Spatial patterns of distribution and abundance of *Harrisia portoricensis*, an endangered Caribbean cactus

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Abstract

Aims

The spatial distribution of biotic and abiotic factors may play a dominant role in determining the distribution and abundance of plants in arid and semiarid environments. In this study, we evaluated how spatial patterns of microhabitat variables and the degree of spatial dependence of these variables influence the distribution and abundance of the endangered cactus *Harrisia portoricensis*.

Methods

We used geostatistical analyses of five microhabitat variables (e.g. vegetation cover, soil cover and light incidence) and recorded the abundance of *H. portoricensis* in 50 permanent plots established across Mona Island, Puerto Rico, by the United States Department of Agriculture Forest Service as part of the Forest Inventory and Analysis (USDA–FIA). We also used partial Mantel tests to evaluate the relationships between microhabitat variables and abundance of *H. portoricensis,* controlling for spatial autocorrelation.

Important findings

Abundance of *H. portoricensis* showed strong affinities with microhabitat variables related to canopy structure, soil cover and light environment. The distribution of this cactus species throughout the island was consistent with the spatial variation patterns of these variables. In general, landscape-level analyses suggested a predictive value of microhabitat traits for the distribution and abundance of this endangered species. For sensitive cacti species, wherein abundance may be influenced by similar variables, these types of analyses may be helpful in developing management plans and identifying critical habitats for conservation.

Keywords: abundance, Caribbean cactus, geostatistics, *Harrisia portoricensis*, Mona Island, spatial correlation, spatial distribution

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INTRODUCTION

One of the major goals of ecological research is to determine the factors that limit the distribution and abundance of species (Elith and Leathwick 2009; Krebs 2002; Zhang *et al.* 2012). For any species, factors limiting its distribution include a combination of biotic and abiotic factors that may operate at different spatial and temporal scales (Collin and Glenn 1991; Elith and Leathwick 2009; Fortin and Dale 2005; Zhang *et al.* 2012). However, in extreme environments, abiotic factors are thought to have a dominant role in species distributions and abundances (Holmgren *et al.* 2006; Reynolds *et al.* 2004). With ongoing regional and global changes in primary climatic variables (IPCC 2001), determining the link between biotic and abiotic factors with species abundance and distribution is a necessary step to understand how species will respond to these impending changes and their adaptive capacities. Spatial analyses combining plant distributions with variations in abiotic and biotic factors could be helpful tools for identifying these links and determining the habitats that may be most suitable for species of conservation concern (Babish 2006; Fortin and Dale 2005).

Cacti are often a dominant component of plant communities in arid and semiarid ecosystems. For species within this family, low temperatures are often the single most important element limiting their latitudinal distribution (Godínez-Alvarez *et al.* 2003; Medel-Narvaez *et al.* 2006). Nevertheless, it is the spatial variability in a combination of factors (i.e. temperature, topography, soil properties, rainfall and availability of nurse plants) that often determines their local patterns of distribution and abundance (Godínez-Alvarez *et al.* 2003; Parker 1988). At local scales, cacti abundance may be highly variable, ranging from a few individuals to thousands per hectare (de Viana *et al.* 1990; Esparza-Olguín *et al.* 2002; Medel-Narvaez *et al.* 2006; Valiente-Banuet and Ezcurra 1991), and to date, most species studied exhibit clumped distributions (Fleming and Valiente-Banuet 2002). Many authors suggest that local distribution and abundance patterns of cacti may be explained by patchy distributions of environmental conditions that enhance germination, seedling establishment and plant growth (Bowers 1997; Valverde *et al.* 2004). However, we still lack landscape-level information about how spatial patterns of environmental variables may affect the final distribution and abundance of cacti.

Harrisia portoricensis (hereafter, *Harrisia*) is a columnar cactus formerly endemic to the Puerto Rican Archipelago and currently restricted to the small islands of Mona, Monito and Desecheo (United States Fish and Wildlife Service 1990). The largest population of *Harrisia* occurs on Mona Island, where a previous study yielded a population size estimate of 59 857 (standard error, SE = 1058) plants (Rojas-Sandoval 2010; Rojas-Sandoval and Meléndez-Ackerman 2013). The demographic profile of this population included plants in all life-history stages (i.e. seedlings, juveniles and adults), indicating that at least some recruitment is occurring at this locality. Recent data on the establishment and growth of early life-history stages of this cactus species indicate that seedlings and juveniles are particularly susceptible to variations in local microclimatic conditions (Rojas-Sandoval and Meléndez-Ackerman 2012a; 2012b). For this species, authors have shown that perennial native shrubs, such as *Croton discolor* and *Reynosia uncinata,* act as nurse plants that provide suitable microclimatic conditions that significantly improve survival, establishment and growth of *Harrisia* seedlings (Rojas-Sandoval and Meléndez-Ackerman 2012a). While the combined results suggest that abiotic factors are indeed important to the successful establishment and growth of *Harrisia*, we currently lack information on how these factors vary in space and how this variation may ultimately influence plant abundance throughout the island.

