LOCAL DISTRIBUTION PATTERNS OF *OPUNTIA ECHIOS ECHIOS*, *BURSERA GRAVEOLENS* AND *SCALESIA CROCKERI* ON SANTA CRUZ ISLAND, GALAPAGOS

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SUMMARY

We mapped stems of three plant species in a 2.36 ha plot in the arid zone near the coast of eastern Santa Cruz Island, Galapagos, Ecuador, to determine factors influencing their local distribution. The three species were *Opuntia echios* var. *echios* (Cactaceae), a large cactus, *Bursera graveolens* (Burseraceae), a small tree that dominates dry woodland near the coast, and the shrub *Scalesia crockeri* (Asteraceae). In our plot, *Opuntia* was most abundant near the coast, while *Bursera* and *Scalesia* increased in density inland and with increased relief. *Scalesia* also increased in density with increases in *Bursera* and decreases in other woody plants and was most abundant 200–250 m from the coast. Both *Opuntia* and *Bursera* were clumped in the plot as a whole but selected stem size classes were randomly dispersed within homogeneous portions of the sample area.

RESUMEN

Patrones de distribución local de *Opuntia echios echios*, *Bursera graveolens* y *Scalesia crockeri* en la Isla Santa Cruz, Galápagos. Registramos la localización de tallos de tres especies de plantas debtro de un cuadrante de 2.36 ha en la zona arida cerca de la costa este de la isla Santa Cruz, Galápagos, Ecuador, para determinar los factores que influencian su distribución local. Las tres especies son: *Opuntia echios* var. *echios* (Cactaceae) una especie de cactus grande, *Bursera graveolens* (Burseraceae) un árbol pequeño que domina el bosque seco cerca de la costa, y el arbusto *Scalesia crockeri* (Asteraceae). En nuestro cuadrante, *Opuntia* resultó más abundante cerca de la costa, mientras la densidad de *Bursera* y *Scalesia* incrementaban tierra adentro y a medida que aumentaba el relieve. La densidad de *Scalesia* también incrementaba al igual que la de *Bursera* y en tanto que decrecía la densidad de otras plantas leñosas, y llegaba a su máxima a 200–250 m desde la costa. Tanto *Opuntia* como *Bursera* se encontraban agrupadas dentro del cuadrante como conjunto, pero las clases de tamaño de tallo especificas estaban dispersas aleatoriamente dentro de porciones homogéneas del área de muestreo.

INTRODUCTION

Factors determining spatial variation in vegetation vary in importance with the scale of the study. Over a range of centimeters, vegetation is influenced by differences in moisture, light availability, soil type, surface features, and other micro-scale factors. At the landscape scale, vegetation varies with elevation and aspect, which determine more widespread temperature and precipitation regimes. Patchiness within a community is intermediate, over distances of meters to tens of meters. Historic events can operate at any of these spatial scales.

Much of the spatial investigation of vegetation in the Galapagos has emphasized the landscape scale. Broad vegetation zones have been used as a basis for describing species distributions (Wiggins & Porter 1971, Jackson 1993, Itow 1995, McMullen 1999). Other studies have compared plots from different locations (Reeder & Riechert 1975, Van der Werff 1978, Hamann 1981) to define naturally occurring plant communities.

Relatively little attention has been paid to patterns of spatial variation within communities or over short distances. Reeder & Riechert (1975) and Van der Werff (1978) found the Arid and Humid Zones respectively to be characterized by much local patchiness in vegetation. They suggested that substrate conditions may cause much of that patchiness. Reeder & Reichert (1975) also noted that the cactus *Opuntia* often forms a low, open forest on the coastal plain in a relatively narrow zone just landward of the Littoral Zone. We wished to study intra-community patchiness of the Arid Zone and determine factors underlying the transition between this *Opuntia* zone and the rest of the Arid Zone. We examined the distribution of three species (*Opuntia echios* var. *echios*, *Bursera graveolens*, and *Scalesia crockeri*) in two coastal plots differing in substrate.

