

Simulated geographic variations of plant species richness, evenness and abundance using climatic constraints on plant functional diversity

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Abstract

Among the most pronounced large-scale geographic patterns of plant biodiversity are the increase in plant species richness towards the tropics, a more even distribution of the relative abundances of plant species in the tropics, and a nearly log-normal relative abundance distribution. Here we use an individual-based plant diversity model that relates climatic constraints to feasible plant growth strategies to show that all three basic diversity patterns can be predicted merely from the climatic constraints acting upon plant ecophysiological trade-offs. Our model predicts that towards objectively 'harsher' environments, the range of feasible growth strategies resulting in reproductive plants is reduced, thus resulting in lower functional plant species richness. The reduction of evenness is attributed to a more rapid decline in productivity from the most productive to less productive plant growth strategies since the particular setup of the strategy becomes more important in maintaining high productivity in harsher environments. This approach is also able to reproduce the increase in the deviation from a log-normal distribution towards more evenly distributed communities of the tropics. Our results imply that these general biodiversity relationships can be understood primarily by considering the climatic constraints on plant ecophysiological trade-offs.

Keywords: biodiversity, climate, relative abundance distribution, neutral theory

1. Introduction

One of the best established and well documented patterns of global biodiversity is the large-scale gradient of species richness, with a general increase of species richness towards the tropics (Wallace 1878, Currie and Paquin 1987, Barthlott *et al* 1999, Krefl and Jetz 2007). Another well established pattern is the distribution of species within communities, which usually follows a near log-normal distribution of relative abundances of species within communities (Preston 1948, Hubbell 2001, McGill 2003). These two patterns are linked by

the observation that plant species are more evenly abundant in communities towards the tropics, i.e. there is an increase in the evenness of relative abundance towards the tropics (Hubbell 1979, 1997).

Several explanations have been provided to explain these patterns. The large-scale pattern of plant species richness has been attributed to climatic and energetic factors that limit plant functioning (Currie and Paquin 1987, O'Brien 1998). Over the last few years, the neutral theory of biodiversity was able to derive relative abundance distributions under the assumption of functional equivalence of species (Hubbell 1979) and confirm

the model predictions with detailed observations from highly diverse tropical rain forests (Hubbell 1997, Volkov *et al* 2003). This neutral view of biodiversity, however, has not yet been fully reconciled with a view that is based on functional differences in species (Shipley *et al* 2006) and large-scale gradients in biodiversity. Process-based models that link plant ecophysiological processes to their climatic environment (Kleidon and Mooney 2000, Pachepsky *et al* 2001, Reineking *et al* 2006, Schwinning and Ehleringer 2001) provide an alternative approach to understand biodiversity patterns and can help to reconcile these different perspectives.

Here we use such a process-based approach to investigate how these two views can be reconciled. The model we use is an individual-based plant diversity model (Kleidon and Mooney 2000) and is based on the assumption that richness mainly reflects differences in ecophysiological trade-offs and how these are constrained by climate. Different 'species' are represented in this approach by using different plant growth strategies, for instance in terms of its allocation of carbon to plant pools and phenology. This model was previously used to simulate the large-scale geographic distribution of the diversity of plant growth strategies that are successful under given climatic conditions (Kleidon and Mooney 2000) and this simulated pattern of functional diversity matches the observed distribution of plant species richness very well (Barthlott *et al* 1999). Even though not all aspects of plant species richness patterns are necessarily attributable to functional diversity, we take this model here as a reasonable approach to understand plant biodiversity patterns. In order to infer relative abundances from the model, we make the basic assumption that 'size matters'. That is, we assume that plants of higher biomass would generally also be more abundant. This should be a reasonable assumption, especially in forest environments, as larger plants are able to better capture resources. However, some exceptions are possible, for instance in mixed tree-grass ecosystems such as savannas. This simple assumption is used to derive relative abundance estimates and to compute the geographic variation of evenness in the relative abundance distributions.

2. Methods

We use a simulation model of a generic individual plant (Kleidon and Mooney 2000). This model simulates the ecophysiological processes of the plant, such as photosynthesis, respiration, allocation, phenology, and reproduction as well as its life cycle using common, ecophysiological relationships. The environmental conditions of the plant are simulated using a land surface model (Roeckner *et al* 1996) that simulates infiltration, evaporation, root water uptake, and runoff using observed daily climatological forcing of solar and terrestrial radiation, surface temperature and precipitation.