In this work, we used information recorded from permanent plots established on Mona Island across the entire island and a geostatistical approach (see the following section) to study how the spatial variation in plant abundance and the demographic structure of *Harrisia* are associated with spatial variation in microhabitat variables. Specifically, the goals of this study were to: (i) reestimate plant density and population

size of *Harrisia* on Mona Island using an island-wide census and a geostatistical approach, (ii) explore the spatial patterns of particular microhabitat variables (i.e. canopy cover; proportions of rock, soil and litter; and light incidence) and evaluate how these might be associated with the abundance and distribution of *Harrisia* and (iii) determine habitat characteristics that would be most suitable for the establishment and growth of *Harrisia*. We hypothesized that the distribution and abundance of *Harrisia* on Mona Island would be closely associated with spatial patterns of microhabitat variables, principally canopy cover and light incidence. In this regard, we expected that areas with intermediate values of canopy cover and light incidence would be optimal for the presence and abundance of *Harrisia*. Given the protected status of *Harrisia,* this information will be valuable in identifying suitable habitats for the conservation and management of this species.

MATERIALS AND METHODS

Study site and study species

This study was conducted on Mona Island, a 5517-ha raised platform of limestone rock located in the Caribbean Sea between Puerto Rico and the Dominican Republic (18°05′N, 67°54′W; Fig. 1). The surface of Mona Island is characterized by exposed rocks, cracks and interspersed sinkholes with accumulated soil. Water on the island is limited to organisms because the limestone rock structure ensures the rapid percolation of water and the shallow soils have low water-holding capacities (Lugo *et al.* 2001). The island has an annual mean temperature of 26.8°C and an average annual rainfall of 895.79 mm. Its climate is considered semiarid because the rainfall received is significantly less than the potential evapotranspiration level throughout the year (Rojas-Sandoval 2010; Rojas-Sandoval and Meléndez-Ackerman 2012b). The vegetation is classified as a subtropical dry forest, with a large proportion of species showing xeromorphic adaptations (Cintrón and Rogers 1991). *Harrisia* is one of three columnar cacti reported on the island (Rojas-Sandoval and Meléndez-Ackerman 2011a). Juveniles of *Harrisia* are unbranched, whereas adults usually are extensively branched and may reach heights >2 m (Rojas-Sandoval and Meléndez-Ackerman 2011b). This species is an iteroparous night-flowering cactus that needs to set seed to propagate under natural conditions (Rojas-Sandoval and Meléndez-Ackerman 2009, 2011a).

Sampling design

In November 2008, we established 50 plots across Mona Island following the methodology described by the Forest Inventory and Analysis protocol (USDA-FS–FIA 2006; Fig. 1). Rojas-Sandoval and Meléndez-Ackerman (2013) provided specific descriptions of the application of this methodology on Mona Island. At each plot, we established two circular subplots (7.3 m radius) located at 36.5 m horizontal at azimuths of 360° and 240° from the center of the plot to generate a total of 100 subplots. Subplot pairs within a plot had a fixed distance
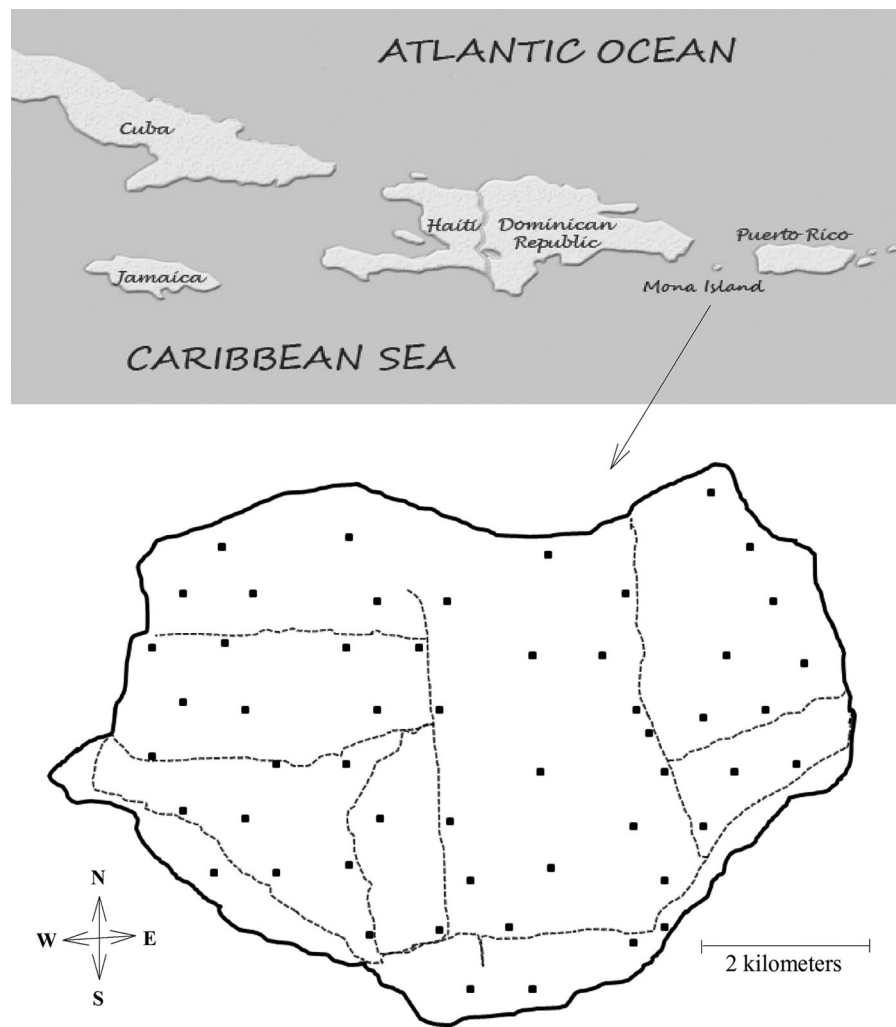
Figure 1: geographical location of Mona Island within the Caribbean and the setting of the 50 plots surveyed in November 2008 on Mona Island to gather information about microhabitat variables and *Harrisia portoricensis*.

