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Vegetation recovery and plant facilitation in a human-disturbed lava field in a megacity: searching tools for ecosystem restoration

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Abstract Unplanned urban development threatens natural ecosystems. Assessing ecosystem recovery after anthropogenic disturbances and identifying plant species that may facilitate vegetation regeneration are critical for the conservation of biodiversity and ecosystem services in urban areas. At the periphery of Mexico City, illegal human settlements produced different levels of disturbance on natural plant communities developed on a lava field near the Ajusco mountain range. We assessed natural regeneration of plant communities 20 years after the abandonment of the settlements, in sites that received low (manual harvesting of non-timber forest products), medium (removal of aboveground vegetation), and high (removal of substrate and whole vegetation) disturbance levels. We also tested the potential facilitative role played by dominant tree and shrub species. Plant diversity and vegetation biomass decreased as disturbance level increased. Sites with high disturbance level showed poor regeneration and the lowest species similarity compared to the least disturbed sites. Six dominant species (i.e., those with the highest abundance, frequency, and/or basal area) were common to all sites. Among them, three species (the tree *Buddleja cordata*, and two shrubs, *Ageratina glabrata* and *Sedum oxypetalum*) were identified as potential facilitators of community regeneration, because plant density and species richness were significantly higher under their canopies than at open sites. We propose that analyzing community structural traits of the successional vegetation (such as species diversity and biomass) and identifying potential facilitator species are useful steps in assessing the recovery ability of plant communities to anthropogenic disturbances, and in designing restoration strategies.

Keywords Biodiversity · Mexico · Oak forest · Secondary succession · Species richness · Xerophytic vegetation

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Introduction

Nowadays human activities are severely damaging natural ecosystems worldwide. In many regions, land conversion to agriculture, mining, and urbanization seriously threaten biodiversity and ecosystem functions (Bullock et al. 2011). While the impacts of some primary activities such as food production, forestry, and mineral extraction have been well documented in several ecosystems (Newton et al. 2009), the environmental impact of urban expansion on natural areas, as well as the reduction in ecosystem resilience in response to such disturbances, is poorly understood (Aguilar 2008). The understanding of such impact is critical as natural areas within and around cities provide ecosystem services of paramount importance for human well-being, including temperature amelioration, water storage, filtration and drainage, and air filtering, among others (Bolund and Hunhammar 1999).

In cities with relatively high poverty levels, housing demands promote the encroachment of illegal settlements on such ecosystems. In the exceptional cases in which illegal settlements have been reverted, ecosystem recovery depends on the intensity, duration, and extension of the disturbance, as well as on the successional mechanisms intrinsic to the ecosystem (Coop et al. 2007). When the severity of the disturbance overcomes ecosystem resilience, restoration activities are required to recover desirable ecosystem properties (Young et al. 2001). Therefore, detecting disturbance thresholds (Briske et al. 2005) and identifying species that may play a facilitation role in the natural regeneration of vegetation are important steps in the design of restoration strategies.

Natural areas surrounding megacities, among which Mexico City is one noticeable example, are constantly under high urbanization pressure. Paradoxically, these areas often are the most important providers of ecosystem services (such as water reservoirs, recreation, and mesoclimate regulation; Bullock et al. 2011) for the very same people who press to settle in them. In Mexico City, the government has responded to this pressure by creating protected areas or nature reserves as a way of facing the increasingly high rate of land use change (Cano-Santana et al. 2006). Our study site, the Parque Ecológico de la Ciudad de México (PECM), is one of such protected areas, which was created by governmental decree in 1991. Between 1980 and 1990, an illegal human settlement affected an area of ca. 200 ha within this park producing a disturbance mosaic. The settlement was dissolved through land expropriation in 1990 and the people were relocated.

After expropriation, some intervention activities aimed at restoring the disturbed areas in the PECM were initiated (Bonfil et al. 1997). Nevertheless, the disturbed area was a lava field, where the basaltic substrate and the reduced amount of organic soil result in harsh environmental conditions that make plant recruitment difficult (Mendoza-Hernández et al. 2010), which invites for a restoration program to be established. To design the most adequate restoration strategies for the recovery of vegetation structure and ecosystem functionality it is necessary to explore several ecological features and processes at different scales. One of these is the capacity of the plant community to recover after a disturbance; this ability may be assessed through a quantitative analysis of structural and compositional attributes of the vegetation (Maestre et al. 2006; Lebrija-Trejos et al. 2008). Also, investigating the potential positive interactions between naturally established plants is a promising approach, which may allow us to identify key tree and shrub species that may facilitate plant establishment by creating micro-sites of reduced radiation and increased soil resources under their canopies (Brooker et al. 2008).

In this article, we report an assessment of vegetation recovery in different areas of the PECM, 20 years after the anthropogenic disturbance described above. Also, we explore the potential of the dominant plant species to act as facilitators of the natural regeneration of the vegetation under the harsh environmental conditions that prevail after the disturbance. Specifically, we address the following questions: (1) To what extent have the structure and composition of the vegetation recovered from increasing levels of anthropogenic disturbance? (2) Do some shrub or tree species have the potential of facilitating the natural regeneration of the vegetation? We hypothesized that increased levels of anthropogenic disturbance reduce the ability of the plant community to recovery on the studied lava field.

Methods

Study area

The Parque Ecológico de la Ciudad de México (PECM) is located on the southern margin of Mexico City (19°15′32.0″N, 99°12′1.9″W; Fig. 1). The climate at this area is temperate with a summer rainfall pattern; over a 3-year period (2008–2010) annual precipitation ranged from 717 to 918 mm (ca. 80 % falling between June and October), mean annual temperature is 15.6 °C, extreme temperatures reach values of −3.3–0.5 °C during the winter, and 27.9–30.2 °C in the summer (Ecoguardas meteorological station). The PECM is one of the largest fragments remaining from the original lava flow created by the eruption of the Xitle volcano between 1650 and 2000 years ago (Siebe 2000). The park area is 727 ha, of which 29 % was affected by illegal human settlements in the 1980s. The disturbed area comprises a mosaic of different vegetation types, among which an oak forest and a xerophytic scrub are prominent. The oak forest occurs on deep andesitic soils and is dominated by *Quercus rugosa*, *Q. crassipes*, and *Q. laurina*; the xerophytic scrub occurs on shallow undeveloped soils and is the most widespread vegetation type, dominated by *Agave salmiana*, *Ageratina glabrata*, *Bouvardia terniflora*, *Dahlia coccinea*, *D. merckii*, *Eupatorium pazcuarense*, *Muhlenbergia macroura*, *Salvia mexicana*, *Sedum oxypetalum*, *Senecio praecox*, and *Verbesina virgata* (González-Hidalgo et al. 2001). The local flora comprises 329 native species of vascular plants, which adds up to 16.8 % of the 2071 species recorded in the entire territory of the Basin of Mexico (ca. 7500 km^2; Rzedowski and de Rzedowski 1989). The PECM also serves as an important refuge to several groups of native fauna (Zaragoza and Miceli 2006). In addition, this area provides very important ecosystem services for the entire Basin of Mexico, among which the most valued ones are climate regulation and the recharge and probably purification of the aquifers (Cano-Santana et al. 2006).