Different species in the model are represented by unique sets of parameters that determine carbon allocation, phenology and other ecophysiological trade-offs. These unique sets are not necessarily synonymous with real-world plant species, so we will refer to these sets of plant growth strategies as a 'proxy'

species in the following for simplicity. A proxy species is taken as successful if an individual plant of that species is able to reproduce itself during its lifetime under the prevalent climatic conditions.

A Monte Carlo approach is used to estimate the range of successful proxy species to obtain a measure for proxy species richness. In this approach, a large, fixed number of randomly assembled parameter combinations are used to generate a pool of potential proxy species. Each proxy species of this pool is tested for success at each grid point of a global grid with a spatial scale of 1.125° longitude and 1.125° latitude that covers all continental land areas except for Greenland and Antarctica. Climatic forcing is taken from the ECMWF reanalysis (Uppala *et al* 2005) for the years 1960–1989. The simulation is run for a period of 100 years to reach a quasi-steady-state. In the simulation, each proxy species is tested in isolation, that is, competition is not explicitly considered. However, the differences in capture of carbon and space between the different species within the community would ultimately be expected to lead to differences in abundance in a competitive environment. Hence, competition is factored into the analysis indirectly as described below in the derivation of the relative abundances.

The geographic variation of proxy species richness is directly taken as the number of proxy species that are successful at any grid point. Note that the richness patterns obtained with our model are always relative to the pool size of tested potential proxy species. Proxy species richness in the following is normalized to the maximum proxy species richness found on the global grid.

We obtain relative abundance estimates from the model by assuming that the relative abundance of the proxy species is proportional to their respective biomass compared to the total biomass of all proxy species at a given location. With the mean simulated biomass $BM(i, j)$ of a given species i at a grid cell j , its relative abundance is calculated as $RABD(i, j) = BM(i, j) / \sum BM(k, j)$ where the sum runs over all proxy species k found at grid cell j .

The relative abundance distributions are averaged over all grid points falling into four ranges of proxy species richness: grid points with low richness ($0 < D < 0.25$ of the maximum simulated richness level) to medium ($0.25 < D < 0.50$), high ($0.50 < D < 0.75$) and very high richness ($0.75 < D < 1.00$), where the richness D is expressed in relation to the maximum value of proxy species richness as mentioned above.

Based on this classification, we also ranked species according to their abundance and their productivity for the four classes.

3. Results

The simulated geographic variation of proxy species richness is shown in figure 1. This simulated map of proxy species richness correlates highly and significantly ($r = 0.84$) with a map derived from observations (Kreft and Jetz 2007).

The associated ranked abundances of proxy species show very clearly that the relative abundance distribution becomes increasingly even with higher richness in the model (figure 2)

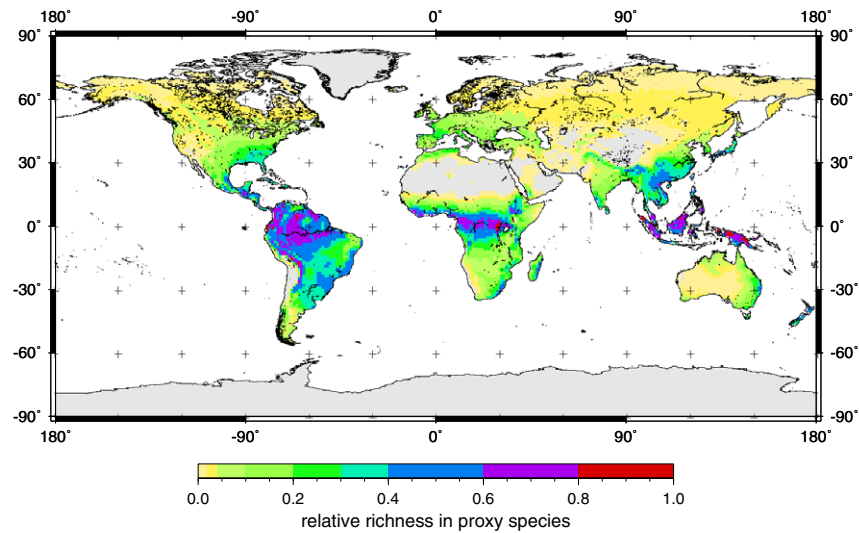


Figure 1. Geographic patterns of the richness of plant growth strategies simulated with a generic, ecophysiology-based plant model forced with present-day climatic conditions. Richness is expressed as a percentage of the maximum value of species richness found in any locality in the model.