of 63.2 m from the center of each other. These subplots were used to characterize the microhabitat and to explore the distribution patterns of *Harrisia* across the island (i.e. degree of aggregation) and how they were associated with the spatial variation of microhabitat variables on an island-wide scale. For the analyses, data from the 100 subplots were pooled to avoid problems of autocorrelation, generating an effective sample size of 50 plots (see the following section).

Data collection

At each subplot, we counted the number of *Harrisia* plants. To evaluate the influence of microhabitat on the spatial distribution of *Harrisia*, we measured a series of microhabitat variables that included vegetation cover at various heights; proportion of ground cover by rock, mineral soil and litter; and estimates of light incidence and canopy cover (estimated as leaf area index). The percentage of vegetation cover was recorded at four different layers above ground: 0–60, 60–180, 180–480 or >480 cm. Vegetation cover was estimated using

a semiquantitative scale ranging from 0 to 4 (0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%), considering the area of the circular subplot as the reference area and estimating the percentage of the area covered by the entire vegetation. We also estimated the percentage of ground area of each subplot covered by mineral soil, litter and rock. To evaluate the spatial variation in light incidence and vegetation structure, sets of three hemispherical photographs were taken within each subplot. Hemispherical photographs were obtained using a Nikon Coolpix 850 digital camera fitted with a fish-eye lens (Nikon FC-E8) mounted on a tripod at 1 m above the ground and photography was conducted in the center of a 1-m² quadrant located at 5 m from the center of the subplot at azimuths of 30°, 150° and 270°. From these digital photos, we extracted estimates for the global site factor (GSF: quantitative measure of light available at each subplot), the proportion of visible sky (the proportion of the canopy containing gaps) and the leaf area index (LAI: one side leaf area per unit of ground area) using the program HemiView

2.1 (Delta-T Devices, Burwell, Cambridge, UK). Given that sampling plots were visited only once and Mona Island is a completely flat platform of limestone (uniform in elevation), variables with high seasonal and daily variability such as soil moisture and soil pH, as well as elevation and slope traits, were not included in this study.

Data analysis

The information on the total number of *Harrisia* recorded within the 100 sampled subplots was used to analyze its distribution and abundance on Mona Island. We transferred the abundance data onto a map for visual examination of its distribution across the island by projecting the number of plants per plot using the pooled frequencies for the two subplots. We used the plant data collected within each subplot to estimate the mean density of *Harrisia* by dividing the total number of adult individuals recorded in all subplots by the total sampled area.

Spatial analysis

Analyses of spatial patterns for microhabitat variables and *Harrisia* abundance were performed using a geostatistical approach. We first carried out exploratory analyses by evaluating the shape of semivariograms to determine the degree of spatial dependence of their variances (Babish 2006; Isaaks and Srivastava 1989). All geostatistical analyses were performed using GS+ version 9 (Gamma Designs Software, Plainwell, MI, USA). To perform the analyses, the latitude/longitude coordinates for each sampling point were converted to Cartesian units (Universal Transverse Mercator, UTM). Semivariograms were built for each variable separately considering an active lag distance equal to 50% of the maximum distance between sampled subplots. The first lag intervals varied between 400 and 450 m and were gradually increased until a lag distance of 4.4 km was reached. Normality of residuals was checked, and the data were transformed when necessary using square-root transformations. For each variable, the resulting semivariogram was then fitted to a spherical, exponential or Gaussian model considering the best reduced sums-of-squares fit (Babish 2006; Isaaks and Srivastava 1989). Spatial dependence was analyzed as the proportion of sampled variance (sill: $C + C_0$) that was explained by the structure variability (C). Spatial dependence was high when the ratio $C/(C_0 + C)$ approached one and low when the ratio was near zero (Robertson *et al*. 1993).

