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Community ecology

The drivers of woody species richness and density in a Neotropical savannah

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Environmental filtering prevents species without certain attributes from occurring in local communities. Traits respond differently to different abiotic factors, assembling communities with varying composition along environmental gradients. Here, we measured proxies of soil fertility, disturbance by fire, response and physiological traits to assess how these variables interact to determine woody species richness and density in a Neotropical savannah. We explicitly incorporated our assumptions about how different abiotic filters influence different subsets of traits into a statistical model using structural equation modelling, yielding a more accurate representation of the assembly process. Fire had an effect on resistance traits, whereas soil fertility influenced physiological traits. Resistance traits explained both the richness and density of plots, whereas physiological traits explained only the density. Fewer fire events led to richer and denser plots. Similarly, areas with lower cation exchange capacity assembled less dense communities. Furthermore, we showed that structural equation modelling yielded a realistic representation of the bivariate interactions of distinct environmental filters with different subsets of traits.

1. Introduction

Environmental filtering prevents species without certain trait values from occurring in local communities. Distinct abiotic factors can filter species at different spatial scales and points in time [1]. Thus, assemblages are likely to be formed by multiple sources of trait filtering [1]. Accordingly, subsets of traits respond differently to different abiotic factors, assembling communities with varying composition along environmental gradients [2,3]. Because some traits are more relevant to certain abiotic filters than others [4], incorporating their functional relevance in models of assembly will yield more realistic translations of how the environment and organisms interact to shape communities and rates of ecosystem processes.

In savannahs, such as the Brazilian cerrado, soil fertility and fire are important promoters of trait filtering [5,6], determining which species from the regional pool are able to co-occur locally [1,2]. In the Brazilian cerrado, studies have indicated that soil characteristics [7] and disturbance caused by fire [6,8,9] play a major role in the composition of communities, influencing the distribution of traits and the richness and density of woody individuals. Indeed, patches of forest formations within the Cerrado domain indicate that both vegetation types share the same climate requirements. However, not all functional traits respond similarly to soil fertility and fire in the cerrado. For instance, only half of the functional traits measured in a cerrado area [10] had distributions correlated with fire frequency. Likewise, the effects of fire on functional diversity are dependent on the subset of traits used to calculate the diversity index [11]. Even though there is an increasing amount of research relating fire and the distribution of traits in the Brazilian cerrado, it is still uncertain how traits mediate the interaction between abiotic factors and the richness and density of plants. Moreover, the role of different subsets of functional traits in this mediation remains to be addressed.

Here, we measured proxies of soil fertility, disturbance by fire, response and physiological traits to assess how these variables interact to determine woody species richness and density, and we describe more generally how structural equation modelling with latent variables can improve assembly models. In ecological studies, several of the concepts that researchers use cannot be directly measured or reduced to a single number. Latent variable modelling allows the inclusion of such concepts in structural models, yielding more accurate mathematical translations of our ecological hypotheses. Thus, the resistance of plants to fire or the physiological challenges imposed by low soil fertility and that are reflected on plant traits are ideas that can be modelled as latent variables. To our knowledge, this is the first study to quantify the joint effects of soil fertility and fire on subsets of traits and the effects of traits on community composition in a Neotropical savannah.

2. Material and methods

We conducted this study in Emas National Park, Central Brazil. Emas is one of the largest cerrado reserves in Brazil, with an area of around 133 000 ha. The cerrado vegetation in the park displays striking variation in the density of woody individuals. We randomly placed one hundred $25 \, m^2$ quadrats in the park and, on each of the 531 woody individuals that occurred in the quadrats, measured the values of six functional traits that represent responses of plants to environmental conditions such as nutrient availability and fire [12]: (i) basal area (m^2), related to space occupation, resource uptake, total biomass and reproductive capability; (ii) height (m), associated with competitive vigour, fecundity and growth after disturbance; (iii) bark thickness (mm), related to resistance to disturbance; (iv) leaf nitrogen ($mg \, g^{-1}$), related to maximum photosynthetic rates and nutrient stress; (v) specific leaf area ($mm^2 \, mg^{-1}$), associated with growth and maximum photosynthetic rate; and (vi) leaf toughness (N), associated with resistance to herbivore and leaf lifespan.

Fire is a major source of disturbance in Emas [13]. Preventive firebreaks, maintenance roads and heterogeneous fuel availability make the fire map of Emas resemble a mosaic, with nearby plots possibly having very distinct fire histories. Using in-field observations and satellite images, we counted the number of fire events between 1984 and 2010 as a proxy for the disturbance caused by burnings.

As cerrado soils generally have low nutrient availability and nutrient levels have been shown to influence the cerrado vegetation [7], we used cation exchange capacity as an indicator of soil fertility. We measured this variable from five soil subsamples from each plot, which we combined into one sample per plot.