Study system

Study sites

Fieldwork was conducted during the dry period of the year, from November 2008 to March 2009. We selected an area of about 20 ha within the zones disturbed by illegal settlements. Within this area, we identified sites with high, medium, and low disturbance levels, which prior to disturbance had similar vegetation structure and composition (open oak forest included in a matrix of xerophytic scrub). The high-disturbance sites were those where settlers used heavy machinery to remove below and above ground vegetation, as well as soil and rocky substrate (this disturbance covered about 25 % of total human affected area); the medium-disturbance sites comprised those where the above ground vegetation was partially removed (some original vegetation patches remained) and substrate was altered using hand tools (about 60 % of the area); the low-disturbance sites were those where the vegetation was altered only through extraction of some forest products (Rzedowski and de Rzedowski 2005), such as firewood and medicinal plants (about 15 % of the area). In total, we selected 30 sites; 10 belonging to each disturbance level. Because at the study area, within the same geomorphological formation, there were no sites that could be taken as an undisturbed reference condition, we used the low disturbance as the reference condition, considering that the soil was not disturbed at these sites and that vegetation alteration was kept to a minimum. At each site, we established a sampling plot of 160 m^2. Within this plot, all trees and shrubs with heights ≥50 cm were tagged. Each plant was taxonomically determined, and its height measured. For shrubs we also measured the basal diameter (D) of each stem, and the diameter at breast height (DBH) of each stem in the case of trees. Finally, for all plants we measured two perpendicular crown diameters (D_1, D_2).

Identification of potential facilitator species

At the high- and medium-disturbance sites, we selected four species based on their dominance across all sites, two tree species (*Buddleja cordata* and *Dodonaea viscosa*, seeders) and two shrub species (*Ageratina glabrata* and *Sedum oxypetalum*, both seeders and sprouters). These stress-tolerant, anemochorous, species are frequently found in early successional communities on the lava fields of this region (Rzedowski and de Rzedowski 2005). Previous observations suggest that under the harsh open conditions that prevail in lava fields, such species may potentially facilitate the establishment of other species under their crowns because (a) they are capable of casting shade during the dry season (they are evergreen or have highly dense branching), (b) they accumulate significant amounts of litter under their crowns thus aiding soil formation, (c) they are abundant in disturbed sites, and (d) small plants of several woody species commonly establish under their

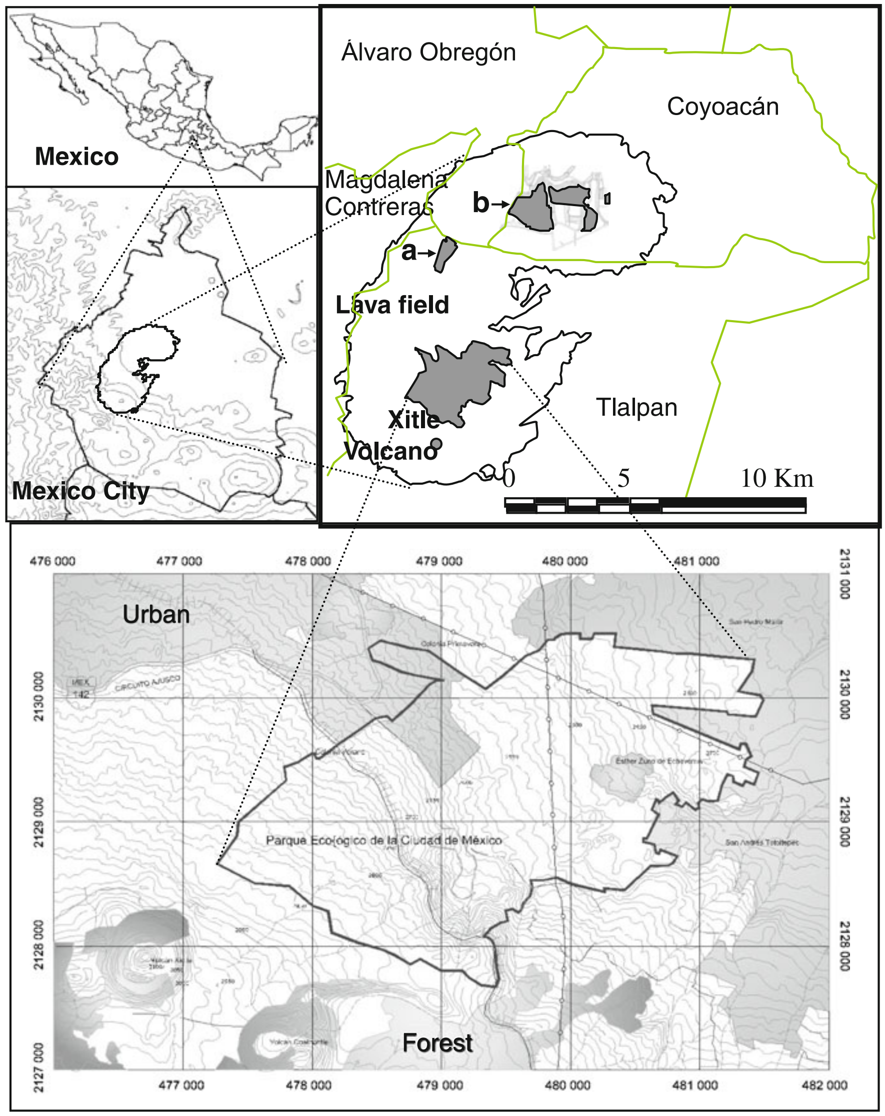


Fig. 1 The Parque Ecológico de la Ciudad de México is one of the largest protected fragments of natural ecosystems developed on the lava field. Two other protected fragments are: **a** Los Encinos and **b** Reserva Ecológica del Pedregal de San Ángel at the Universidad Nacional Autónoma de México (Modified from Castillo-Argüero et al. 2004)

crowns. We randomly selected 50 individuals of each of these potential facilitator species (PFS, 200 in total) and measured their height and crown area. We refer to the woody plants present beneath the crown of these PFS as protégé plants (sensu Flores and Jurado 2003). We counted the number of protégé plants and species under the projected crown cover of each focal PFS individual. Additionally, we randomly selected 50 circular plots 2 m in diameter within open areas deprived of shrubs or trees; these plots represented the mean environmental conditions in areas without a woody vegetation cover. We counted the number of plants (<30 cm in height) and species in each of these plots.

