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The effects of habitat filtering on the phylogenetic structure of the urban flora of Brussels (Belgium)

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Abstract: Community ecologists have become increasingly interested in analyzing the phylogenetic diversity of species assemblages. Species that co-occur in the same habitats often share a common phylogenetic history such that at coarse spatial scales a species assemblage with a locally clustered phylogenetic structure is usually associated with the presence of habitat filtering mechanisms. However, more recently it has been hypothesized that environmental filters act primarily on the relative abundance of species rather than on their simple presences and absences, reducing the species' probabilities to persist in given environmental conditions. This process may produce a non-random distribution of species abundances in the regional phylogeny even in the absence of a locally clustered phylogenetic structure. In this paper, using data from the urban flora of Brussels (Belgium) we tested for the presence of non-randomness in the distribution of abundances among the species phylogenetic structure. We argue that the observed pattern of low species phylogenetic distinctiveness at increasing species abundances is compatible with environmental filtering processes.

Abbreviations: OLS–Ordinary Least Squares, SOF–Species Occupancy Frequency.

Introduction

It is usually assumed that the processes that drive community assembly are highly scale-dependent. At small spatial scales, species coexistence has been typically associated with local processes that promote limiting similarity; at larger scales species assembly is driven mainly by habitat filters, such that species that co-occur in the same habitats often share a similar set of adaptations to the environment, reflected by a shared set of functional traits (Kraft and Ackerly 2010).

Given the strong link between phylogeny and variation in functional traits (Losos 2008), functionally related species are likely to share a common phylogenetic history such that phenotypic attraction (habitat filtering) promotes a phylogenetically clumped assemblage in which co-occurring species that are adapted to similar niches are more related than expected by chance (Cavender-Bares et al. 2009). Therefore, if the assumption that traits exhibit phylogenetic signal is supported, integrating phylogenetic information into the analysis of diversity patterns can help reveal ecological processes that drive species co-occurrence (Cavender-Bares et al. 2009, Kraft and Ackerly 2010). On the other hand, besides its ecological relevance, studying the phylogenetic structure of species assemblages is important per se, for example for the selection of sites to be preserved that maximize future options, like the number of species of medicinal or economic importance (Forest et al. 2007).

In his seminal paper on phylogenetic community ecology, Webb (2000) considered a locally clustered phylogenetic structure as a clear fingerprint of habitat filtering (for a thorough review on this topic, see Vamosi et al. 2009). However, it has been also hypothesized that environmental filters act more on the relative abundance of species, reducing their probabilities to persist in given environmental conditions, rather than on the crude species' presences or absences (Ricotta et al. 2008, de Bello et al. 2011). For instance, species that occur as dominants or subordinates in more favorable ecological conditions may be occasionally recruited into 'unsuitable' ecosystems as a consequence of their dispersal across the landscape, while other species may persist in unfavorable habitats as a legacy of former more suitable conditions (Grime 1998).

This effect may lead to a non-random species distribution of abundances in the regional phylogeny even in the absence of a locally clustered phylogenetic structure. On the other hand, as shown by Hardy (2008), non randomness in the distribution of species abundances across the phylogeny is not necessarily caused by environmental filtering. In this paper, using data from the urban flora of Brussels (Belgium), we will show that the observed presence of a non-random distribution of abundances in the regional phylogeny is compatible with habitat filtering mechanisms.

Materials and methods

Study area

The city of Brussels covers an area of roughly 161 km^2 and hosts approximately 1 million inhabitants. The climate is temperate with mean annual temperature of 9.9°C and mean annual rainfall of 798 mm. The flora of Brussels was comprehensively surveyed from 1992 to 1994 (IBGE 1999). For sampling the urban flora, a systematic grid composed of 159 grid cells of 1 km^2 that are included in the administrative limits of the city for at least 75% was used. Within each of these cells all spontaneous seed species were recorded systematically avoiding planted species. Except private gardens, the whole city area has been prospected, including managed areas (e.g., parks and lawns). In order to avoid undersampling because of the seasonal variation, each cell was surveyed twice along the growing season (early spring and summer or early autumn). This census recorded 670 angiosperms and only one gymnosperm (*Taxus baccata)*, which was excluded from subsequent analysis (Godefroid 2001).