Once we established that variability in *Harrisia* density and microhabitat variables had a significant spatial dependence, we then used the semivariogram results to interpolate variable values at unsampled areas and to create interpolation maps to examine the variables (biotic vs. abiotic) that exhibited similar spatial distribution patterns. To construct interpolation maps, we used ordinary block kriging (2×2) with a search neighborhood having a minimum of 1 and a maximum of 16 neighbors to be considered in the weighted moving spatial average and the generation of interpolation

plots. Cross-validation analysis was then used to check the effectiveness of kriging parameters (Babish 2006). Because most variables were spatially autocorrelated (see Results), we used partial Mantel tests to perform correlation analyses to explore the association between the five microhabitat variables (those with the highest values of variance explained by spatial structure and with the highest fit to the model) and abundance of *Harrisia* (Casgrain and Legendre 2000; Legendre and Fortin 1989). Partial Mantel tests examined the relationship between (i) GSF, vegetation cover in the 180- to 480-cm layer, percentage of soil cover by rock, soil and litter and (ii) the abundance of *Harrisia,* controlling for spatial autocorrelation among variables. For this analysis, distance matrices (dissimilarity) were constructed for all variables and the spatial matrix was calculated as the distance between all pairs of plots. The statistical significance was determined by comparison with 999 randomized permutations using the Bonferroni-corrected significance level ($\alpha = 0.05/7 = 0.007$). Calculations of partial Mantel tests were completed with the R software version 2.15 (R Development Core Team 2012). Finally, an interpolation map for *Harrisia* density generated by kriging was used to estimate the population size of this species on Mona Island considering the area of each interpolated value (Babish 2006).

RESULTS

There were a total of 112 individuals of *Harrisia* in 29 out of the 50 plots censused. The number of individuals of *Harrisia* detected within plots varied from 1 to 19 plants, with mean density values equal to 0.001 plants m^{-2} (Fig. 2).

Spatial variation in microhabitat variables

Most variables exhibited a strong spatial dependence and showed moderate to strong autocorrelations at distances ranging between 945 and 2085 m (Table 1). For microhabitat variables, LAI had the lowest values for the amount of variance explained by spatial structure (50%; Table 1) and was also the microhabitat variable with the lowest fit to the model (Table 2). Visual examination of interpolation maps showed that most of the microhabitat variables exhibited a gradient-like variation along the east–west axis of the island. We detected that the percentage of vegetation cover in the layer between 0 and 60 cm tended to be highest in the northeastern portion and lowest in the southwestern and central portions of the island (Fig. 3a). The percentage of vegetation cover in the layer between 60 and 80 cm also varied along the east–west axis, with highest values recorded in the western and lowest values in the northeastern portion of Mona (Fig. 3b). The percentage of vegetation cover in the 180- to 480-cm layer exhibited a degree of clustering in the central part of the island and a general trend to form a gradient of vegetation cover along the east–west axis (lowest cover in the east; Fig. 3c). The highest percentages of ground cover by rock were detected in the eastern portion of the island and the lowest ones in the
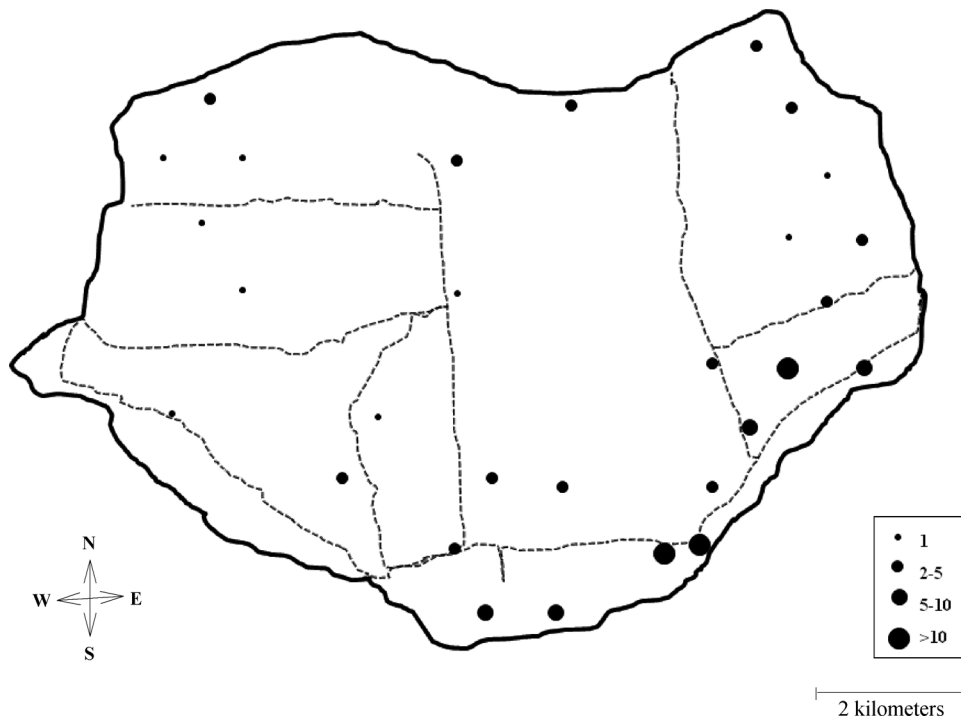
Figure 2: abundance of *Harrisia portoricensis* within each plot surveyed on Mona Island.