Data analysis

Assessing the recovery of structural attributes of plant communities

For each plant that we tagged within the study plots, we quantified crown cover ($CC = ((D_1/2) \times (D_2/2) \times \pi)$ and basal area ($BA = (D/2)^2 \times \pi$). For each of the 10 plots per disturbance level, we calculated plant density (number of individual plants in 160 m^2), mean plant height (m), total crown cover area (m^2), total basal area (m^2), and species density (number of species in 160 m^2). Each plot represented a replicate for its disturbance level. Diversity per plot was assessed using Shannon–Wiener index (Magurran 2004). For each plot, we calculated rarified species richness and diversity using the lowest number of individuals per plot, with ECOSIM v7.72 (http://garyentsminger.com/ecosim.htm). We used a Kruskal–Wallis test to assess the significance of the differences in vegetation structural traits among disturbance levels.

To explore disturbance effects on global species richness, we obtained smoothed cumulative species-curves for each disturbance level. Moreover, we calculated a relative importance value for each species i (RIV_i) as an indicator of its structural contribution to the community in each disturbance level, by adding its relative values of frequency (RF), density (RD), and cover (RC). We constructed a species–rank curve per disturbance level by plotting RIV_i values (on a log scale) as a function of the species RIV_i rank. The resulting curves were fitted to the exponential model, $y = a + b\exp(-x/c)$, using Table Curve 2D v5.01 (Systat Software Inc., Richmond, CA, USA). The slope of the curve indicates community evenness. We used the first minimal derivatives of these curves to test for differences in evenness among disturbance levels using a t test.

We used Sørensen index to quantify species similarities between all possible plot pairs. Then, we used Kruskal–Wallis tests to assess differences in mean similarity between plots of the same and different disturbance levels. Furthermore, we carried out an ordination of the plots through non-metric multidimensional scaling (NMDS, McCune and Mefford 2006) applied to a Bray–Curtis similarity matrix (Austin 1977). The matrix was constructed considering the RIV values per species at each of the 30 studied plots. A multivariate analysis of variance (MANOVA) and a posteriori Bonferroni tests were performed to assess statistical differences among the scores corresponding to each disturbance level on the ordination dimensions extracted by the NMDS. We performed the NMDS using PRIMER-E Enterprises v.5, and MANOVA using DATA DESK (Data Description Inc., Ithaca, New York, USA).

Protégé plant density and species richness associated to potential facilitator species

To test the hypothesis that PFS maintain higher plant densities and species densities under their canopies compared to open sites, we used one-way ANOVAs after log-transformation of the variables. In this analysis we had five treatments, including the open sites and the four PFS, each with 50 replicates. Plant density and species density, the two response variables, were obtained by dividing the total number of recorded plants or species, respectively, by the crown cover area of each PFS individual. When an ANOVA detected a significant effect of the treatment, we performed post hoc Bonferroni tests.

To assess whether the PFS effectively affected the abundance of particular species, we compared separately plant density of each protégé species among the four PFS and the open sites. To do this, and because PFS crown area differed widely in size between species, we scaled the plant density of every protégé species (recorded across all 50 individuals of each PFS) to an area of 100 m^2. Because of the nature of the response variable (i.e., counts), we used a generalized linear model (GLM) with a Poisson error and a log-link function (GLIM v4.0, NAG, Jordan Hill Road, Oxford, UK). We used a t test, adjusted for multiple comparisons, to identify significant differences among treatments (Crawley 1993).

Results

Recovery of structural attributes of plant communities

A total of 1,828 individuals and 71 species (38 identified to the species level, 19 to the genus level, and 14 not identified; Table 2 in Appendix) were found in the 30 sampled plots. The plant families with the higher number of species were Asteraceae (20 species), Lamiaceae (6), and Fagaceae (5). After 20 years of secondary succession, the low-disturbance sites had twice as many individuals (45 % of the total) and species (55) than high-disturbance sites (22 % and 26), while medium-disturbance sites had intermediate values (33 % and 34). From the total number of recorded species, 4 % occurred exclusively at high-disturbance sites, 10 % in sites with medium-disturbance, and 47 % were exclusively recorded at sites with low-disturbance level (Table 2 in Appendix).

As expected, for most structural vegetation traits (mean plant height, total crown cover area, total basal area, and diversity indices), low-disturbance sites showed the highest values, followed in decreasing order by the medium- and the high-disturbance sites (Fig. 2). The only exception was plant density, which was highest at the medium-disturbance sites (Fig. 2c). In particular, high-disturbance sites showed low values in biomass indicators, basal area and cover, which were three to four times smaller than in the low-disturbance sites. The slopes of the species–rank curves (Fig. 3A–C) indicated that the high- and medium-disturbance sites were dominated only by a few species, while the low-disturbance sites showed a noticeably higher evenness (i.e., less steep slopes; $P < 0.0001$). At the low-disturbance sites, *Quercus rugosa* was dominant (Fig. 3C), while the medium- and high-disturbance sites were dominated by *Buddleja cordata* (Fig. 3A, B). Among the ten species with the highest RIVs (Fig. 3), six were shared among all disturbance levels; however, the rank of these species differed markedly among them (Fig. 3A–C). The estimated global species richness values based on species–area curves were similar for the high- and medium-disturbance sites, while the low-disturbance sites exhibited twice as many species considering the total sampled area (Fig. 3D).

Two decades after abandonment, species similarity (Sørensen index) was still low (0.33) between sites with low- and high-disturbance levels, intermediate (0.41) between sites with medium- and high-disturbance levels, and highest (0.53) between sites with medium- and low-disturbance levels ($P < 0.0001$). NMDS and MANOVA showed that sites with high- and medium-disturbance levels were similar in species composition and structure and both differed from the low-disturbance sites ($P < 0.0001$; Fig. 4).

