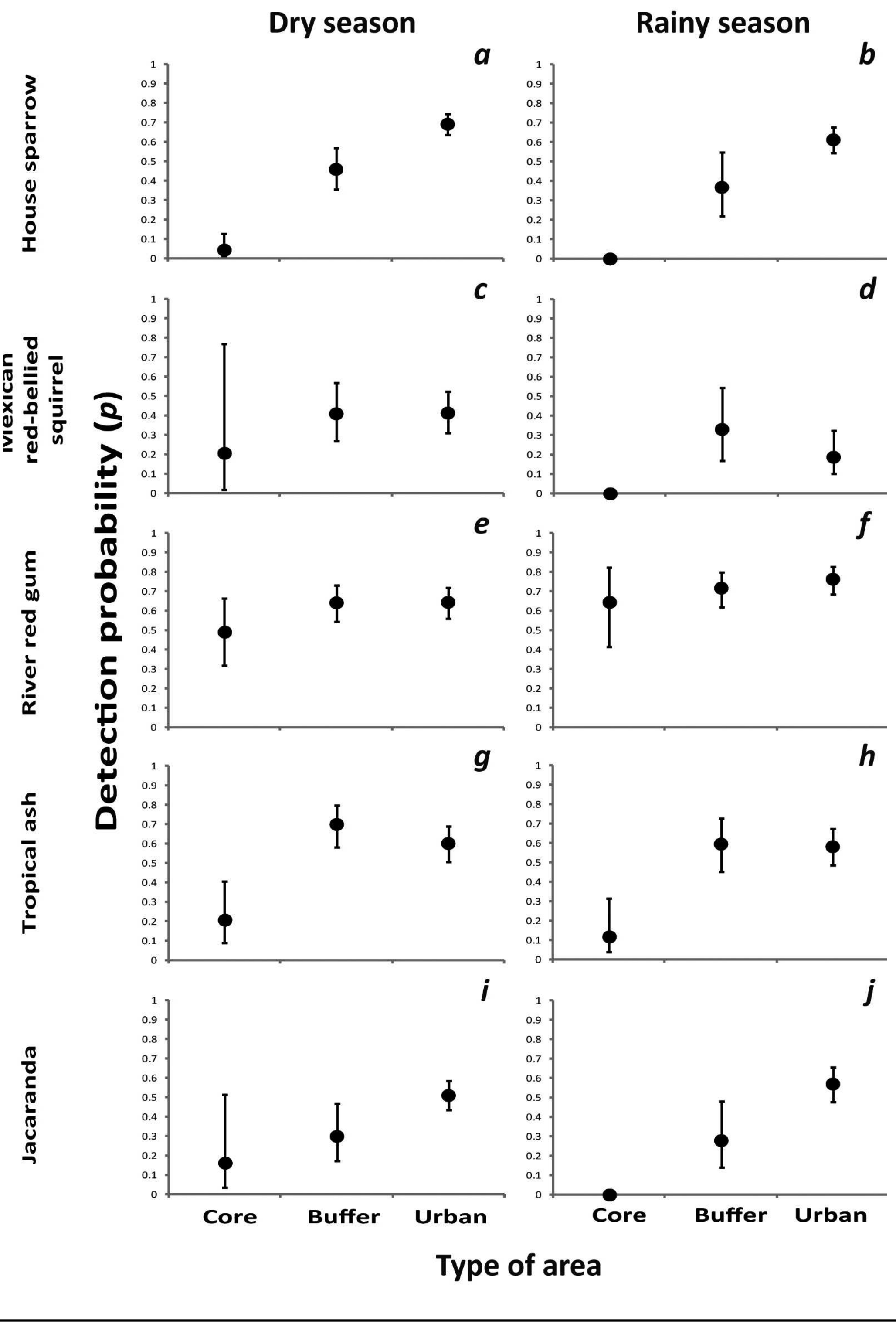
With, K.A. 2002. The landscape ecology of invasive spread. Conservation Biology 16:1192-1203.

Xiangzhen, Q., L. Zhenshan, and L Huiyu. 2016. Modeling the interactive effects of competition and landscape patterns on exotic species spread. Ecological Informatics 31:30-38.

