

## SHORT COMMUNICATION

# Habitat differentiation of sympatric *Geonoma macrostachys* (Arecaceae) varieties in Peruvian lowland forests

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Among the hypotheses invoked to explain high species richness in tropical forests, the niche differentiation hypothesis has received observational and experimental support (Ashton 1969, Chesson 2000, Clark *et al.* 1999, Souza & Martins 2004, Svenning 2001, Terborgh & Mathews 1999). Habitat specialization with regard to edaphic factors and topography has been observed in several plant groups including trees, lianas, shrubs, ferns and palms (Clark *et al.* 1999, Ibarra-Manriquez & Martinez-Ramos 2002, Svenning 1999, Tuomisto & Ruokolainen 1993). Treefall gaps and light gradients have also been found to be important ecological factors affecting plant distribution and niche differentiation in the understory (Chazdon 1986, Poorter & Arets 2003, Terborgh & Mathews 1999). It is suggested that such habitat heterogeneity may not only maintain biodiversity but also may lead to the origin of new species through the process of parapatric speciation (Gentry 1989, Haffer 1997, Patton & Smith 1992).

The high biodiversity of tropical forests is due in large part to species-rich genera with coexisting closely related species. This pattern is exemplified in palms by the presence of many sympatric congeneric species or varieties, notably in *Bactris*, *Chamaedorea* and *Geonoma* (Svenning 2001). *Geonoma macrostachys* Martius is a palm complex that has received attention because of its abundance, small size and highly variable morphology. Two common and widespread varieties in Western Amazonia have been recognized (Henderson 1995): *acaulis* (Mart.) A. J. Hend and *macrostachys* Mart., which differ primarily in leaf shape.

Svenning (2001) indicated that if both processes involved in parapatric speciation (genetic adaptation to

habitat differentiation and reproductive isolation) were present for a given set of taxa, this mode of speciation could be suggested to occur in those taxa. In this context, Listabarth (1993) found that *G. macrostachys* var. *acaulis* (as *G. acaulis*) and *G. macrostachys* var. *macrostachys* (as *G. macrostachys*) were reproductively isolated due to differences in phenology, flowering activity, and pollinator spectrum in a tropical moist forest of central Peru. However, these two varieties did not form discrete entities in a molecular study that used inter-simple sequence repeat (ISSR) variation in a sample of 31 individuals collected from four localities in Peru. Individuals clustered by locality and an infraspecific genetic classification was not possible (Roncal 2005). The *Geonoma macrostachys* sympatric varieties or forms appear to be mainly a local phenomenon offering a good study case to analyse in detail the habitat differentiation between them.

Here I evaluated the habitat differences between sympatric *G. macrostachys* varieties through the analysis of 16 environmental characteristics in three Peruvian lowland forests. I examined the following questions: (1) do sympatric varieties of *G. macrostachys* occur in different habitats, (2) if so, what are the major environmental differences between them? and (3) is there a consistent habitat preference pattern across field sites?

Fieldwork was carried out in three tropical moist forests. The Amazon Conservatory of Tropical Studies (ACTS, 03°15'S 72°54'W) located in north-eastern Peru within the Explornapo Reserve, 1725 ha of mostly primary forest, property of Explorama Tours. Most of the reserve is covered by tierra firme forest but the area adjacent to the Sucusari river was classified as Igapo or floodplain (Vasquez 1997). The Loma Linda Native Reserve (LLNR, 10°19'S 75°03'W) is a 332-ha protected area located adjacent to the Palcazu river in central Peru. Two main habitat types were recognized: a topographically irregular

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**Table 1.** Number of transects established, area sampled, and densities at which each variety was found on each habitat for every locality. TF = tierra firme, FP = floodplain, ACTS = Amazon Conservatory of Tropical Studies, LLNR = Loma Linda Native Reserve, EBCC = Cocha Cashu Biological Station

