SPECIES RICHNESS AND FLOOD PULSES: EVALUATING MULTIVARIATE RELATIONS ALONG A DISTURBANCE GRADIENT IN A RIVERINE FOREST OF SOUTHERN BRAZIL

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INTRODUCTION

Several hypotheses have been developed concerning different subjects that affect or control plant species richness. Major specific factors include productivity and competition, disturbance and the species pool capable to establish in a site.

Generally, univariate models of productivity or disturbance were described as unimodal predictors of plant species richness and according to Cardinale *et al*. (2006) they had some success in explaining such patterns. By other hand, environmental variables are frequently associated with the presence or absence of some species, according to its capacity to establish at a site or, the environmental influences on plant biomass. In the first case, environmental variables and disturbance may be associated once disturbance can affect the availability or heterogeneity of specific variables in a system. This approach of disturbance defines it as processes leading to either the survivors of disturbance or new colonists to respond to increased resources availability, then, accelerated growth of small individuals released from competition is a response pattern to disturbance. The direct influence of disturbance on biomass led us to a second approach where distribution limits plant biomass by causing its partial or total destruction or as a change in conditions which interferes in the current functioning of a given biological system

The conceptual model of Dynamic Equilibrium (Huston 1994) proposed diversity is the result of community biomass production which led to competitive exclusion and, disturbance, which may reduces, by itself, species density. In the past few years, multivariate hypotheses development and testing methods have conducted to increasing efforts in evaluate hypotheses concerning networks of controlling factors on species richness, specially the structural equation modelling (Laughlin & Grace 2006).

In this study we seek to evaluate a multivariate model of the relationships among environmental variables, disturbance and biomass in predict tree species richness in riparian forests. Here, we hypothesized once flooding is a direct promoter of disturbance within riparian forests, then it is also the main resource of tree species variation across these systems. Our approach started by test a general multivariate model linking environmental variables, disturbance and biomass in predict tree species richness and provide and alternative model if necessary. Then, we decompose disturbance (measured as flooding frequency per year) and biomass (measured in m^2. ha^{-1}) in a separated bivariate model to seek for specific contribution of these resources on tree species richness.

MATERIAL AND METHODS

Study area and sampling design

This research was conducted in the riparian fringes of Rio Botucaraí near its confluence with Rio Jacuí (30º01'S, 52º47'W), Southern Brazil (Budke et al. 2007). Floods in the area are highly unpredictable because there is no one marked seasonal rainy period and rainfall is relatively well distributed throughout the year. As a consequence, floods occur at any time of the year. The duration of overflow periods may vary from some days to a few weeks. We distributed four 1 ha (100 × 100 m) plots in a toposequence from the river margin of the Rio Botucaraí to a non-flooded forest site. Each plot comprised ten contiguous 100 × 10 m transects parallels to the river margin. All individual living trees, having at least one stem with perimeter at breast height (pbh) e" 15 cm were sampled. We carried out a detailed topographic survey of the transects as well as topsoil (0-20 cm depth) samples, from 60 sites distributed in different positions, in such a way that its overall topographic variation was encompassed.

Data analysis

We used Principal Coordinates Analysis (PCoA) to obtain orthogonal axes describing the community resemblance among transects with Jaccard's coefficient as the similarity measure. We modelled a multivariate model by using structural equation modelling to seek for relations among soil properties, flooding frequency, biomass and species richness. Prior the evaluation of the full model, we examine bivariate relations among variables, all of which in the 40 transects (0.1 ha). To evaluate whether species richness will be a function of disturbance frequency and biomass as an increasing function of their interactions, we evaluated this prediction testing richness to a second-order polynomial function, according to the equation: $S = b_0 + b_1B + b_2D + b_3B^2 + b_4D^2 + b_5B \times D + e$ where; D is the disturbance frequency (mean no. floods year^{-1}) and B is a estimative of biomass (estimated by basal area (m^2.ha^{-1})).

RESULTS AND DISCUSSION

The studied area has well-defined geomorphic features that include point bars with recent-deposited sediments, meanders and small ponds located in the lower sites, which reflect river dynamics and associated sedimentation. Across the entire topographical range, we observed soil texture to correspond such variations. Frequently flooded transects presented high proportion of silt or sand, in some cases. Sand proportion was higher at upper non-flooded sites, although, some upper transects also presented low sand proportion. Clay, by other hand presented low proportion among all transects and varied only from 10 to 30 percent. Silt proportion was higher at low to moderate elevated sites but it also varied lesser than sand proportions.

Field inventory yielded a total of 5,779 trees belonging to 96 species and 36 families, from which, Myrtaceae (14) and Fabaceae (13) were the richest families, followed by Euphorbiaceae, Rubiaceae, Salicaceae and Sapotaceae with five tree species. The first two axes of the PCoA ordination explained *ca*. 30% of the total variation (Axis 1 = 21.9%; Axes 2 = 8%) and the transects arrangement indicated there is a strong species gradient, starting at the left side, with non-flooded forest transects and ends at the right side, with frequently flooded forest transects.

All predictor variables included in the analysis presented strong relationships with tree species richness, which had its maximum at intermediate elevation. Peak richness occurred at high fertility soils, high organic matter and intermediate levels of aluminium saturation. Only seven transects presented high proportion of aluminium (saturation > 50%) and most transects had intermediate-low fertility (saturation < 50%) which means soils presented low to moderated fertility but without major aluminium restrictions to nutrient absorption by plants. Richness declined severely with the increase of disturbance and it reached a peak at low disturbance frequency. By other hand, highest richness appeared at intermediate to high biomass levels. Disturbance fit a linear relationship with biomass fairly well ($r^2 = 0.45$), with decreasing biomass toward higher disturbance.

After analyzing for the adequacy of our initial model, with major interest on the relationships among latent variables, a preliminary fit indicated some measured variables did not figure as consistent variables in the model and did not contributed in explain any additional information when considered as isolated latent variables, thus, they were deleted from the final model. These variables were: proportions of silt and clay, aluminium saturation and pH. Furthermore, some pathways were also deleted from the model, including those from soil chemistry and soil texture on biomass and soil texture on richness. Three pathways were included in the final model and represented direct interactions among soil texture and soil chemistry on soil organic and soil texture on soil chemistry. Final analysis of the revised full model indicated that the model obtained a close fit with the data ($c^2_{df=3} = 1.724$, $P = 0.63$; RMSEA = 0.000, $P = 0.667$; GFI = 0.988), where GFI values higher than 0.9 indicate good fit between model and data. The final model explained 79% of variation in richness and 67% of variation on biomass. Disturbance was clearly associated to elevation, as a direct function of topography. Soil chemistry (expressed in the final model only by fertility), organic and texture (expressed by sand proportion only) were also well explained in the final model and, additional paths among them helped to explain organic matter contents and soil chemistry. Together, disturbance and elevation explained well the variation on soil texture ($r^2 = 0.34$).

The interaction between disturbance and biomass on tree species richness revealed a concave-down function with an increasing function of their interaction. Contrary to our expectation and previous models, richness reached a peak at increased biomass and at decreased disturbance frequency. The quadratic term explained 32.5% of variation on tree species richness ($F = 4.2$, $P < 0.001$).

Flooding, as a direct measure of disturbance, presented different frequencies across the topographical range and it was a causal variable to most of the other environmental parameters. Also, inundation is acting in this basin by unpredictable events and it is playing a substantial role in structuring tree species, not only by seed bank removal or sediment dynamics but also by it high variable flow regime. In this case, flexible and opportunistic live history strategies are more likely to develop (Walker et al. 1995).

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