We used structural equation modelling with robust estimators ([14]; electronic supplementary material, appendix S2) to test two competing models of the causal connections between abiotic factors, traits and community composition. We proposed two *a priori* structural equation models (figure 1). In the first model (figure 1a), all traits are caused by only one latent variable. In the second model (figure 1b), observed traits are further divided into resistance and physiological traits. Each trait value in our proposed models was the average of that trait for all individuals in a quadrat. We had, thus, 100 observations for each trait. We determined density as the number of woody individuals per square metre. Prior to testing the full structural equation models, we did a confirmatory factor analysis with all traits caused by one latent variable and another one with resistance and physiological traits (see the electronic supplementary material, appendix S1). Poor fit in these confirmatory models would indicate that the choice of latent variables did not
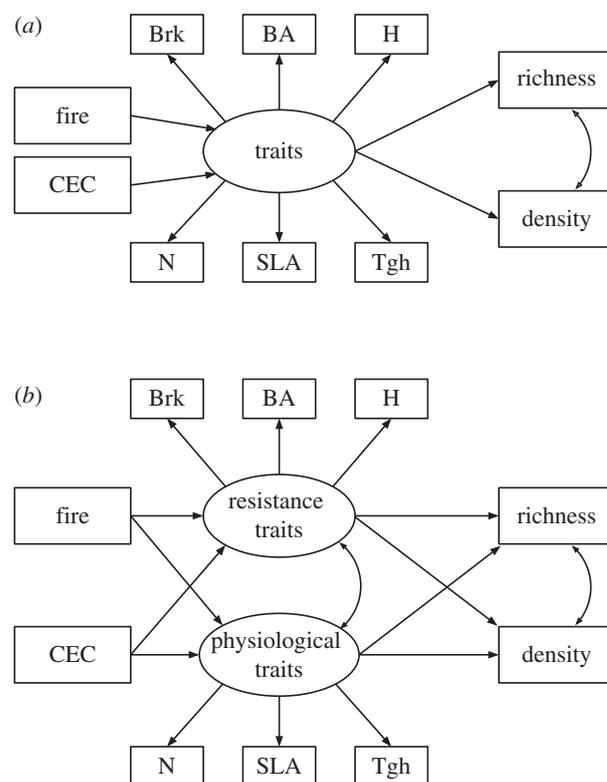

Figure 1. Competing causal models relating the environment, traits, richness and density. In the first model (a), we considered all measured traits to be caused by a unique latent variable, whereas in the second model (b), we incorporated trait multi-dimensionality by further dividing traits into two latent variables. Fire, number of fire events between 1984 and 2010; CEC, cation exchange capacity ($mmol \, kg^{-1}$); Brk, bark thickness (mm); BA, basal area (m^2); H, height (m); N, leaf nitrogen content ($mg \, g^{-1}$); SLA, specific leaf area ($mm^2 \, mg^{-1}$); Tgh, leaf toughness (N).

accurately represent the role of resistance and physiological traits in the interaction between plants and the environment.

3. Results

The causal structure with all traits represented by one latent variable exhibited a poor fit with the data ($\chi^2 = 92.319$, d.f. = 33, $p = 0$). The confirmatory factor analysis of the single latent variable in this model also showed poor fit ($\chi^2 = 53.249$, d.f. = 9, $p = 0$). The factor analysis indicated that all the traits we measured were not caused by a single latent variable, because bark thickness, basal area and height had non-significant path coefficients, whereas leaf nitrogen content, specific leaf area and leaf toughness had significant coefficients. Separating traits into two latent variables yielded a confirmatory factor model with a much better fit ($\chi^2 = 7.304$, d.f. = 8, $p = 0.50$; electronic supplementary material, appendix S1). All indicators of the two factors were significant.

The structural equation model with two sets of traits represented by two latent variables quickly converged to a solution and fit the data well (figure 2, $\chi^2 = 38.250$, d.f. = 28, $p = 0.094$). The loadings of both latent variables were significant. Of all the paths we initially considered plausible, the estimates of the effects of fire on physiological traits, cation exchange capacity on resistance traits, physiological traits on richness and the covariance between physiological and resistance traits were non-significant. Fire had a strong influence on resistance traits and a non-significant influence on