Protégé plant density and species richness associated to potential facilitator species

Total crown cover for the 50 plants of the different PFS was 66.3 m^2 for *Sedum oxypetalum*; 78.0 m^2 for *Ageratina glabrata*; 221.6 m^2 for *Buddleja cordata*; and 330.3 m^2 for *Dodonaea viscosa*. Both mean height and mean crown cover differed significantly between PFSs (Table 1). Overall, plant density beneath the canopies of PFS was significantly higher than at open sites ($F_{(4,245)} = 6.66$, $P < 0.0001$) and the same was true for species density ($F_{(4,245)} = 15.02$, $P < 0.0001$). Specifically, the canopies of *Sedum oxypetalum*, *Ageratina glabrata*, and *Buddleja cordata* resulted in increased plant and species density compared to open sites, while the canopy of *Dodonaea viscosa* did not differ from the open sites in this respect (Fig. 5).

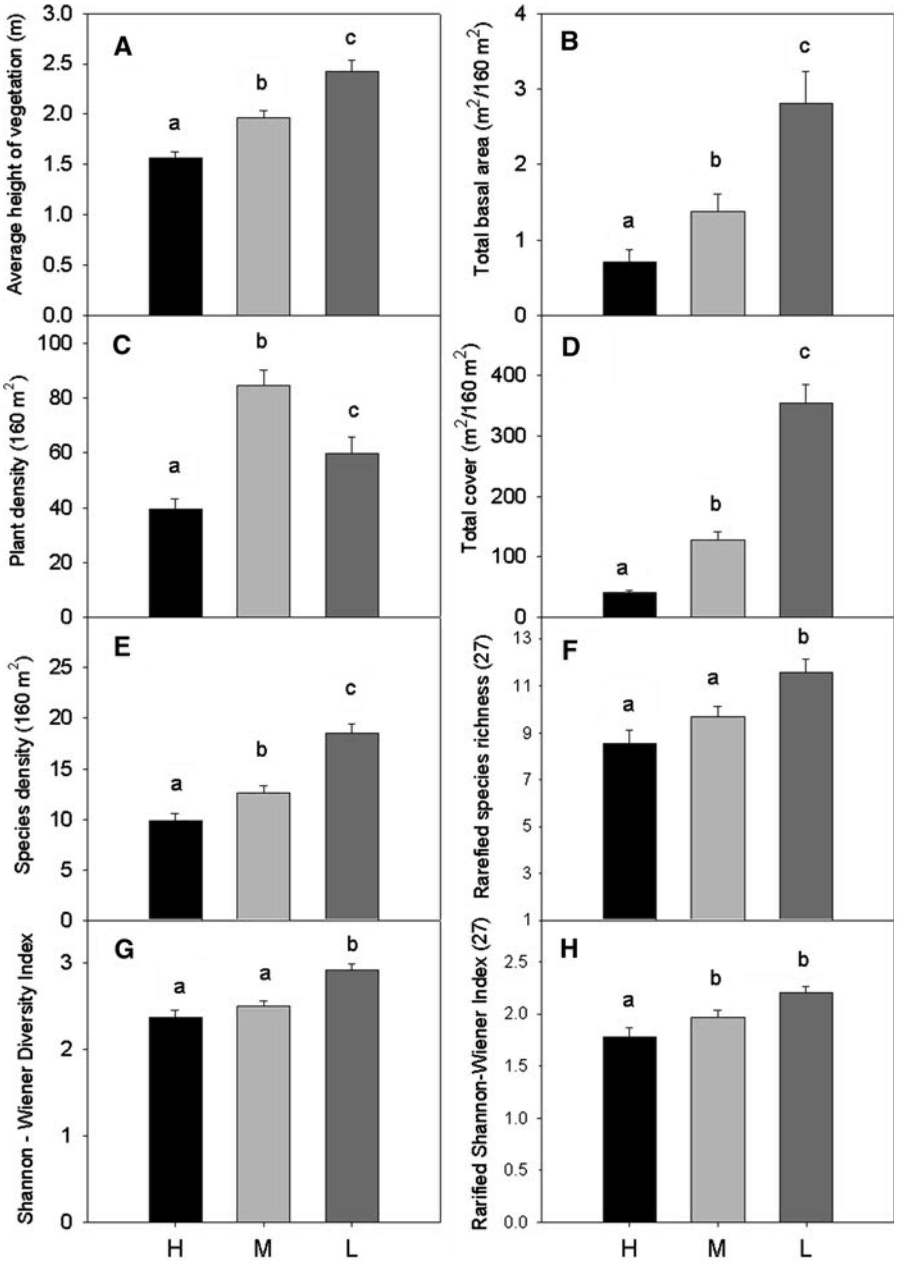
We analyzed the effect of PFS on the abundance of eleven protégé plant species. We found significant positive effects of the PFS on seven protégé species, but these effects were non-uniform across PFS (Fig. 6). Seven species of protégé plants (*Agave salmiana*, *Ageratina glabrata*, *Buddleja cordata*, *Echeveria gibbiflora*, *Opuntia* spp., *Quercus rugosa*, and *Sedum oxypetalum*) had significantly higher densities under the crown cover of *Ageratina glabrata* than in open sites (Fig. 6). In contrast, only two species (*Agave salmiana* and *Sedum oxypetalum*) showed higher densities under the canopies of *Buddleja cordata* and *Sedum oxypetalum*. In turn, only one species (*Sedum oxypetalum*) had a higher density under the canopy of *Dodonaea viscosa* than in open sites. Moreover, for some species we found evidence of negative associations with various PFS, as indicated by the lower densities of *Ageratina glabrata*, *Buddleja cordata*, *Senecio praecox*, and *Wigandia urens* under the canopies of some PFSs than in open sites (Fig. 6). On the other hand, *Dodonaea viscosa* and *Mammillaria magnimmama* showed similar densities under all PFS and in open sites (neutral response), whereas *Echeverria gibbiflora*, *Opuntia* spp., and *Quercus rugosa* showed a neutral response to *Dodonaea viscosa*, *Buddleja cordata*, and *Sedum oxypetalum*. Finally, *Senecio praecox*, and *Wigandia urens* also displayed a neutral response to the presence of more than one PFS (Fig. 6).