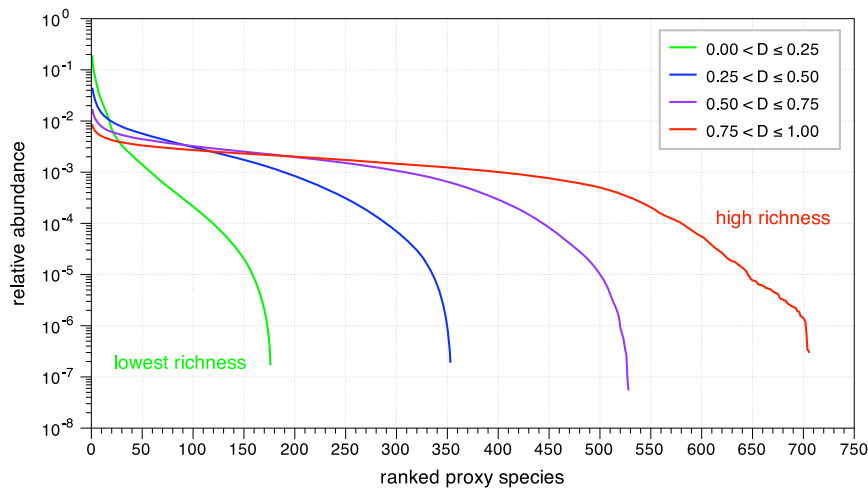


Figure 2. Simulated relative abundance versus proxy species rank for four classes of proxy species richness D . On the x -axis, proxy species are ranked according to their abundance, which in turn is plotted on the y -axis.

even if the effect of richness is removed by normalization from the results (not shown). This trend reproduces qualitatively the observed trend in rank–abundance plots of forests that show a much steeper decline in abundance in boreal forests than in tropical rainforests (Hubbell 1979, 1997).

The mean relative abundance distributions for the four richness classes are close to the common, near log-normal distribution with a noticeable increase in left skewed bias with diversity (figure 3). This left skew means that rare species are greater in number than abundant ones, another commonly observed attribute, especially in tropical rainforests (Hubbell 1997). With increasing levels of proxy species richness, the mean as well as the variance of the relative abundance distribution is successively shifting to lower values. What is surprising about our results is that they are entirely based on climatic conditions and how these constrain plant growth strategies (in combination with the simple, ‘size matters’

assumption of community assemblage). The cause for the patterns should therefore lie mainly in the constraints that the climatic conditions impose on proxy species richness and their relative abundances.

We can understand the results as follows: the pattern of proxy species richness is directly a consequence of increased climatic constraints on the range of feasible plant growth strategies (Kleidon and Mooney 2000). As climate becomes more constraining, in terms of decreasing availability of precipitation, light and temperature, the range of feasible plant growth strategies is increasingly constrained, therefore reducing richness. To understand the decrease in evenness, we ranked proxy species according to their gross primary productivity (per unit area) for the four richness classes (figure 4). This figure shows that in regions with lower richness, the productivity of the less productive proxy species declines much faster than in diverse regions with more

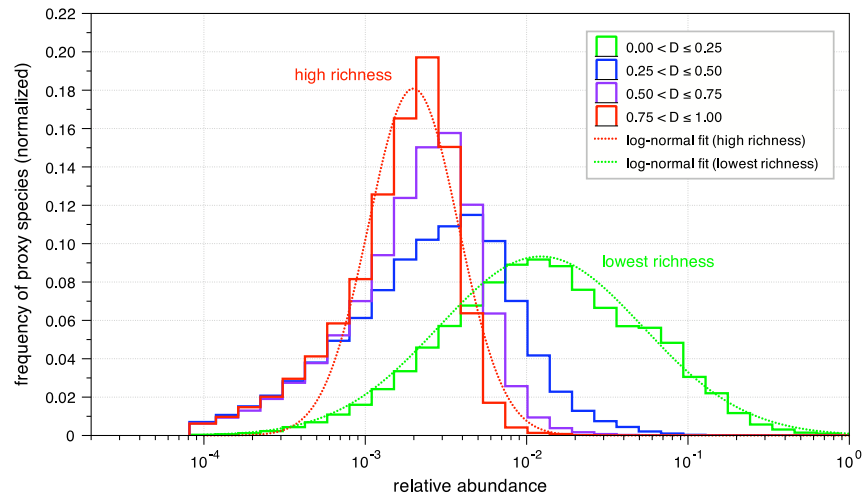


Figure 3. Simulated relative abundance distributions of plant growth strategies for four classes of proxy species richness D . The dotted lines show two log-normal distributions that closely match the respective relative abundance distributions for comparison.