	ACTS	LLNR	EBCC
Number of TF transects (area ha)	5 (0.75)	6 (0.9)	5 (0.75)
var. <i>acaulis</i> density (indiv. ha <sup>-1</sup> )	2.66	12.22	0
var. <i>macrostachys</i> density (indiv. ha <sup>-1</sup> )	321.33	35.55	221.33
Number of FP transects (area ha)	5 (0.75)	6 (0.9)	6 (0.9)
var. <i>acaulis</i> density (indiv. ha <sup>-1</sup> )	2805.33	200	28.88
var. <i>macrostachys</i> density (indiv. ha <sup>-1</sup> )	57.33	11.11	72.22
Total sampled area (ha)	1.5	1.8	1.65

tierra firme and a floodplain forest (Roncal pers. obs.). Finally, the 1000-ha study area of Cocha Cashu biological station (EBCC, 11°50'S 71°23'W) is located within the lowlands of the Manu National Park in south-eastern Peru. Soils at EBCC within the meander belt of the Manu River are composed of young alluvial silt and clay, while soils in the uplands are sandy (Terborgh 1990). We used the morphological descriptions of Henderson (1995) to identify *G. macrostachys* varieties in the field. Voucher specimens were deposited at the Herbario Forestal of the Universidad Nacional Agraria La Molina in Lima, Peru and at Fairchild Tropical Botanic Garden in Miami, USA.

At each site, transects of 10 m wide and 290 m long were established haphazardly on each main habitat or soil type and separated from one another by at least 200 m. The number of transects at each habitat and site (Table 1) was determined by the availability of area. Transects were divided into plots of 10 m × 10 m and all *G. macrostachys* adult individuals were recorded in every other plot. The total area sampled in this study was 4.95 ha. The inclination of every other plot along each transect was measured with a clinometer (PM5/360PC, Suunto<sup>®</sup>, Finland) in the middle of the plot.

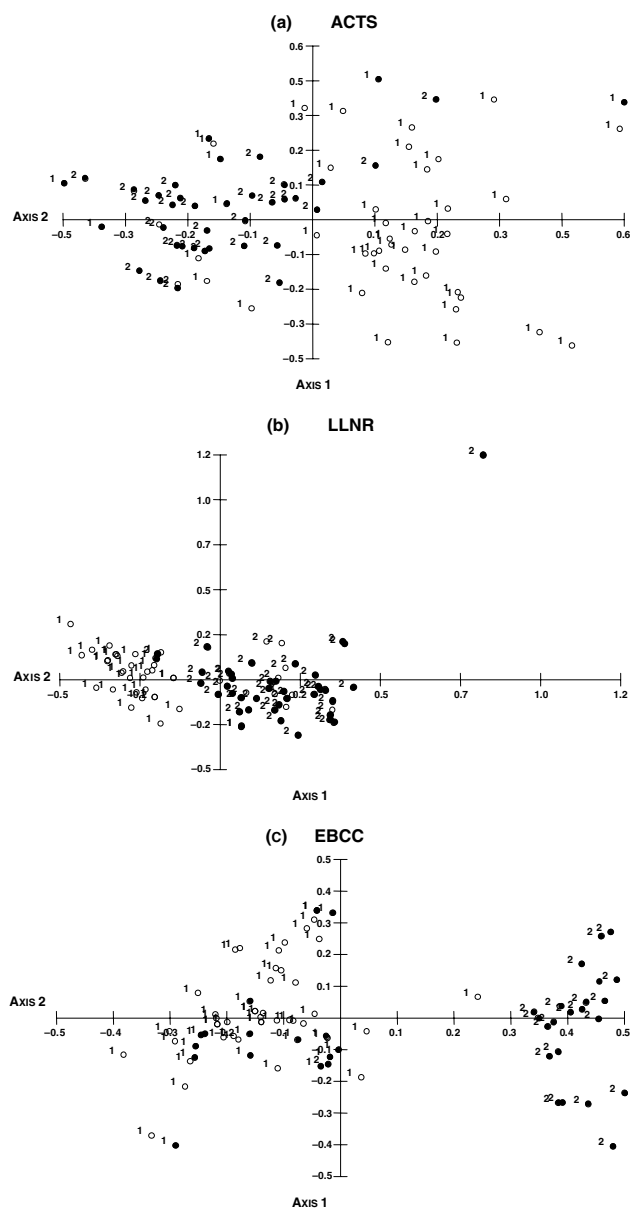
Composite soil samples from the top 20 cm of soil profile and within 0.5-m radius of the palms, were taken from 78, 76 and 71 plots from ACTS, LLNR and EBCC, respectively (225 soil samples in total). Plots were randomly chosen along transects so that at least 40 soil samples per variety at each site were collected with no more than nine soil samples per transect. Since at EBCC fewer than 40 plots were recorded to have *G. macrostachys* var. *acaulis* individuals, 17 additional soil samples were collected from haphazardly selected individuals in the forest. For the same reason, nine soil samples from haphazardly chosen *G. macrostachys* var. *macrostachys* individuals were collected at LLNR. This procedure was also followed for plots where the two varieties were found, collecting only one composite sample. Soil texture was quantified using a hydrometer (WLS75026, Sargent-Welch, NY). Soil chemical analyses included pH, and the following extractable cations: Ca, Mg, P, K, Zn, Mn, Cu, B and Na, using the Mehlich 1 extractant and an Inductively Coupled Plasma (TJA 61E, Thermo Electron Corporation, FL).