Discussion

Vegetation recovery at sites with different disturbance levels

Our results show that the anthropogenic disturbance that took place in the 1980s in the PECM had a strong effect on the plant community. Twenty years after land reclamation in the year 1989, attributes of the

Fig. 2 Natural regeneration of vegetation 20 years after land reclamation, as measured by different structural vegetation traits, in sites with high (*H*), medium (*M*), and low (*L*) human disturbance levels at the Parque Ecológico de la Ciudad de México. *Bars* not sharing *same letter* are significantly different ($P < 0.05$)



vegetation still show a poor recovery at sites with high- and medium-disturbance levels. Particularly, the low values of basal area and cover and species diversity, as well as the species composition recorded at the high-disturbance sites, are evidence of such poor recovery. The disturbance inflicted on the substrate and the extirpation of below and above ground vegetation with machinery or above ground with hand tools was of such magnitude that, after two decades, the ecosystem is far from attaining at least the structure and composition of the low disturbance sites. Such impact is significant if we take into account that the high- and medium-disturbance levels occurred in about 85 % of the total area affected in the PECM. Thus, the establishment of the protected area was an important first step toward the recovery of the original plant community (Crosti et al. 2007), albeit insufficient to guarantee its complete recovery.

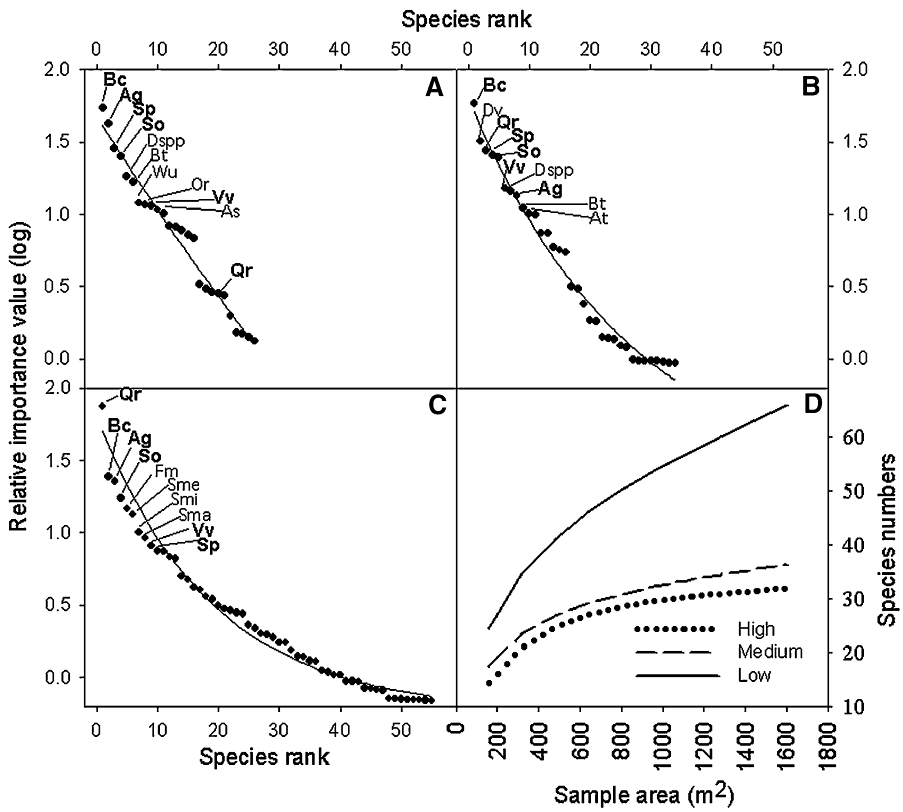


Fig. 3 Species diversity of regenerating vegetation 20 years after land reclamation in sites that suffered different levels of anthropogenic disturbance at the Parque Ecológico de la Ciudad de México. **A**, **B**, and **C** Dominance–diversity curves for sites with high-, medium-, and low-disturbance level, respectively; the ten species with highest relative importance value at each disturbance conditions are shown with acronyms (in *bold letters* are indicated the six species common to all disturbance levels). **D** The cumulative species–area curves for each one of the three studied disturbance levels. *Ag Ageratina glabrata*, *As Agave salmiana*, *At Arracacia tolucensis*, *Bc Buddleja cordata*, *Bt Bouvardia ternifolia*, *Dv Dodonaea viscosa*, *Dspp Dahlia* spp., *Fm Fuchsia microphylla*, *Or Opuntia rzedowskii*, *Qr Quercus rugosa*, *Sm Salvia mexicana*, *Smi Stevia micrantha*, *Sma Satureja macrostema*, *So Sedum oxypetalum*, *Sp Senecio praecox*, *Vv Verbesina virgata*, and *Wu Wigandia urens*

Soil and vegetation removal created environmental conditions similar to those occurring during early primary succession. Under such harsh conditions, typical early successional species at these sites (most of them anemochorous and stress-tolerant plants) are *Agave salmiana*, *Ageratina glabrata*, *Buddleja cordata*, *Dodonaea viscosa*, *Opuntia rzedowskii*, *Sedum oxypetalum*, and *Senecio praecox* (Rzedowski and de Rzedowski 2005). Precisely these species were dominant at sites with high- and medium-disturbance levels (Table 2 in Appendix). Medium-disturbance sites were dominated by *Sedum oxypetalum*, which is a clonal shrub that produces a large numbers of wind-dispersed, orthodox seeds (Martínez-Villegas et al. 2012), and has a high capacity for vegetative propagation. In contrast, at the low-disturbance sites the soil remained almost unaltered while the vegetation was directly disturbed through the harvest of herbaceous plants and woody branches for medicinal and firewood purposes. In the low-disturbance sites, *Quercus rugosa* was the dominant species, which was also dominant in the old growth forest of the PECM before human disturbance (Rzedowski 1954); also, in these sites a relatively high number of late successional species were found as co-dominants.

Although low-disturbance sites may act as seed sources of late successional species (such as *Quercus rugosa*) for the regeneration of high- and medium-disturbance sites, such species may face recruitment limitations due to distance effects (dispersal limitation), lack or scarcity of dispersal agents, or high seed or seedling mortality due to harsh abiotic and biotic factors (Fattorini and Halle 2004). For example, *Q. rugosa* is a long-lived, slow-growing tree that is