STUDY AREAS AND SPECIES

We studied the three species on the NE coast of Santa Cruz Island near the hill Cerro Colorado (0°34´S, 90°10´W). The location, across a narrow strait from the Plazas islets, a popular tour destination, allowed convenient access. Previous studies of feral cats (Konecny 1987a, b, Stone *et al*. 1994) showed that the site contained relatively natural vegetation with some substrate heterogeneity and little direct human impact, although feral donkeys and goats have been recorded there (Snell, unpublished field trip reports 1988, 1993, 1994 on file at Charles Darwin Research Station, Santa Cruz, Galapagos; personal observation) and may impact the vegetation. Precipitation in the Arid Zone is highly variable year to year (Snell & Rea 1999). The present study was conducted during one of the wettest episodes in the last 35 years.

The tree-like cactus *Opuntia echios* var. *echios* was most apparent near the coast. The small tree *Bursera graveolens* dominated (in both size and cover) areas further inland. The site also included many species of thorny shrubs (e.g. *Acacia insulae-iacobi*, *Castela galapageia*, *Lycium minimum*, *Parkinsonia aculeata*, and *Scutia pauciflora*) and the shrub *Scalesia crockeri*. Another large cactus, *Jasminocereus thouarsii*, was present in very low numbers. Structurally the site fit the dry-season deciduous forest type of Van der Werff (1978), which he described as leafless most of the year, located from sea level to 150 m altitude on the east coast of Santa Cruz, and dominated by trees 5–10 m tall. Van der Werff (1978) also said of this structural type that *Bursera* is the most common tree species; shrub cover is 70% at 2–4 m height; herbaceous cover occurs between shrub clumps; *Opuntia* is common; and lava boulders cover over 30% of the surface. Floristically, our site best matched the Alliance Burserion graveolentis, Association Abutiletum depauperati, Subassociation abutiletum depauperati typicum, Vicariant Opuntia echios var gigantea (Van der Werff 1978).

The Galapagos endemic *Scalesia crockeri* is a low, rounded shrub found on bluffs and lava crevices, mostly near the shore (Wiggins & Porter 1971, Eliasson 1974), but up to 1 km inland at Cerro Colorado. It grows singly or in small, often widely separated groups (Eliasson 1974). Its seeds have no obvious adaptations for long-distance dispersal. It is one of several *Scalesia* with very restricted distributions. It is found only on the north and northeast slopes of Santa Cruz, and the nearby islands Baltra and North Seymour (Adsersen 1990, Snell *et al*. 1995). It is currently classified as Vulnerable, owing to its small range (Tye 2000, 2002). Its life history has not been studied but may resemble that of *S. helleri* on Santa Fe or *S. baurii* on Pinta (Hamann 1993, 2001).

METHODS

We established a 2.36 ha plot that ran a maximum of 100 m N–S (parallel to the coast) and 300 m E–W (Fig. 1). It reached the ocean approximately 100 m north of Cerro Colorado and formed a transect from the coast inland with relatively little change in elevation from its S edge to its N edge. Although it reached the coast, mangroves and other species characteristic of the Littoral Zone (Wiggins & Porter 1971) were not present. The plot was located on volcanic rock containing cracks, mounding and other lava features. The first 100 m westward marked the rise from sea level to a relatively flat plain. We established a 10-m grid in the plot and mapped all stems of *Opuntia echios*, *Bursera graveolens*, and *Scalesia crockeri* to the nearest 0.1 m. Where several stems of *S. crockeri* were too close together to separate we recorded one central location and the number of stems in the cluster. For each 10 x 10 m section of the plot we estimated by eye the % of bare ground and shrub cover (excluding the three species above) and the local relief (vertical distance from lowest to highest point). These three factors partly indicate the light and moisture regimes available to the target species. They also influence the likely impact of grazing, especially on small plants, because bare rock is easier to traverse than dense, often thorny shrubs and so should be more heavily grazed. High relief is often associated with cracks and crevices that may provide refuges from grazing and relatively moist micro-sites for seedling establishment. We estimated height and measured dbh (diameter at breast height, *i.e.* at 137 cm above ground) for each stem of *Opuntia* and *Bursera,* and counted the number of stems in two height classes (>1 m and ≤1 m) for *S. crockeri*.