Hemispherical photographs were used to obtain an indirect measure of light availability for 40 palm individuals of each variety at each locality (240 palms in total). Individuals selected for this purpose were the same as those selected for soil analyses. I used a Nikon 8 mm fisheye lens (180° field of view) mounted on a Nikon COOLPIX 995 digital camera. Hemispherical photographs were analysed with Gap Light Analyzer software version 2.0 (Frazer *et al.* 1999) for percentage of canopy openness, leaf area index and total (direct plus diffuse) transmitted light in mol m<sup>-2</sup> d<sup>-1</sup>.

After calculating the densities at which each variety occurred at each habitat and field site, a chi-square test ( $\chi^2$ ) was used to test the null hypothesis of independence between variety density and habitat type. A principal components analysis (PCA) using the Multi-Variate Statistical Package (MVSP) version 3.1 (Kovach Computer Services, Wales, UK) was performed on the plot by 16 environmental variables matrix of standardized data for each field site separately. PCA permitted the evaluation of the contribution of each environmental variable to any habitat differences between the sympatric varieties. The spatial autocorrelation between plots within transects was evaluated through correlograms using Moran's *I* statistics (Sawada 1999) on each of the 16 environmental variables at each site. Plots separated by 20 m were found to be spatially correlated with respect to some variables and were therefore excluded in the analyses.

The two varieties were mostly encountered in different habitats (Table 1). At ACTS and LLNR, *G. macrostachys* var. *acaulis* was more abundant than *G. macrostachys* var. *macrostachys* and significantly preferred the floodplain forest, while the latter variety was more common in tierra firme ( $\chi^2 = 2620$ ,  $P < 0.001$ ,  $df = 1$  and  $\chi^2 = 128$ ,  $P < 0.001$ ,  $df = 1$ ; for ACTS and LLNR, respectively). At EBCC, var. *acaulis* was less abundant than var. *macrostachys* and as in the other two localities var. *macrostachys* occurred preferentially in tierra firme ( $\chi^2 = 69.7$ ,  $P < 0.001$ ,  $df = 1$ ). No *G. macrostachys* var. *acaulis* individual was found in the tierra firme forest at EBCC (Table 1).