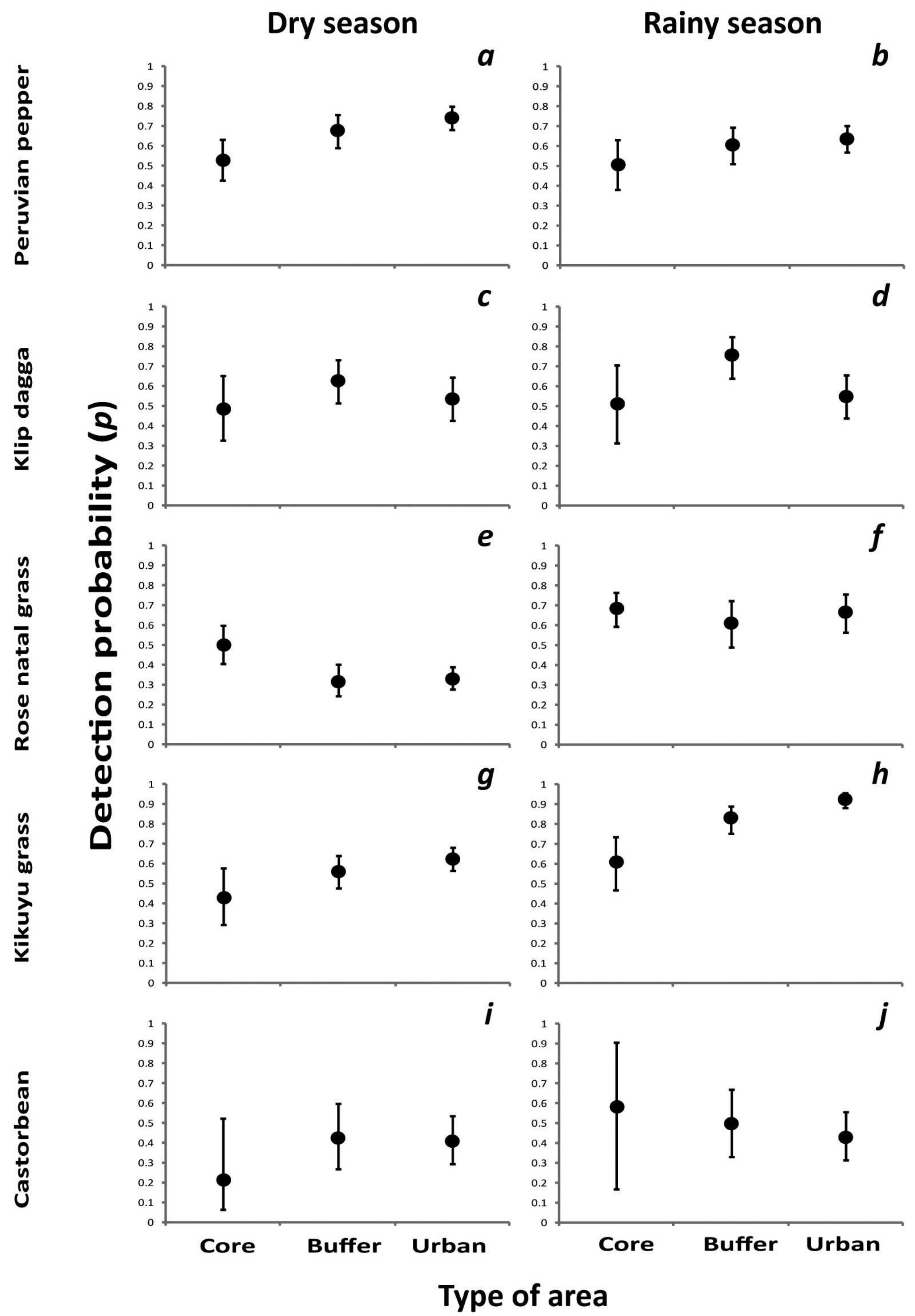
Xiao, S., R.M. Callaway, R. Graebner, J.L. Hierro, and D. Montesinos. 2016. Modeling the relative importance of ecological factors in exotic invasion: The origin of competitors matters, but disturbance in the non-native range tips the balance. Ecological Modelling 335:39-47.

Zambrano L., S. Rodríguez-Palacios, M. Pérez-Escobedo, G. Gil-Alarcón, P. Camarena, and A. Lot. 2016. La Reserva Ecológica del Pedregal de San Ángel: Atlas de Riesgos, 2da edición. Coordinación de la Investigación Científica, Secretaría Ejecutiva de la Reserva Ecológica del Pedregal de San Ángel, UNAM. Ciudad de México.

Zavaleta, E.S., R.J. Hobbs, and H.A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology & Evolution 16:454-459.



Appendix 1. Estimated detection probabilities (*p*) of house sparrow (a, b), Mexican red-bellied squirrel (c, d), river red gum (e, f), tropical ash (g, h), and jacaranda (i, j) within core, buffer, and urban areas during dry and rainy seasons. Error bars represent 95% confidence intervals.



Appendix 2. Estimated detection probabilities (*p*) of Peruvian pepper (a, b), klip dagga (c, d), rose natal grass (e, f), kikuyu grass (g, h), and castorbean (i, j) within core, buffer, and urban areas during dry and rainy seasons. Error bars represent 95% confidence intervals.