Table 1: semivariogram parameters estimated for kriging interpolation of *Harrisia portoricensis* and for microhabitat variables

Variable	n	Model	Nugget	Sill	$C/(C_0 + C)$	Range (m)	r^2
% Vegetation cover							
0–60 cm	50	Exponential	41.0	619.7	0.93	2040	0.85
60–180 cm	50	Exponential	10.3	231.6	0.96	945	0.70
180–480 cm	50	Exponential	11.6	183.7	0.94	1737	0.74
Percentages of							
Rock	50	Gaussian	1.0	488.7	0.99	1785	0.73
Soil	50	Gaussian	0.1	114.8	0.99	1500	0.71
Litter	50	Gaussian	1.0	602.5	0.99	1635	0.63
Proportions of							
Visible sky	50	Gaussian	0.00001	0.025	1	1227	0.83
GSF	50	Exponential	0.001	0.032	1	2085	0.85
LAI (m²·m⁻²)	50	Exponential	0.1	0.18	0.50	1855	0.51
Harrisia (plants m⁻²)	50	Exponential	0.5	7.5	0.93	8571	0.74

n = number of plots; GSF = global site factor; LAI = leaf area index; $C/(C_0 + C)$ = spatial dependence; r^2 = proportion of variation explained by the semivariogram.

western portion (Fig. 3d). For the percentage of ground cover by soil, spatial patterns were more complex across the island, but in general, major accumulations of soils occurred in the southwestern part of the island and minor accumulations of soils were observed in the northern and eastern portions of Mona (Fig. 3e). The percentage of ground cover by litter also exhibited a gradient-like variation along the east–west axis of the island, with the highest percentages of litter observed in the west and the lowest percentages observed in the east, coinciding with areas in which ground cover was dominated

by rock (Fig. 4f). Visible sky and GSF had maximum values in the northeastern portion of the island and minimum values in the southwest (Fig. 4a and b). In contrast, LAI had maximum values in the southwestern portion of the island and lowest values in the northeastern portion (Fig. 4c).

Spatial variation in the distribution and abundance of *Harrisia*

Semivariogram analyses for *Harrisia* revealed a strong spatial dependence for this species, with 93% of the total variance

Table 2: results of cross-validation analysis to evaluate the effectiveness of kriging for *Harrisia portoricensis* and for microhabitat variables

Variable	RC	r^2
% Vegetation cover		
0–60 cm	0.80	0.68
60–180 cm	0.84	0.66
180–480 cm	1.05	0.75
Percentages of		
Rock	1.15	0.94
Soil	−1.19	0.88
Litter	−1.14	0.87
Proportions of		
Visible sky	0.75	0.69
GSF	1.15	0.83
LAI ($m^2 \cdot m^{-2}$)	1.01	0.48
Harrisia (plants m^{-2})	1.26	0.88

RC = regression coefficient; GSF = global site factor; LAI = leaf area index; r^2 = proportion of variation explained by the best-fit line while kriging.

in plant abundance explained by spatial structure (Table 1). Similarly, the interpolation map produced for this species indicated that 88% of the variation was explained by the best-fit line achieved by kriging (Table 2). *Harrisia portoricensis* was widely distributed throughout the island, but plants had higher densities in the southeastern and northeastern portions of the island, where abundance ranged from 0.008 to 0.013 plants m^{-2}, and were less frequent in the western side, where the estimated density value was 0.0001 plants m^{-2} (Fig. 4d). Based on these interpolated density values, we estimated a population size of 63 708 (SE = 986) plants on Mona Island. The partial Mantel results for the relationship between microhabitat variables and abundance of *Harrisia*, controlling for spatial autocorrelation, show that the percentages of ground cover by rock (partial Mantel $r = 0.52$, $P = 0.008$), ground cover by litter (partial Mantel $r = 0.44$, $P = 0.005$) and vegetation cover in the 180- to 480-cm layer (partial Mantel $r = 0.48$, $P = 0.006$) influence the spatial pattern of abundance of this cactus species. In general, *Harrisia* were more abundant in areas with the highest percentage of ground cover by rock (cover class range 40–60%), lowest percentage of ground cover by litter (<22%) and lowest canopy cover in the vegetation layer between 180 and 480 cm (<15% cover). We did not detect a significant relationship with the abundance of *Harrisia* for the other two microhabitat variables analyzed (percentage of the ground cover by soil: partial Mantel $r = 0.24$, $P = 0.34$; and GSF: partial Mantel $r = 0.19$, $P = 0.16$).