At ACTS the first component allowed discrimination of plots by habitat types (Figure 1a). Plots from the floodplain forest showed for the most part positive values along the



**Figure 1.** Scatter plot of the sampling plots along the first two components of the principal components analysis (PCA) for 16 environmental variables collected in (a) ACTS, (b) LLNR and (c) EBCC. 1 = plot in floodplain forest, 2 = plot in tierra firme. ● = *Geonoma macrostachys* var. *macrostachys*, ○ = *G. macrostachys* var. *acaulis*.

first axis, while tierra firme plots were in the negative part of this axis. The variables that separated plots along the first component were (with loadings in parentheses): K (0.39), sand content (−0.39), Cu (0.38), clay content (0.36) and Mg (0.35). At LLNR the segregation of plots by habitat along the first component was also clear (Figure 1b). The most significant contributors to axis one were (with loadings in parenthesis): K (0.39), inclination (0.34), sand content (−0.34), clay content (0.33), Cu (0.31) and Na (0.30). At EBCC tierra firme plots occupied the positive side of the first axis while floodplain plots

appeared on the negative part (Figure 1c). Component one was correlated primarily with Ca (−0.38), sand content (0.36), pH (−0.36), clay content (−0.34), Mg (−0.33), and K (−0.32). As in the other localities, light factors did not have high loadings in the first component. Edaphic factors were therefore better contributors than light conditions to distinguish habitats and also to differentiate the two varieties given that the segregation of plots by habitat in all three PCAs also allowed segregation of local sympatric varieties.

In a study of a palm community in the north-eastern Peruvian Amazon, Ruokolainen & Vormisto (2000) classified both *G. macrostachys* varieties as generalists as they were found in rich and poor soil classes according to a cation content gradient. These authors, however, used the presence or absence of individual taxa to define edaphic preferences; results presented in this study, based on abundance data, showed different habitat responses for these two varieties. The use of concepts such as specialist or generalist should be therefore carefully interpreted, as they are highly dependent upon sampling strategies.

Most studies on plant distribution patterns have focused on the effects of edaphic and topographic factors. However, few studies have analysed the effects of both light availability and soil characteristics. For example, the distribution of *Geonoma brevispatha* genets in a swamp forest in Brazil was not correlated with canopy openness but was correlated with soil moisture (Souza & Martins 2004). The present study is in concordance with these reports since light variables did not explain the variation between varieties within the first PCA axis. Edaphic factors, mostly texture and K content, separated sympatric varieties of *G. macrostachys* more readily.

In a community-level study across four forest transects in Peruvian Amazonia, Vormisto *et al.* (2004) found that *acaulis* individuals occurred more on hills than expected while *macrostachys* individuals were more abundant in the valleys. These patterns occurred only in one of the four transects analysed. When compared with the study conducted by Svenning (1999) in Yasuni, Ecuador, it becomes clearer that the distribution pattern of this species may not be consistent across forests. In Yasuni, var. *macrostachys* did not show a significant preference for any topographic position. Topographic position was not tested in the present study; however, plot inclination was an important component in the differentiation of LLNR plots where var. *acaulis* was found consistently in flat areas and var. *macrostachys* was associated with terrain of irregular topography.

Finally, it appears that the local reproductive isolation and habitat differentiation achieved by these varieties might have arisen quickly with little genetic foundation or that more polymorphic loci are needed to detect the genetic differentiation (Roncal 2005). Phenotypic plasticity of *G. macrostachys* in response to edaphic

conditions is another potential explanation for the morphological variation of this species. From this and other studies it is clear that habitat heterogeneity is an important factor that allows coexistence of closely related tropical plants. However, as Svenning (2001) argued, habitat differentiation and reproductive isolation do not guarantee parapatric speciation, it may just reflect niche competition between species already formed by other mechanisms (Bush 1994, Haffer 1997, Levin 2001, Losos & Glor 2003). Future studies specifically designed to test parapatric speciation are needed to elucidate the importance of this mechanism in tropical plant richness.

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