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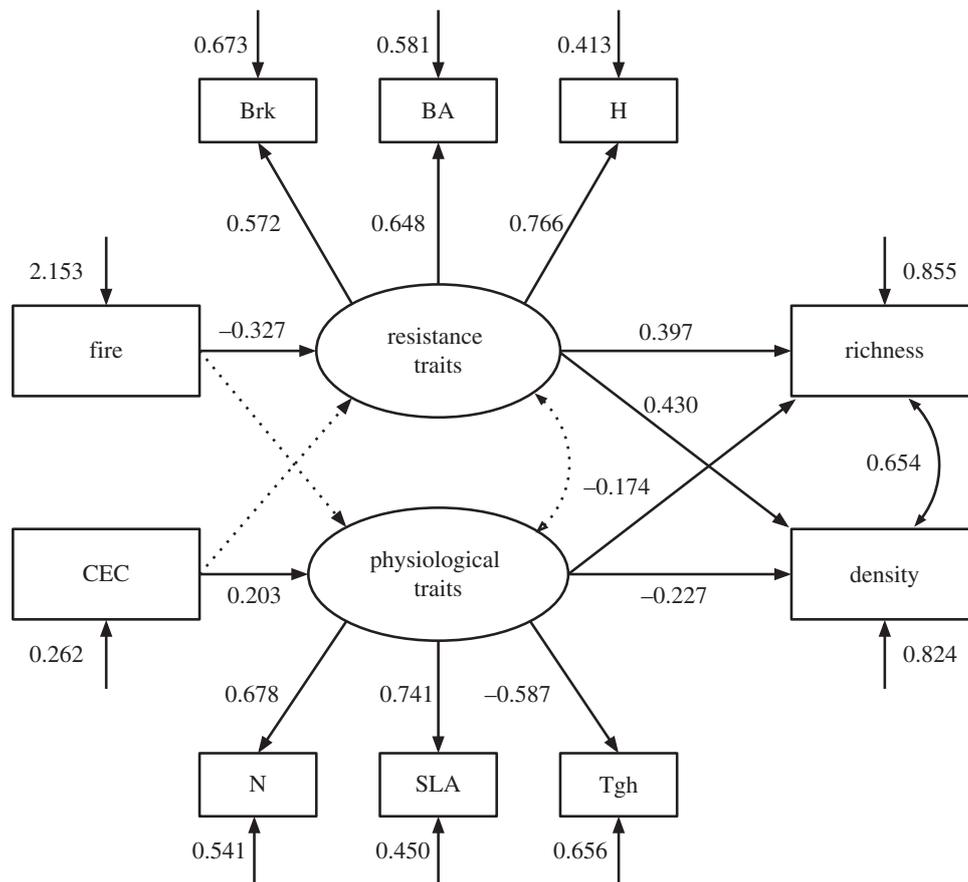
Figure 2. Standardized estimates of the model with best fit to the data ($\chi^2 = 38.284$, d.f. $= 28$, $p = 0.093$). Solid arrows indicate significant paths. Dotted arrows indicate paths not significantly different from 0. See the legend of figure 1 for abbreviations.

physiological traits. Similarly, the path coefficient connecting cation exchange capacity and physiological traits was significant, whereas the estimate of the effect of cation exchange capacity on resistance traits was not. Resistance and physiological traits explained both richness and density.

4. Discussion

Our results offered support to our expectation that separating functional traits into latent variables better representing their functional roles would yield more accurate models of how the environment and traits interact. The structural equation model with one latent variable representing all traits had a poor fit with data, indicating that even if all measured traits are influenced by habitat filtering, different subsets of traits are subjected to different abiotic filters. Furthermore, including subsets of traits as latent factors according to their main role in the interaction between plants and the environment allowed us to accurately represent the importance of different traits for community assembly. Finally, models with latent variables account for the covariance between traits and our imprecision in measuring them, leading to more reliable estimates [14].

Our model corroborated the observation that careful selection of traits has an impact on models of community assembly [11,15]. Instead of simply removing or doing individual statistical analysis for each subset of traits based on their functional roles, we incorporated these roles in the analysis by using latent variables. Indeed, we were able to corroborate that fire did influence resistance traits, as previously described

[9,11], but not physiological traits. Physiological and resistance traits were correlated in the confirmatory factor analysis, although they were not correlated in the structural model, indicating that the inclusion of fire and cation exchange capacity accounted for most of the variation between these latent variables.

We showed that plots that burn less have taller and thicker individuals, with thicker bark, which supports previous findings [6,10]. High numbers of fires led, via the indirect effects of fire on richness and density through resistance traits, to plots with fewer species and individuals, probably owing to recurrent top-killing [16]. Similarly to our results, fire suppression has been shown to result in richer and denser communities [8].

Cation exchange capacity did not influence resistance traits. Physiological traits, on the other hand, were significantly related to cation exchange capacity. Plots with higher fertility had individuals with higher leaf nitrogen content, higher specific leaf area and softer leaves, which, in turn, led to lower richness and density. This plastic response of woody plants might increase competition for light owing to bigger leaves, allowing for fewer species and individuals along a fertility gradient. Previous findings described either positive [7] or non-significant [8,17] relationships between soil nutrient availability and the density and richness of woody plants. However, they did not directly consider the role of different sets of plant traits in these relationships. Thus, our approach also unveiled a novel negative path between soil fertility and the density and richness of woody individuals in the cerrado.

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