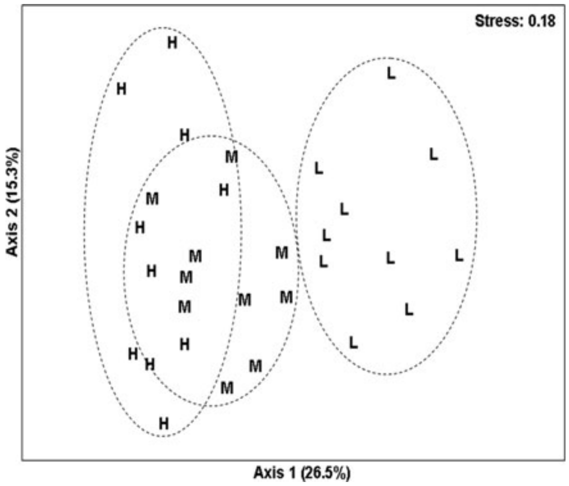


Fig. 4 Result of the NMDS ordination for 30 sites that suffered human disturbance in the Parque Ecológico de la Ciudad de México. *L* low disturbed sites, *M* medium-disturbed sites, *H* high disturbed sites. Dashed ellipses include sites of same disturbance level (see text for further details)

highly sensitive to disturbance and which every 2 years produces recalcitrant seeds that lose viability a few months after dispersal, especially at open sites (Castro-Colina et al. 2011). Additionally, this species establishes mainly at shaded microsites with high soil accumulation (Bonfil and Soberón 1999). In fact, *Quercus rugosa* showed an important reduction in its dominance along the disturbance gradient, displaying the highest RIV at the low-disturbance sites, the third RIV at the medium-, and the twentieth RIV at the high-disturbance sites, suggesting a high sensitivity of this species to anthropogenic disturbance.

For each disturbance level, we identified a list of ten dominant species according to their RIVs (Fig. 3A–C). *Ageratina glabrata*, *Buddleja cordata*, *Sedum oxypetalum*, *Senecio praecox*, and *Verbesina virgata* were among them at all sites, indicating that these species play an important role in the structuring of this plant community across the vegetation mosaic present at the PECM. We propose that these widespread, stress-tolerant species show resilience to disturbance and hence could be useful for restoration activities. They could be used as a core plant group capable of triggering the natural regeneration of the vegetation and creating micro-environmental conditions (e.g., shadow and soil) favorable for species of later successional stages. Planting native species at micro-sites under the canopy of potential facilitator species emerges as a promising restoration strategy at highly disturbed sites, in particular for the eventual re-introduction of species that are sensitive to human disturbances such as *Quercus rugosa*. Such restoration programs may be planned following the planting scheme of synthetic communities, which is an active restoration tool for native species re-introduction (Díaz et al. 2003). In selecting the native species to be reintroduced, naturally scarce species should also be considered (for example, those that were recorded as singletons in this study), which in the PECM accounted for over 50 % of total species richness (Table 2 in Appendix).

Our NMDS ordination results (Fig. 4) confirmed the effects of the anthropic disturbance and were related to the successional gradient in our study system, along which species were grouped or segregated. Such a gradient has been reported in ecosystems experiencing severe human disturbances in deserts (Rao et al. 2011), tropical deciduous forests (Lebrija-Trejos et al. 2008), and oak forests (Olvera-Vargas et al. 2010). Taking into consideration the observed changes in floristic composition over the disturbance gradient, and designing experimental plantings as outlined above seem appropriate as potential empirical scenarios to explore the

Table 1 Mean structural trait values (±SE) of the four studied potential facilitator species (PFS), based on 50 plants measured per PFS, at the Parque Ecológico de la Ciudad de México

Potential facilitator species	Mean crown cover (m^2)	Crown cover upper limit (m^2)	Mean height (m)	Height upper limit (m)
Buddleja cordata	4.43^b (0.41)	12.0	2.66^b (0.12)	4.4
Dodonaea viscosa	6.61^a (0.56)	18.1	3.68^a (0.13)	6.0
Ageratina glabrata	1.56^c (0.19)	7.6	1.74^c (0.05)	2.7
Sedum oxypetalum	1.33^d (0.09)	2.9	1.51^d (0.03)	2.0

Different superscript letters indicate statistical differences ($P < 0.05$)

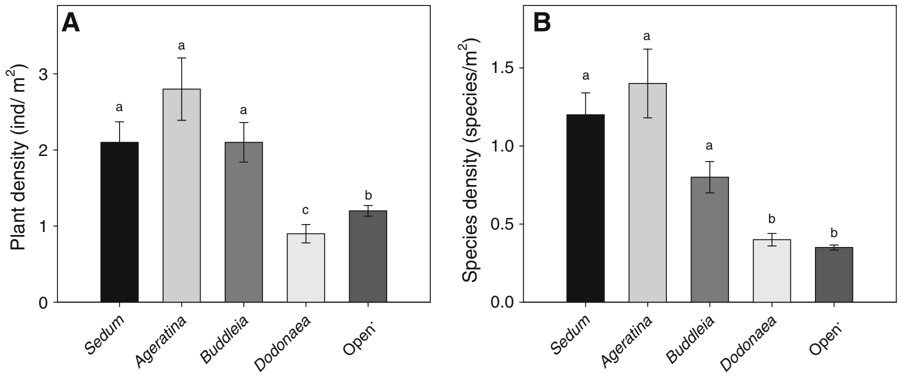


Fig. 5 Plant density (**A**) and species density (**B**) of regenerating vegetation under the canopies of four potential facilitator species and in open sites deprived of shrubs and trees, in highly human disturbed sites of the Parque Ecológico de la Ciudad de México. *Columns* not sharing *same letter* are significantly different ($P < 0.05$)

order of arrival of key species to the recovering system, and to assess ecological factors and mechanisms driving the assembly of successional communities. Similarly, to plan restoration actions in the PECM at the landscape level, the use of the hemeroby index should be considered in the future, which includes such an approach (Kim et al. 2002; Ziarnek 2007).

Potential effects of facilitator species (PFS)

The four tested PFS had differential effects on plant density of purportedly protégé species. Three of these PFS, *Ageratina glabrata*, *Buddleja cordata*, and *Sedum oxypetalum*, belong to the above-mentioned resilient core plant group: under their canopies, plant assemblages were denser and species-richer than at open sites. It is worth mentioning that among the 11 species recorded as protégé plants (Fig. 6), four were seedlings of the species considered PFS. *Ageratina glabrata* was the species with the highest potential to play a facilitation role, as 64 % (7 out of 11) of the analyzed protégé species exhibited higher plant densities under its canopy. In contrast, the potential facilitative role of *Sedum oxypetalum* and *Buddleja cordata* were restricted to two species (*S. oxypetalum* and *Agave salmiana*), while some species displayed negative associations with these PFS, and most species (64 %) were neutral to their presence. The fourth PFS studied (*D. viscosa*) mainly had a neutral effect on seven (64 %), and a negative one on the remaining species (Fig. 5); interestingly, under its own canopy were established mostly seedlings or small plants of this species. This result is suggestive of both an allelopathic effect of this species, and an important resprouting capacity in it, which seems to be responsible for the existence of communities strongly dominated by this species in other regions (Maraschin-Silva and Aqüila 2005; Barkatullah and Ibrar 2010). Thus, this species does not seem to be carrying out a facilitator role in this community; in fact, it may even arrest succession in the lava field by creating a barrier that may effectively prevent the establishment of other species (Hobbs et al. 2007).