We also sampled a 20 x 500 m transect on a sandy plain dominated by burr-bearing grasses and scattered *Cordia lutea* trees, located *c.* 100 m north and upslope from the other plot. The transect lay between GPS-read coordinates 0°34.558´S, 90°10.198´W and 0°34.521´S, 90°10.449´W, starting about 5 m from the bluff overlooking the ocean at this point and running due west. This bluff did not extend into the 2.36 ha plot. Exposed rocks were not present

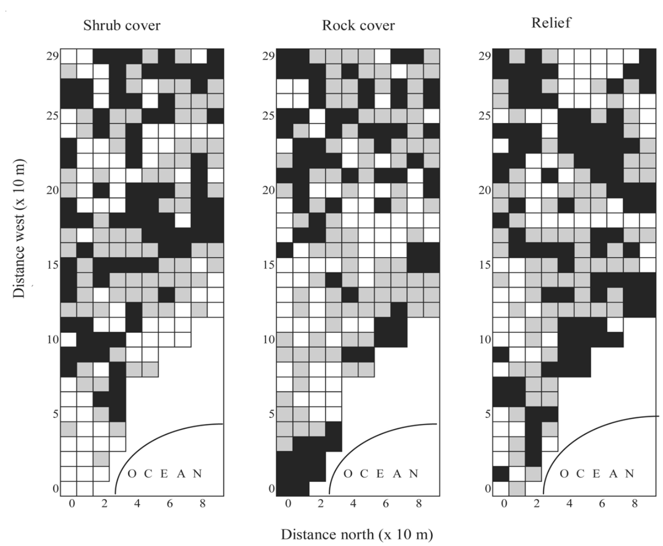

Figure 1. Study plot grid showing variation in shrub cover, rock cover, and relief. For shrubs, white indicates cover ≤20%, shaded 25–45%, and black ≥50%. For rock, white indicates cover ≤10%, shaded 15–40%, and black ≥45%. For relief, white indicates a maximum vertical difference ≤1.5 m, shaded 2 m and black ≥2.5 m.

and local relief was minimal. We recorded the height, dbh, and location of all stems of *Bursera* and *Opuntia*; *Scalesia* was not present.

Field sampling was conducted 18–26 January 1998. We related species densities in each plot to location (west and north of the SE corner of the plot, where west and north refer to the number of 10-m sub-plots in the given direction), shrub cover, bare ground and relief, using stepwise regression (SAS 1985). In this procedure variables are added until the marginal probability of an additional variable is >0.05. Squared terms for distances west and north were included, to check for non-linear relationships. We used stepwise regression to investigate the relation-ships between *S. crockeri* and *Bursera* and between small (≤2 m height) and larger stems of *Bursera* and *Opuntia*. We related shrub cover, rock cover and relief to location (including distances squared). For *Opuntia* and *Bursera*, $\log_{10}$(height in m) was related to $\log_{10}$(dbh in cm) by regression. We related the maximum height of *Opuntia*, in each 10 x 10 m sub-plot that contained *Opuntia* stems >2 m high, to plot characteristics.

The Clark-Evans ratio (Clark & Evans 1954) is the observed distance between nearest neighbors divided by the distance expected if the stems are randomly distributed. Converting the ratio to %, a value <100 indicates clumping, 100 indicates randomness, and >100 a regular distribution. These values were adjusted for edge effects and significance levels calculated using the method of Donnelly (1978; see also Runkle 1990, Ward *et al.* 1996). For some analyses we divided stems into small (≤2 m height) and large (>2 m) size classes. We also divided the large plot into coastal (row ≤10) and inland (row ≥20) regions. We calculated dispersion values for *Opuntia* and *Bursera*, both of which tend to grow as single stems. We did not calculate dispersion values for *Scalesia*, which usually grows in tight clusters.