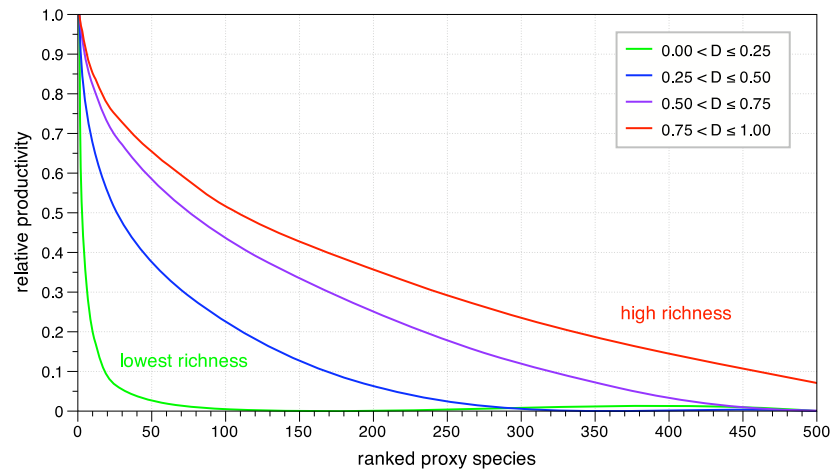


Figure 4. Simulated relative productivity versus proxy species ranked by their productivity for four classes of proxy species richness D . Productivity is expressed relative to the maximum productivity of all proxy species at a given grid point and averaged over all grid points within a given class.

benign climate. This is the direct consequence of the more constraining climate in less diverse regions, which makes the particularities of the plant’s growth strategy more relevant for maintaining high productivity. In the less constraining tropical climates, the productivity of a plant species is less dependent on its strategy. Based on this interpretation, tropical climates should inherently result in more species rich and more evenly distributed plant assemblages.

The class-averaged frequency distributions of the values of the 12 model parameters do not show a clear trend in the restrictions of the traits with lower richness except that the frequency distribution becomes less evenly distributed with lower diversity. This trend is quantified in an average increase in the Shannon entropy of the frequency distributions of the parameters from a value of 0.86 for the lowest richness class to a value of 0.99 for the highest class with a value of unity for a perfectly evenly parameter value distribution. This result suggests that (a) the classification used here may be too coarse to resolve functional restrictions for particular climatic environments in a clear way or that (b) there is no clear

restriction in the range of plant functional diversity, but rather a more fragmented space of feasible parameter combinations. A clarification of this result requires further investigations.

Even though our results suggest climatic constraints as the dominant force that shapes biodiversity patterns, there are clearly some limitations in our approach. For instance, our relative abundance distributions do not include lower limits of minimum population densities that are required to maintain a feasible population of a species. The cutoff value of such a minimum density would affect the left edge of the relative abundance distributions in figures 2 and 3, and thereby affect how close the distribution would be to a log-normal. This aspect would be needed for an adequate comparison of the simulated abundance distributions with observations.

Also, our ‘size matters’ assumption only holds in communities of similar plant sizes. It would unlikely to work in a mixed grass-tree environment where sizes differ substantially, but both plant types show relatively high abundance. Note, however, that our interpretation of the unevenness in the distribution is derived from the model

simulation without any assumptions of abundances and hence the explanation of the geographic variation in evenness should nevertheless hold.

The results suggest that history does not matter much in shaping present large-scale patterns of plant biodiversity. This could be understood as follows: plant species have evolved for sufficiently long time to generate such high levels of functional diversity that the variation in functioning is not limited by evolutionary innovations, but only limited by the imposed environmental constraints on plant ecophysiological functioning. Hence, patterns of species diversity would then be predictable by the relevant environmental constraints on plant functional diversity alone.

4. Conclusions

The results of our model simulations show that the large-scale variations in plant species richness, evenness, and relative abundance distributions can be derived from the assumption that these mainly reflect functional differences in species and the climatic constraints that plants are subjected to. In this light the main reason why the neutral theory and the assumption of functional equivalence (Hubbell 2001) works so well in tropical rainforests is the less constrained climatic environment that—as our results show—is associated with the productivity associated with different plant growth strategies being more evenly balanced. On the other hand, our results support the statistical mechanistic approach that treats the assemblage of plant communities as a constrained, random process (Shipley *et al* 2006, McGill 2006) which relates the relative abundance of each species with how closely its functional traits agree with the community traits. In our approach, we explicitly simulate these relevant constraints as far as these concern large-scale climate variations and how these constrain the range of plant traits, thus being able to predict large-scale geographic patterns of plant biodiversity from climate.

The functional interpretation of these biodiversity relationships has the important implication that it allows biodiversity to play a critical role in Earth system functioning (Tilman 2000) and it sets the foundation to quantify how community compositions and diversity patterns may change under global climatic changes.

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