In the case of the PFS *Ageratina glabrata* and *Sedum oxypetalum*, their positive effects were conspecific to a large extent. However, their seedlings shared more uniformly with other species the available space under their respective canopies. The relatively favorable micro-environmental conditions under the canopy of these two PFSs, and their relatively limited seed dispersal ability may explain such high conspecific protégé plant density. In turn, their positive heterospecific effects were mainly on *Agave salmiana* (Agavaceae), *Opuntia* sp. (Cactaceae), and *Echeveria gibbiflora* (Crassulaceae), all of which are succulent species. These plants possess adaptive traits that allow them to inhabit arid environments, such as CAM metabolism and water-storing parenchymatic tissues (Solbrig 1994). However, during the early establishment phases even succulent plants require some shelter from solar radiation (Olvera-Carrillo et al. 2009) and may benefit by the improved soil conditions that prevail under the canopies of PFS. Also, PFS are likely to provide perches for animals that disperse

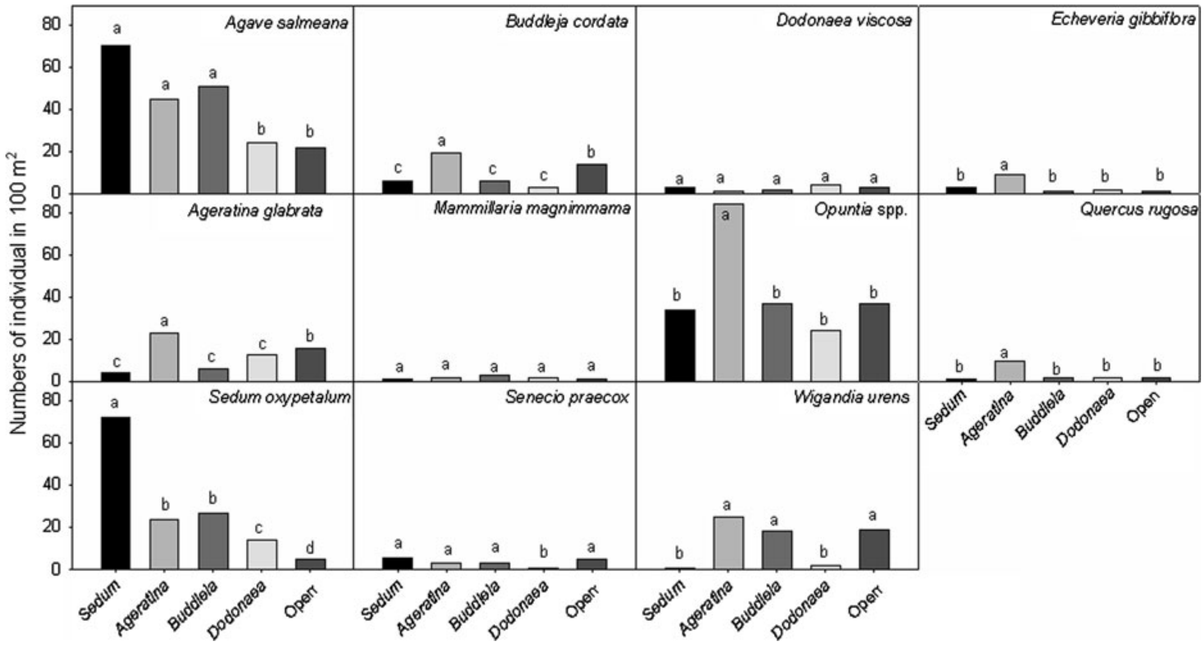


Fig. 6 Change in plant density of species regenerating under the canopies of four potential facilitator species and open sites, in highly human disturbed sites of the Parque Ecológico de la Ciudad de México. *Columns* not sharing *same letter* are significantly different ($P < 0.05$)

seeds of these succulent species (e.g., *Opuntia rzedowskii*). A denser seed rain under PFS enhances plant density of protégé plants, as has been reported in cacti forests (Godínez-Alvarez et al. 2002).

Overall, PFS may promote positive changes in soil retention, litter accumulation, microclimatic amelioration, and seed deposition, as has been reported for facilitating species in various harsh habitats (Brooker et al. 2008). The observed significant effects of PFS on densities of purportedly protégé plants suggest that they may act as nucleation spots (sensu Yarranton and Morrison 1974), from which the natural regeneration may spread out. In particular, the positive effect of *Ageratina glabrata* on the density of the late-successional *Quercus rugosa* is promising.

The positive effects of PFS on the plant density of other species documented in our study may support the design of experimental manipulations of the vegetation recovery process. Several studies have proposed that the reintroduction of species assemblages beneath PFS may be an intervention practice with a large restoration potential (Castro et al. 2002; Rey Benayas et al. 2008). However, gaining a deeper understanding of the effects of both biotic (plant–plant) and abiotic interactions on introduced plants and on PFS remains a central task in restoration ecology, given the magnitude of the challenge of recovering the natural complexity of ecosystems affected by human disturbance (Crosti et al. 2007; Kikvidze and Armas 2010). In this context, our findings provide strong evidence that the shrubs *Ageratina glabrata* and *Sedum oxypetalum*, and the tree *Buddleja cordata*, play a facilitating role in the natural regeneration of several native species in this highly disturbed ecosystem. Ultimately, these species could be useful to create nucleation spots that may be crucial for restoration actions of disturbed lava-field ecosystems.

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Appendix

See Table 2.