Some regression equations related parameters to location (north or west in the plot) and location squared. Using calculus, derivatives were taken to determine the distance at which the parameter value reached its minimum or maximum and its value at that distance.

RESULTS

Shrub cover, rock cover, and relief varied over the plot (Fig. 1). Values are related to position within the plot by the following equations:

shrub cover (%) = $13.1 + 2.59W - 0.05595W^2$ ($r^2 = 0.0794$, $P < 0.0001$);
rock cover (%) = $45.6 - 2.89W + 0.0978W^2$ ($r^2 = 0.0751$, $P = 0.0001$);
relief (m) = $1.85 + 0.205N - 0.020N^2$ ($r^2 = 0.0250$, $P = 0.0552$);
where W = distance (in units of 10 m) west of the coast, N = distance (10 m units) north.

According to these equations, shrub cover increased to a maximum of 43% at 230 m from the coast and then decreased further inland. Rock cover decreased to a minimum of 24% at 148 m, about half way through the plot. Relief was largest at about the north midpoint of the plot, with a fitted maximum of 2.4 m at a north distance of 51 m. The low r^2 values for the equations demonstrate pronounced local heterogeneity.

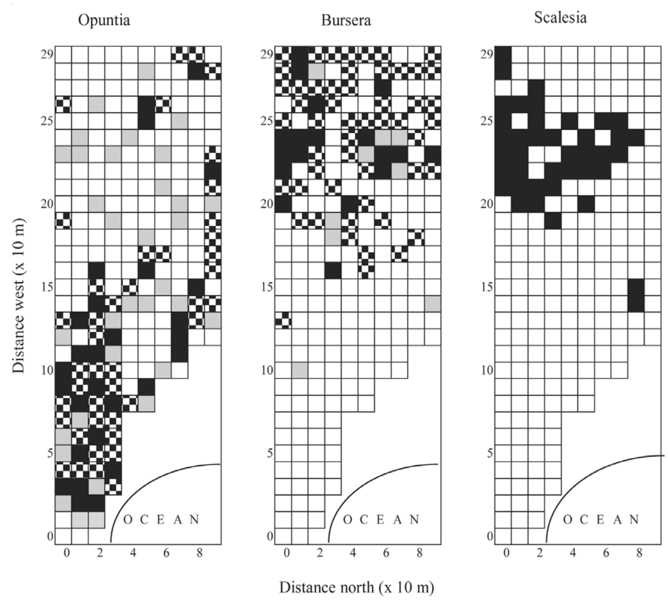

Figure 2. Study plot grids showing distributions of *Opuntia echios*, *Bursera graveolens* and *Scalesia crockeri*. For *Opuntia* and *Bursera*, white indicates no stems present, light shade indicates only stems ≤2 m tall present, dark shade indicates only stems ≥2 m present, and black indicates both small and large stems present. For *Scalesia* black indicates species present.

The three species studied had different distributions (Fig. 2). Most *Opuntia* were on the slope between the coast and a relatively flat upland area: densities were 1–4.5 stems per 100 m^2 on the slope but <1 further inland (Fig. 3). *Bursera* began to appear *c.* 160 m from the coast and soon reached a steady level of 1–2.5 plants per 100 m^2 plot. *Scalesia crockeri* was most abundant 200–260 m from the coast.