DISCUSSION

Our sampling methods and combined results provide a better understanding of the abundance and spatial distribution

of *Harrisia* and the factors that may underlie its distribution on Mona Island. The estimated density values (which varied from 1 to 137 plants ha^{-1}) were comparable with values estimated for other columnar cacti in arid and semiarid environments that have low to moderate densities (Esparza-Olguín *et al.* 2002; Medel-Narvaez *et al.* 2006; Zou *et al.* 2010). The estimated population size of *Harrisia* on Mona Island presented in this study is slightly higher than that previously reported (Rojas-Sandoval 2010). This discrepancy is probably the result of the different approaches used to estimate the population size (Rojas-Sandoval and Meléndez-Ackerman 2013; Wu *et al.* 2005).

The spatial analyses suggest the existence of a transitional gradient of microhabitat conditions associated with *Harrisia* density distribution along the east–west axis of Mona Island. This gradient is characterized by a transition from dense vegetation, with high percentage of canopy cover in the layers between 60 and 180 cm (shrubs and trees) and between 180 and 480 cm (trees) and ground with more accumulation of mineral soil and litter in the western portion of the island, to less dense vegetation in the eastern portion of Mona, characterized by high percentage of vegetation cover in the layer between 0 and 60 cm (herbs and shrubs) and high percentage of ground cover by rock. These results are consistent with those of Martinuzzi *et al.* (2008), who also reported an east–west direction gradient for the vegetation on Mona Island using remotely sensed data. In their study, it was suggested that prevailing trade winds (which on Mona Island blow from a northeastern direction) and the associated action of salt spray falling upon the vegetation were the driving factors behind this gradient (Martinuzzi *et al.* 2008).

Along this gradient of environmental conditions, our data suggest that areas located in the southeastern and northeastern portions of the island are the most favorable for the establishment and growth of *Harrisia*. In this regard, the observed spatial distribution of *Harrisia* on Mona Island could be a response to microclimatic conditions that may affect the various life stages (i.e. seedlings, juveniles and adults) differently. One possibility is that the observed spatial distribution of *Harrisia* on Mona Island is a response to the influence of microhabitat variables that favor seed germination and the survival and establishment of seedlings. In this study, we detected that *Harrisia* plants were most common in areas where the percentage of ground cover by rock was highest and the percentage cover by litter was lowest. To the extent that rock cover is a limiting factor for the establishment of large competitors (i.e. trees), one possibility is that rocky areas may provide more opportunities for cacti establishment than areas with considerable soil cover. For many cacti species, the availability of rocks and other surface irregularities, such as cavities, holes and cracks, between rocks appear to be very important for seed germination and seedling survival, in addition to the presence of nurse plants. These surface irregularities and rocks may act as potential facilitators of germination and seedling survival because they reduce solar
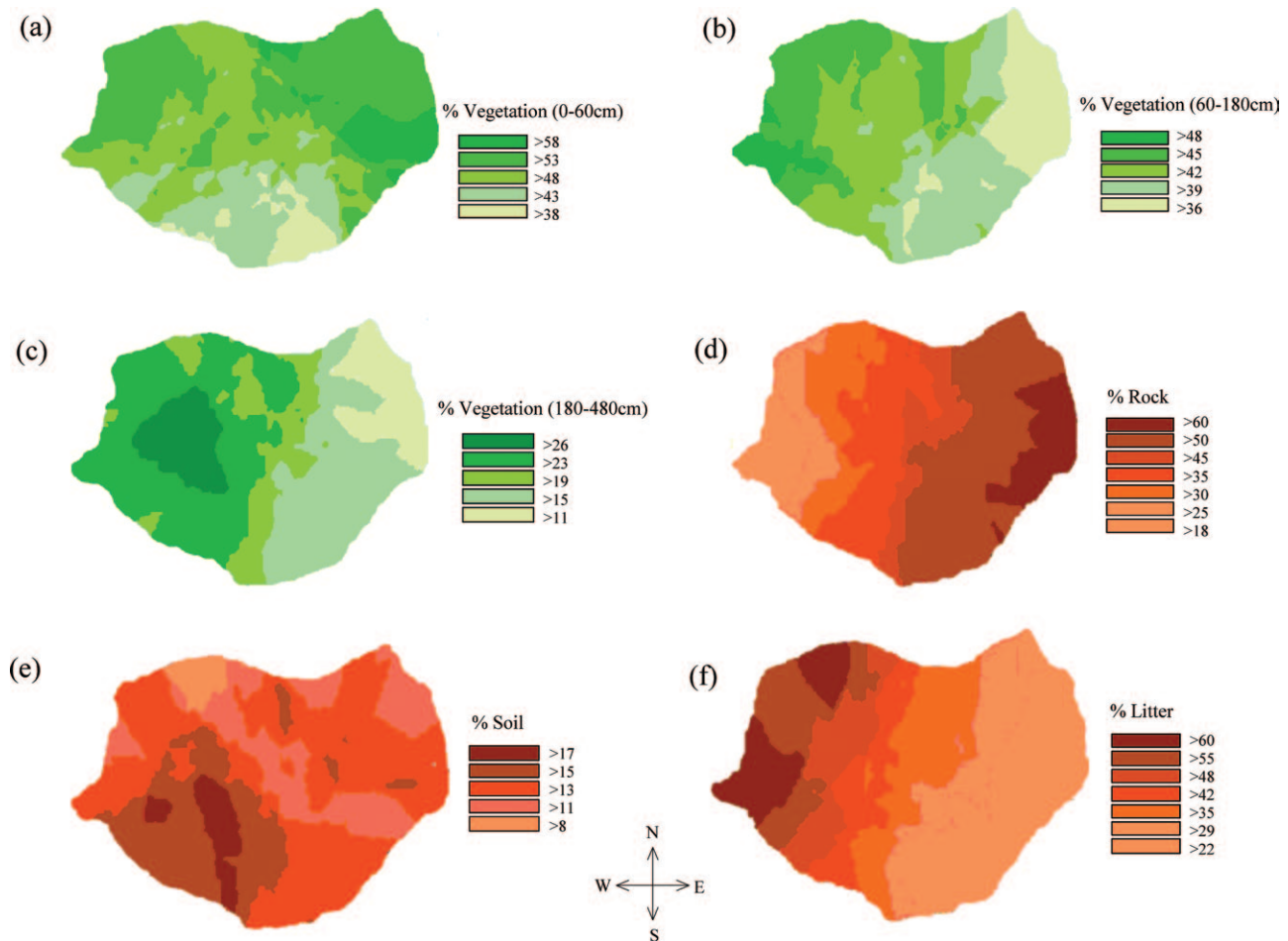
Figure 3: interpolation maps generated by kriging for microhabitat variables. Percentages of vegetation cover in the layers of (**a**) 0–60 cm (**b**) 60–180 cm and (**c**) 180–480 cm. Percentages of ground cover by (**d**) rock, (**e**) soil and (**f**) litter.

