

## Directional changes in plant assemblages along an altitudinal gradient in northeast Brazil

Santos, BA.<sup>a</sup>, Barbosa, DCA.<sup>b</sup> and Tabarelli, M.<sup>b\*</sup>

<sup>a</sup>Coordenação de Pesquisas em Silvicultura Tropical, Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo 2936, CEP 69060-001, Manaus, AM, Brazil

<sup>b</sup>Departamento de Botânica, Universidade Federal de Pernambuco, Av. Prof Moraes Rego s/n, CEP 50670-901, Recife, PE, Brazil

\*e-mail: mtrelli@ufpe.br

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(With 1 figure)

Plant assemblage organization along physical environmental gradients remains a central issue of community ecology whether it is analyzed on local, regional or continental scales. In the case of neotropical forests, several studies have identified remarkable differences between dry and moist forests in terms of vegetation structure, woody plant species composition, plant species richness and the relative contribution of life-history strategies including life form, seed dispersal and pollination mode (see Gentry, 1983, 1988; Bullock, 1995; Medina, 1995; Murphy and Lugo, 1996). Similar patterns have been found in neotropical forests covering altitudinal gradients (Vázquez and Givnish, 1998). More than remarkable differences between patches of forests, the studies referred to earlier support the idea of gradual, directional and consequently predictable changes in the attributes of woody plant assemblages covering such gradients.

The caatinga vegetation is a kind of dry forest and scrub vegetation (sensu Pennington et al., 2000) which covers 730,000 km<sup>2</sup> of northeastern Brazil. Throughout this region, caatinga vegetation covers flattened surfaces located preferentially between 300 and 500 m a.s.l. Vegetation types are constrained by 240-900 mm of annual rainfall (see a synthesis in Leal et al., 2003). Moreover, the caatinga surrounds dozens of high hills where the annual rainfall exceeds 1000 mm. Tracts of the Brazilian Atlantic forest cover the top of these hills, and such enclaves of humid forests located in the caatinga semiarid region have been locally referred to as 'brejo forests' sensu Pôrto et al. (2004). Briefly, the caatinga and Atlantic forest border each other for hundreds of kilometres and form continuums of vegetation from dry seasonal forests or scrub vegetation in the inter planaltic depressions to semi-deciduous or even evergreen forests on the top of the hills – hereafter caatinga-brejo forest continuums. These continuous have already been completely cleared in most of the 47 brejos once recorded in the northeast of Brazil (see a synthesis in Pôrto et al. (2004).

Based on the ideas briefly discussed earlier, it is reasonable to expect both gradual and directional changes in the attributes of plant assemblages, which form the caatinga-brejo forest continuums. Precisely, we should

expect a gradual increase in plant species richness and in the relative contribution of species within categories of life form, seed dispersal mode, fruit type and size as altitude/annual rainfall become higher (i.e., caatinga to Atlantic forest). In this paper, we test this prediction by analyzing species richness and the ecological composition of woody plant assemblages at four altitudinal levels along a caatinga-brejo forest continuum (500-1100 m a.s.l.), which is located between Triunfo and Serra Talhada municipalities (Pernambuco State). In this area, increasing levels of altitude are also correlated with (1) increasing levels of annual rainfall – nearly 600 mm at 500 m up to 1200 mm at 1100 m; and (2) decreasing scores of average annual temperature (26-18 °C respectively; Ferraz et al., 1998).

Remaining patches of this vegetation continuum are currently distributed over 23 km of extension and they were assessed via plant surveys by Ferraz et al. (1998). These authors recorded liana, shrub and tree species at four altitudinal levels – 500, 700, 900, and 1100 m a.s.l. by a total sample of thirty 200-m<sup>2</sup> plots and random plant collections outside plots. We used the checklist provided by Ferraz et al. (1998), and classified its 149 woody plant species within categories of life form, seed dispersal, fruit type and fruit size according to criteria and procedures described by Tabarelli et al. (2003). By these procedures, we obtained the proportion of species within ecological categories in the four levels of altitude. Lack of information at two levels of altitude avoided comparisons based on rainfall.

In contrast to our expectations, plant species richness did not show a gradual increase along the gradient ( $r_s = 0.5$ ,  $P > 0.05$ ) yet species richness in 900 and 1100 m of elevation was higher than in 500 m ( $\chi^2 = 17.1$ ,  $df = 1$ ,  $P < 0.001$ ;  $\chi^2 = 11.2$ ,  $df = 1$ ,  $P < 0.001$ , respectively). This was also higher than in 700 m ( $\chi^2 = 27.8$ ,  $df = 1$ ,  $P < 0.0001$ ;  $\chi^2 = 9.5$ ,  $df = 1$ ,  $P < 0.0001$ , respectively). Precisely, species richness ranged from 42 to 70 species at 1100 m of altitude, which represented a significant increase of 71.4%. The proportion of tree species also differed significantly within altitudinal categories ( $\chi^2 = 9.5$ ;  $df = 3$ ;  $P = 0.02$ ). At 500 m of altitude, 52.4% of the species were trees, increasing gradually by 57.6%, 67.1%