Densities were significantly related to plot characteristics. Letting n = number of live stems per 100 m^2 sub-plot, R = relief (vertical distance in m between the

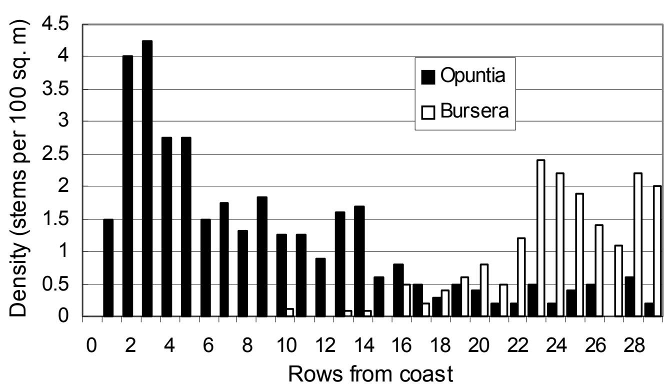

Figure 3. Species densities as a function of distance from the coast for *Opuntia* and *Bursera*.

highest and lowest points within each sub-plot), and S = % of the plot covered by woody plants other than the three target species, we obtained the following fitted stepwise regression equations:
Opuntia $n = 2.7 - 0.16W + 0.00026W^2$ ($r^2 = 0.22$, $P < 0.0001$);
Bursera $n = -0.63 + 0.0033W^2 - 0.14N + 0.35R$ ($r^2 = 0.35$, $P < 0.0001$);
Scalesia $n = -1.8 + 0.26W - 0.36N + 1.0R - 0.46S$ ($r^2 = 0.13$, $P < 0.0001$).

Thus *Opuntia* is influenced mostly by distance from the coast, declining inland (the equation above extrapolates to a minimum at row 31, beyond the edge of the actual plot). *Bursera* increases sharply with distance from the coast and is found more on the south part of the plot. *Bursera* is also found more often on sub-plots with greater relief. The local relief in sub-plots was up to 7 m (mean ± SD: 2.2 ± 1.1 m).

S. crockeri, like *Bursera*, was more abundant in the west (inland) and south parts of the plot. It was more strongly positively associated with relief than *Bursera* and was negatively associated with shrub cover. *S. crockeri* and *Bursera* were positively associated with each other (Spearman $r_s = 0.46$, $P < 0.05$). A stepwise regression relating *Scalesia* density to the environmental features listed above plus the density of *Bursera* resulted in:
Scalesia $n = 2.1 + 1.4B - 0.0349S$ ($r^2 = 0.12$, $P < 0.0001$), where B = *Bursera* density.

Thus, the relationship with *Bursera* was stronger than that with any other environmental variable (*Bursera* was added first to the stepwise regression), suggesting that *S. crockeri* is favored under the open canopy of *Bursera* or that both prefer the same open, rocky substrates where relatively few other species grow. Of 45 *S. crockeri* stems whose heights were measured, 29% were ≤1 m and 33% were >1.5 m (max. height 2.5 m).

Most *Bursera* and *Opuntia* stems were ≤5 m tall (Fig. 4). Stepwise regressions relating the density (number per100 m^2 sub-plot) of small stems (≤2 m high) to environmental features plus the density of larger stems for each species are:
Opuntia (small stems):
$n = 1.5 - 0.11W + 0.0022W^2$ ($r^2 = 0.15$, $P < 0.0001$);

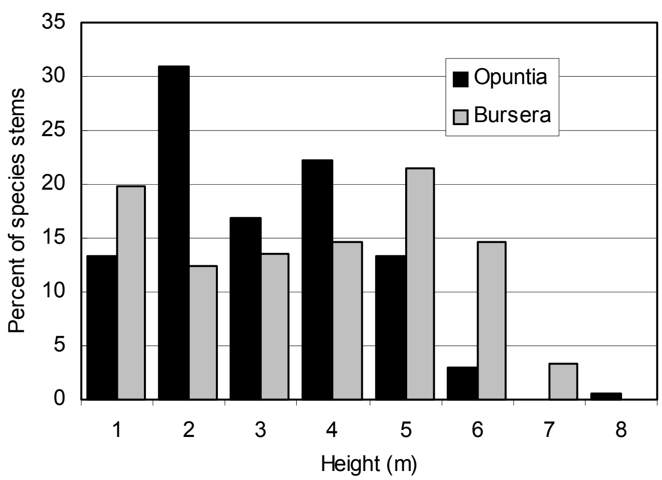

Figure 4. Height distributions of *Bursera* (n = 177) and *Opuntia* (n = 203).