Phylogenetic tree construction

We constructed a time-calibrated phylogenetic tree for the seed plants of Brussels using the Phylomatic online software; a tool for the construction of phylogenetic relationships among taxa freely available at http://www.phylodiversity.net/phylomatic (Webb and Donoghue 2005). One well-known shortcoming of Phylomatic is that the output phylogenetic tree usually contains many polytomies below the family level (Swenson 2009). Due to this lack of resolution, information on the phylogenetic organization of species assemblages is inevitably lost. Nonetheless, Phylomatic is virtually the sole freely available operational tool that enables ecologists to reconstruct a meaningful time-calibrated phylogeny for large species assemblages, while, to the best of our knowledge, none of the more sophisticated methods of phylogenetic reconstruction are able to provide time-calibrated phylogenies for large and taxonomically heterogeneous numbers of species. Rather, they have been usually applied to selected taxonomic groups (e.g., Buerki et al. 2011) or for selected growth forms like trees (e.g., Kress et al. 2010). Accordingly, although Phylomatic is only a 'suboptimal' tool for the integration of phylogenetic information into studies of community ecology, since in this paper all analyses are based on the same phylogenetic tree, they are cross-interpretable, and internally unbiased. Overall, the accuracy of our analyses will increase as more resolved plant phylogenies are produced.

Testing for non-randomness in the distribution of abundances within the phylogeny

To test for non-randomness in the distribution of abundances in the species phylogenetic structure, we first computed the phylogenetic distinctiveness of all species as the mean phylogenetic distance separating each species from all other species in the urban flora (Warwick and Clarke 2001), where the phylogenetic distance between two species is the total branch length separating those species along the aged phylogenetic tree. For an aged ultrametric tree, this will be twice the time since divergence from the most recent common ancestor (branch length from species 1 to the most recent common ancestor plus branch length from the most recent common ancestor to species 2). Next, we used quantile regressions for analyzing the occupancy frequencies of the Brussels species in the sampling grid as a function of their phylogenetic distinctiveness. Our working hypothesis is that, if habitat filtering plays a role in driving the distribution of abundances in the Brussels phylogeny, frequent species will show on average a lower phylogenetic distinctiveness than less frequent ones. This is because, under the assumption of phylogenetic signal, frequent species that are on average better adapted to the ecological conditions of the urban environment as compared to the rarest species will be also phylogenetically closer to each other, giving rise to a negative relationship between the species abundances and their phylogenetic distinctiveness (Ricotta et al. 2008).

Although a number of different definitions of species commonness and rarity can be found in the ecological literature (for a review, see Gaston 1994), in this paper, we equate species commonness with the species occupancy frequencies (SOFs) in the sampled grid cells. This approach is particularly adequate at coarse spatial scales where data on species abundances are usually unknown. Also, for our scope, the comparison of species abundances is largely meaningless between individuals with different growth forms such as herbs and trees, while the species coarse-scale spatial distribution may be reasonably assumed as an estimator of their ability to spread through the study area. According to Ricotta et al. (2008), the occupancy frequency distribution of the seed plants of Brussels is unimodal with a few common species and many rare ones.

Quantile regression seeks to complement classical linear regression analysis by estimating all parts of the response distribution conditional on the predictor variable, thus providing a more comprehensive characterization of the effects than those provided by estimates of the conditional mean as made with ordinary least squares (OLS) regression. In ecology, quantile regression has been used for discovering relationships between variables in cases where the complexity of interactions between different factors leads to data with unequal variation of one variable for different ranges of another variable (Cade and Noon 2003). Quantile-based fitting gives different weights to positive and negative residuals, leading to an asymmetric minimization. Let $\{\rho_1, \rho_2, \ldots, \rho_n\}$ denote the values of the response variable within the scatter plot of the occupancy frequencies of all urban species in the sampled grid as a function of their phylogenetic distinctiveness. OLS regression minimizes residuals by solving