Table 2 List of species registered at sites with high-, medium-, and low-disturbance level in the Parque Ecológico de la Ciudad de México

Family	Species	Growth form	Habitat	Disturbance level, RIV values (%)		
				High	Medium	Low
Agavaceae	*Agave salmiana* Otto ex Salm-Dyck	RLB	XS, OF	10.73	7.39	4.05
Asteraceae	*Ageratina glabrata* (Kunth) R.M. King & H. Rob.	S	XS, OF	42.14	13.36	22.70
Asteraceae	*Ageratina* sp.	S	XS		0.98	
Asteraceae	*Ageratina* sp.	S	XS	3.04	1.20	4.78
Ericaceae	*Arbutus xalapensis* Kunth	T	OF			3.48
Asteraceae	*Archibaccharis hirtella* (DC.) Heering	S	XS, OF		1.40	9.23
Umbelliferae	*Arracacia tolucensis* (Kunth) Hemsl.	EL	XS	7.75	10.04	0.71
Asteraceae	*Baccharis conferta* Kunth	S	XS, OF		0.97	2.19
Rubiaceae	*Bouvardia ternifolia* (Cav.) Schltdl.	S	XS	16.58	10.99	5.03
Asteraceae	*Brickellia pendula* (Schrad.) A. Gray	S	XS, OF			1.29
Loganiaceae	*Buddleja cordata* Kunth	T	XS, OF	54.35	58.16	24.49
Loganiaceae	*Buddleja parviflora* Kunth	T	XS, OF			3.14
Asteraceae	*Castilleja* sp.	DS	XS			0.69
Solanaceae	*Cestrum oblongifolium* Schltdl.	S	OF			6.62
Cupressaceae	*Cupressus lusitanica* var. lindleyi Klotzsch enx Endl. Carrière	T	XS, OF			1.04
Asteraceae	*Dahlia* sp.	EL	XS	18.15	14.49	2.02
Sapindaceae	*Dodonaea viscosa* Jacq.	T	XS, OF	8.13	31.96	
Asteraceae	*Eupatorium* sp.	S	XS			2.30
Onagraceae	*Fuchsia microphylla* Kunth	S	OF		5.90	14.75
Onagraceae	*Fuchsia* sp.	S	OF			0.71
Garryaceae	*Garrya laurifolia* Hartw. ex Benth.	T	OF			3.00
Asteraceae	*Gnaphalium* sp.	DS	XS		1.40	
Polemoniaceae	*Loeselia mexicana* (Lam.) Brand	S	XS, OF	7.21	7.40	0.82
Polygalaceae	*Monnina schlechtendaliana* D. Dietr.	S	OF			0.84
Poaceae	*Muhlenbergia robusta* (E. Fourn.) Hitchc.	TU	XS, OF	6.86	9.97	0.70
Cactaceae	*Opuntia rzedowskii* Scheinvar	TS	XS	11.62	5.64	2.91
Cactaceae	*Opuntia* sp.	TS	XS	2.72	0.94	
Scrophulariaceae	*Penstemom roseus* (Cav. ex Sweet) G. Don	S	XS, OF			1.30
Scrophulariaceae	*Penstemom* sp.	S	XS	1.33	0.94	
Solanaceae	*Physalis* sp.	DS	XS			0.85
Rosaceae	*Prunus serotina* Ehrh.	T	XS, OF			7.43
Fagacea	*Quercus crassipes* Humb. & Bonpl.	T	OF			1.04
Fagacea	*Quercus rugosa* Neé	T	XS, OF	2.82	27.56	74.80
Fagaceae	*Quercus* sp.	T	OF			1.76
Fagaceae	*Quercus* sp.	T	OF			2.76

Table 2 continued

Family	Species	Growth form	Habitat	Disturbance level, RIV values (%)		
				High	Medium	Low
Fagaceae	*Quercus* sp.	T	OF			1.11
Fagaceae	*Quercus* sp.	T	OF			0.94
Asteraceae	*Roldana angulifolia* (DC.) H. Rob. & Brettell	S				4.21
Asteraceae	*Roldana barba-johannis* (DC.) H. Rob. & Brettell	S	XS, OF			0.94
Lamiaceae	*Salvia elegans* Vahl	S	XS, OF			0.71
Lamiaceae	*Salvia mexicana* L.	S	XS, OF			13.49
Lamiaceae	*Salvia* sect Polystachyae Epling	S	XS, OF			1.99
Lamiaceae	*Salvia* sp.	S	XS, OF		1.83	
Lamiaceae	*Salvia* sp.	S	XS, OF			1.38
Lamiaceae	*Satureja macrostema* (Moc. & Sessés ex Benth.) Briq.	S	OF	3.27	5.44	6.81
Anacardiaceae	*Schinus molle* L.	T	XS, OF	2.00		
Crassulaceae	*Sedum oxypetalum* Kunth	S	XS, OF	25.23	24.55	17.35
Asteraceae	*Senecio praecox* (Cav.) DC.	S	XS	28.38	25.56	7.50
Asteraceae	*Simsia amplexicaulis* (Cav.) Pers.	S	XS			1.89
Asteraceae	*Stevia micrantha* Lag.	S	XS	10.12	3.14	1.40
Asteraceae	*Stevia salicifolia* Cav.	S	OF		2.39	10.02
Asteraceae	*Stevia* sp.	S	XS	1.53	3.05	0.70
Asteraceae	*Stevia* sp.	S	XS		1.36	
Asteraceae	*Stevia* sp.	S	XS			3.63
Scrophulariaceae	*Verbascum virgatum* Stokes	RSB	XS, OF	2.90		
Asteraceae	*Verbesina virgata* Cav.	S	XS	11.38	15.08	8.12
Hydrophyllaceae	*Wigandia urens* (Ruiz & Pav.) Kunth	S	XS, OF	11.97	1.81	
MT1						0.94
MS1						0.70
MS2						1.75
MS3						1.55
MS4					1.24	
MS5				8.31	0.95	
MS6					0.97	
MS7						2.82
MS8				1.48		0.82
MS9					0.97	
MS10						1.09
MS11				1.41		
MS12					0.97	
MS13						0.72
Species number		Total = 71		26	34	55
Shared species in all the disturbance levels (%)		23.94				
Species present only in the high disturbance level (%)		4.22				

Table 2 continued

Family	Species	Growth form	Habitat	Disturbance level, RIV values (%)		
				High	Medium	Low
Species present only in the medium disturbance level (%)		9.85				
Species present only in the low disturbance level (%)		46.48				

For each species, their taxonomic family, growth form, their relative importance value, and the habitat(s) are indicated, where is more abundant; *XS* xerophytic scrub and *OF*, oak forest, according to Rzedowski (1954). Growth forms according to Cornelissen et al. (2003): rosette short basal (RSB, leaves shorter than 0.5 m, concentrated close to the soil surface); rosette long basal (RLB, leaves longer than 0.5 m rising from the soil surface); scrubs (S); dwarf scrubs (DS, shorter than 0.8 m); tree (T); erect leafy (EL, erect plants with the leaves concentrated in the middle and/or the top part); tussocks (TU, many leaves with basal meristem forming prominent tufts); tall succulents (TS, taller than 0.5 m with green stems)

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