radiation, prolong the presence of moisture, facilitate the deposition of humidity from the ocean and protect seeds and seedlings from predation (Munguía-Rosas and Sosa 2008; Peters *et al*. 2008; Ramírez 2011). The germination process of many plant species may also be affected by direct interference from litter accumulation. Large amounts of litter produced by dominant perennial species may reduce and even eliminate the occurrence of suitable sites for seed germination and seedling establishment for a variety of plant species in natural communities (Coleman and Levine 2007; Gioria and Osborne 2009; Myers *et al*. 2004; Reynolds *et al*. 2001). In our study, litter cover was positively associated with vegetation cover and thus experimental manipulations of leaf litter may help determine whether indeed the negative association between leaf litter and *Harrisia* abundance is the result of negative effects of litter accumulation on seed germination. Overall, the effect of litter accumulation on the germination of cacti seeds is an area that is largely understudied (Munguía-Rosas and Sosa 2008).

Another possible explanation for the spatial distribution patterns of *Harrisia* on Mona Island may relate to the distribution of environmental conditions that enhance growth and reproductive success of adults. Plants in this survey were more abundant when canopy cover in the tallest layer (180–480 cm) was the lowest. Previous studies on Mona Island with *H. portoricensis* and in Florida with *H. fragrans* have demonstrated that individuals growing in areas with high canopy cover were less abundant, less branched, rarely produced flowers and fruits and were more susceptible to die young by loss of vigor than plants growing between vegetation and open areas (Breckon and Kolterman 1994; Rae and Ebert 2002). Studies evaluating nurse-plant interactions in long-lived plants (including cacti species) have shown that facilitation turns gradually into competition as plants become adults (Callaway and Walker 1997; Holmgren *et al*. 1997; Valiente-Banuet and Verdú 2008; Wang *et al*. 2012). In the case of cacti species, after seed germination and seedling establishment, the environmental requirements of established plants change as they mature and competition for light and water with nurse plants may occur (McAuliffe 1984; Yeaton 1978; Yeaton and Romero-Manzanares 1986). For example, mature *Carnegia gigantea* cacti in the Sonoran Desert were
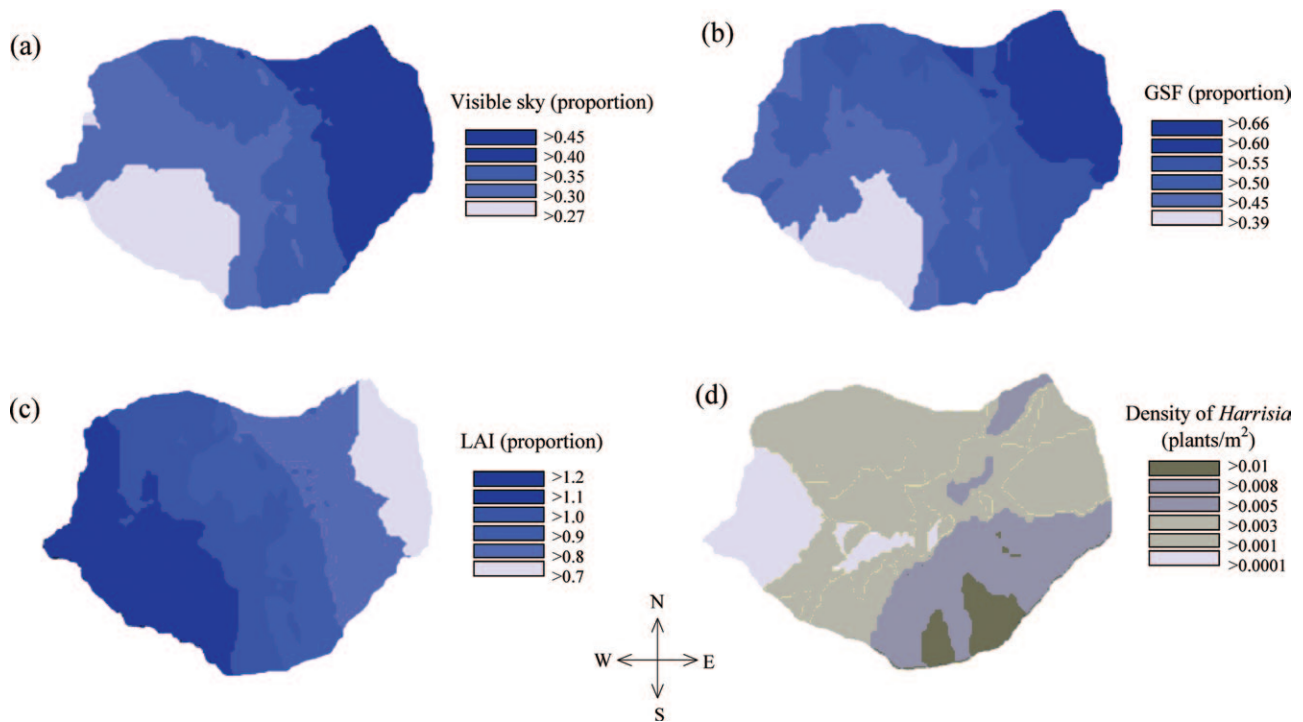
Figure 4: interpolation maps generated by kriging for light incidence variables (**a**) Proportion of visible sky, (**b**) Global site factor (GSF), (**c**) Leaf area index (LAI) and for (**d**) Density of *Harrisia* (plants m^{-2}).