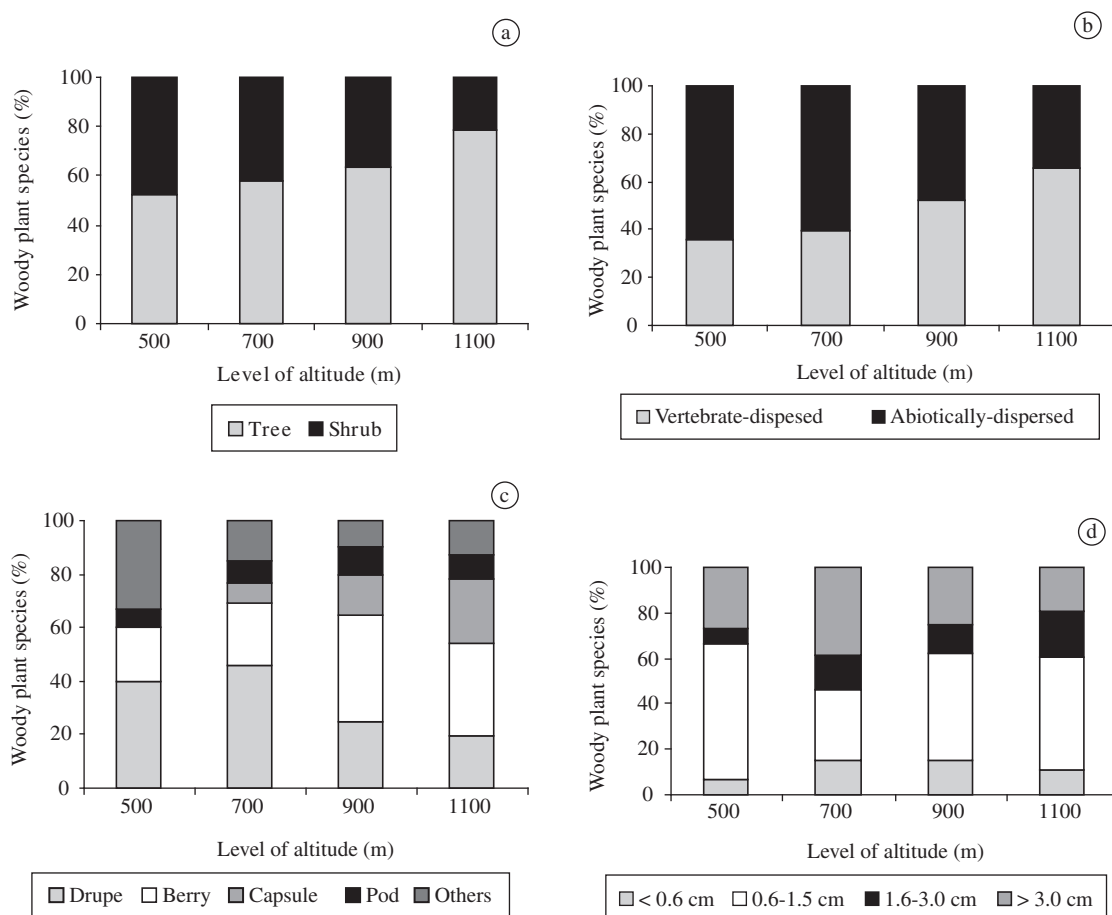
and 78.6% at 1100 m, respectively (Figure 1a). Similarly, the percentage of vertebrate-dispersed species gradually increased from 35.7% (500 m) to 65.7% (1100 m; Figure 1b;  $\chi^2 = 11.79$ ;  $df = 3$ ;  $P = 0.008$ ). In contrast, we did not find any significant relationship between the altitude and both fruit type and size (Figures 1c,d).

Altitude is probably a spurious variable, which is in our site significantly correlated with those promoting more conspicuous biological effects such as average rainfall and temperature (see Lütge, 1997). To give one example, the relative contribution of shrubs decreases sharply while the contribution of trees increases within stands of caatinga vegetation covering gradients from very dry sites (<400 mm of average annual rainfall) to sites receiving > 800 mm (Andrade-Lima, 1981; Leal et al., 2003). The relative and absolute increase in trees, which usually replace part of the shrub species, also explain why moister patches of tropical forest and savannas are richer than drier sites (Andrade-Lima, 1981; Gentry, 1988) as observed in this study.

The underlying mechanisms driving these spatial variations of the attributes of plant assemblages certainly

include differences in the water required by plant species showing different life-history traits, i.e. mechanisms based on plant-response to physical factors. Tabarelli et al. (2003), for example, argued that tree and shrub species that produce and have to maintain small or large fleshy fruits (i.e., moist-but-soft-skinned fruit) in low-rainfall areas within the caatinga or in those areas where rainfall is erratic would be negatively affected by long dry seasons and high evaporation/insolation during the moist season. On the other hand, several studies (e.g., Vázquez and Givnish, 1998; Brose and Tielbörger, 2005) have shown plant-plant and animal-plant interactions as biotic drivers of species distribution along physical gradients with remarkable impacts on the attributes of plant assemblages, particularly species richness, species composition and abundance of life-forms.

In the case of the caatinga-brejo forest continuums, further studies should investigate whether the patterns documented here result from the occurrence of narrow-distributed species (high habitat-specificity) and the consequent establishment of particular assemblages or alternatively if they result from the presence of large ecotonal



**Figure 1.** Percentage of woody plant species within categories of life form (a); seed dispersal mode (b); fruit type (c); and fruit size (d) in four altitudinal levels in northeast Brazil (n = 149 species).

plant assemblages. Additionally, mechanisms driving plant species spatial distribution, which ultimately explain the attributes of plant assemblages, must be identified. Answers to these questions are essential to extend our knowledge concerning the evolutionary history of neotropical biotas, as well as the organization of plant assemblages along physical environmental gradients.

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