Bursera (small stems):
$n = -0.88 + 0.032W - 0.066N + 0.28R + 0.0071K$ ($r^2 = 0.21$, $P < 0.0001$); where K = % rock.

Thus, for both species, the distribution of small stems was more closely related to the physical environment than to the density of large stems. The equations for small stems are similar to those for all stems except that small stems of *Bursera* tend to occur where much bare rock is visible.

Opuntia height (m) was significantly related to dbh (cm) according to the equation:
$\log_{10}$height = 0.79$\log_{10}$dbh − 0.57 ($r^2 = 0.31$, n = 161, $P < 0.0001$). Maximum height of *Opuntia* stems was not significantly correlated with the plot characteristics measured. *Bursera* height was significantly related to diameter according to the equation:
$\log_{10}$height = 0.35 $\log_{10}$dbh + 0.23 ($r^2 = 0.73$, n = 138, $P < 0.0001$).

Opuntia (living and dead stems) and *Bursera* were both clumped (Table 1). However, for more homogeneous parts of the plot (coastal 0–100 m; inland 200–300 m), *Opuntia* was randomly distributed except that large inland stems were clumped. For the inland plots small *Bursera* were clumped and large *Bursera* were randomly distributed. Nearest neighbors for both *Bursera* and *Opuntia* were usually 4–6 m away except that inland *Opuntia* were usually 11–14 m apart (Table 1).

S. crockeri requires rocky substrates and complex local relief and was absent from the grassy plain transect. Both *Bursera* and *Opuntia* were much less abundant on the transect than on the rockier plot. On the plain we found 39 *Bursera* (=39 per ha), 19 live *Opuntia* (19 per ha) and five dead *Opuntia* (5 per ha). We found 32% of *Opuntia* stems and 5% of *Bursera* stems to be ≤2 m tall but no stems of either species <1 m tall. In contrast, proportionally more small stems were found in the plot, where 44.3% of 203 *Opuntia* stems were ≤2 m high and 11.8% were <1 m high, and 32.2% of 177 *Bursera* stems were ≤2 m high and 16.9% <1 m high.

DISCUSSION

Opuntia echios

Opuntia decreased rapidly away from the coast and occurred at very low densities on the flat grassy plain. Wiggins & Porter (1971) say it grows on thin soil and bare lava near the coast. Reeder & Riechert (1975) found it most abundant only to an altitude of 5 m and present only to an altitude of 79 m in their transect located on the SSW of Santa Cruz Island. The maximum plant height at Cerro Colorado (Fig. 4) fits into the pattern noted by Hicks & Mauchamp (1996): 10 m on the S side of Santa Cruz (var. *gigantea*); 5–6 m near Cerro Colorado (our data); 4 m on the north side of Santa Cruz (var. *echios*); <4 m on islets just north of Santa Cruz (vars. *echios* and *zacana*). Hicks & Mauchamp (2000) did not find *Opuntia* maximum height to vary between the lower and upper Arid Zones, although they did find it to be significantly greater in the Transition

Zone. Hamann (1979) measured height growth at 7 cm per year and estimated that a 2.8 m stem would be about 50 years old. Therefore, the largest stems we sampled could be close to 100 years old. Other Galapagos Opuntia taxa may live up to 150 years, with adult mortality rates of only 2–6% per year in most years (Hamann 2001). In our sample, dead stems (74) totaled 37% the number of live stems (203). This seemingly high fraction may be related to the observations of Hamann (1993), Snell *et al*. (1994), and Tye & Aldaz (1999) that high *Opuntia* mortality occurs during high rainfall (El Niño) years. We found proportionally fewer small stems than in areas with fewer introduced browsers (Hicks & Mauchamp 1996, 2000). Recruitment is sporadic and may depend on high rainfall years such as the major El Niño events of 1982–3 and 1997–8 (Hicks & Mauchamp 2000). During these events more of the area may be suitable for growth than usual, leading to the pattern we observed of small stems in the interior being more randomly dispersed than large stems, which are perhaps clumped in sites favorable for long term growth. However, large stems near the coast were also randomly dispersed. Conditions may be more uniformly favorable there, perhaps associated with the lower shrub cover. Hicks & Mauchamp (2000) also found stems to be more clustered inland than near the coast.