found to be associated with the presence of dead palo verde trees (*Cercidium microphyllum*), which commonly function as nurse plants to seedlings (McAuliffe 1984). Similarly, in the Tehuacan Valley of Mexico, *Neobuxbaumia tetetzo* is nursed by *Mimosa luisana* (Valiente-Banuet *et al*. 1991), but it eventually suppresses the growth and reproduction of its benefactor (Flores-Martínez *et al*. 1994). In the case of *Harrisia*, available data suggest that the positive effects of shade provided by shrubs (mainly cooler temperature and higher moisture) are strong for seedlings and juvenile stages (Rojas-Sandoval and Meléndez-Ackerman 2012a).

The combined results of this study suggest that *Harrisia* has strong environmental affinities, which are likely to influence plant distribution in space. Mona Island's vegetation is deemed vulnerable due to the presence of invasive grasses (Rojas-Sandoval and Meléndez-Ackerman 2012b) and feral goats (Cintrón and Rogers 1991; Meléndez-Ackerman 2011). These mammals are considered some of the most destructive fauna worldwide and have been known to cause severe structural changes in the native vegetation of many insular systems (Coblentz 1978; Rainbolt and Coblentz 1999). These changes may, in turn, also threaten *Harrisia*, considering the affinities for certain vegetation structure and soil characteristics shown by adult plants. Our results are consistent with findings elsewhere, which emphasize the significant role of habitat characteristics, in particular those related to habitat structure, in the final distribution and abundance of cacti species. They also emphasize the potential use of long-term

monitoring programs such as the Forest Inventory Analysis, which provide indicators of habitat quality or habitat health that may be relevant to sensitive species. Landscape-level analyses that are based on such programs, similar to those presented here, suggest a predictive value of habitat characteristics for an endangered cactus species and may be a helpful tool for the development of management plans. The information derived from these analyses can be used to identify critical areas for species conservation, develop vulnerability analyses based on different habitat quality scenarios, predict plant abundance under different scenarios of habitat change and monitor potential habitat changes for critical species. Finally, results presented here also show the potential value of incorporating available data from inventories such as the Forest Inventory Analysis to develop hypotheses about the potential drivers of plant distributions.

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