Bursera graveolens

Hamann (2001) found adult mortality of *Bursera* to be only 1–2% per year in studies from 1970 to 1998 and suggested that its life expectancy may thus be up to 200 years. Our observed distribution of *Bursera* (near but not on the coast; at higher densities on lava rocks than the grassy plain) fits descriptions in Reeder & Riechert (1975), who found it on exposed lava at 15–70 m altitude, and Porter (1971), who found it on inclined lava flows and shallow soils. Wiggins & Porter (1971) found extensive open forests of nearly pure stands of *Bursera* on several islands, including the north slopes of Santa Cruz. It has a capsular drupe with edible pseudaril (Wiggins & Porter 1971), which is eaten and the seed dispersed by birds, land iguanas and endemic rats (Clark & Clark 1981). Although most seeds fall under adult canopies, Clark & Clark (1981) found that 86% of juveniles were ≥3 m from an adult. They found the median dispersal distance to be 20 m and the maximum 35 m. Combining juveniles and adults we found nearest neighbors to be 4–5 m apart. Clark & Clark (1981) found seedlings in a variety of substrates, with 40% between rocks, where we also found many small stems. *Bursera* juveniles did not obviously avoid other woody plants (Clark & Clark 1981) but may even be helped by a moderate vegetative cover (Hamann 1993). Our largest individuals (Fig. 4) were similar in size to those described in Clark & Clark (1981) and Hamann (1979).

Bursera was positively associated with topographic relief, cracks and other partly protected sites for germination and growth. No relationship to shrub cover was found. Small inland stems were clumped, presumably responding to the clumping of micro-sites favorable for their initial establishment. The impact of El Niño events on this pattern is not clear (Hamann 2001). Mature stems were randomly distributed.

Scalesia crockeri

We found *S. crockeri* most abundant 200–250 m from the sea. It was associated with high relief (where crevices associated with lava features occurred) and low cover of other shrubs. It was found in many of the same areas as *Bursera* though was not as abundant as *Bursera* >270 m from the shore or in the sandy plain. This distribution fits the general species description from the literature given earlier.

Table 1. Dispersion patterns at Cerro Colorado.

Genus	Living?	Ht[1]	Location	Distrib.[2]	CE(%)[3]	n[4]	n/ha	D[5]
Opuntia	Live	All	All	Clumped	79	203	86	4.4
Opuntia	Dead	All	All	Clumped	64	74	31	6.0
Opuntia	Live	All	Inland	Random	101	32	32	9.7
Opuntia	Live	All	Coastal	Random	97	92	230	3.4
Opuntia	Live	>2	Inland	Clumped	64	13	13	11.3
Opuntia	Live	≤2	Inland	Random	98	19	19	13.7
Opuntia	Live	>2	Coastal	Random	95	51	128	4.6
Opuntia	Live	≤2	Coastal	Random	82	41	102	4.4
Bursera	Live	All	All	Clumped	72	177	75	4.3
Bursera	Live	>2	Inland	Random	97	105	105	5.0
Bursera	Live	<2	Inland	Clumped	66	52	52	4.9

[1]Ht = height (m).
[2]Clumped and Regular indicate patterns significantly ($P \leq 0.05$) different from random.
[3]Clark-Evans index.
[4]n = number of individuals.
[5]D = mean of the distances between nearest neighbors.

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