$$residual = \min \sum (\rho_i - \hat{\rho}_i)^2 \qquad (1)$$

where $\hat{\rho}_i$ is the estimated value for each ρ_i. Quantile regression gives different weights to positive and negative residuals and considers absolute rather than squared residuals, such that

$$residual = \min \sum |\rho_i - \hat{\rho}_i| T \qquad (2)$$

where T is a multiplier term that is equal to τ (the quantile value) for positive deviations (i.e., $(\rho_i - \hat{\rho}_i) > 0$) and to $1 - \tau$ for negative deviations. This asymmetric minimization fits a regression model through the upper tail of the response distribution for $\tau > 0.5$ and through the lower tail of the distribution for $\tau < 0.5$. For $\tau = 0.5$ we obtain the median regression, which can be used as a central regression line similar to the mean regression estimated with OLS regression. In this paper, to look for non-random patterns in the distribution of species abundances as a function of their phylogeny, quantile values $\tau = 0.90$, 0.75, 0.50, 0.25 and 0.10 were considered. We used the 'quantreg' package of R-software (Koenker 2009). Statistical significance for quantile regression estimates was tested using the bootstrap test procedure implemented into the R package (R development Core Team, 2012).

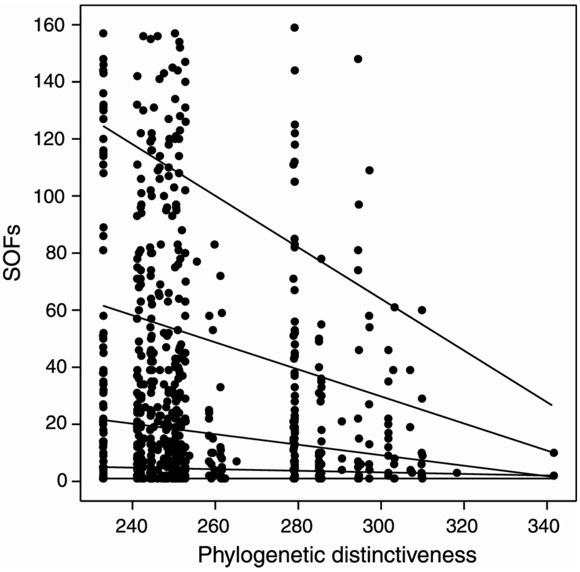

Figure 1. Plot of the species occupancy frequencies (SOFs) of the urban plants of Brussels versus their phylogenetic distinctiveness (Myr). Results of the quantile regressions with four different quantile values (from upper to lower lines) are: $\tau = 0.90$ ($s = -0.90^*$), $\tau = 0.75$ ($s = -0.47^*$), $\tau = 0.50$ ($s = -0.18^*$), $\tau = 0.25$ ($s = -0.03$), $\tau = 0.10$ ($s < -0.01$). * = significant at $p < 0.05$ (two-tailed test); s = slope.

Results

The results of the quantile regressions of the occupancy frequencies of the Brussels species as a function of their phylogenetic distinctiveness are shown in Figure 1. Overall, the roughly triangular shape of the plot in Figure 1 together with the negative slopes of the regression lines provide evidence for non-randomness in the distribution of SOFs within the Brussels phylogeny. The left portion of Figure 1 is mainly composed of species belonging to the most frequent eudicot families, like Asteraceae, or Brassicaceae, while the right portion includes the more phylogenetically distinct monocot species together with species of the orders Ranunculales or Nymphaeales.

In this view, the steeper regression slopes associated with the highest quantile values indicate that for the most abundant species, the values of SOFs decrease more rapidly with increasing phylogenetic distinctiveness when compared to the corresponding median ($\tau = 0.50$). For $\tau = 0.25$ and $\tau = 0.10$ the regression lines are not significant meaning that for rare species phylogenetic distinctiveness does not significantly influence their occupancy frequency. That is, irrespective of the species' higher taxonomic ranks (i.e., families, orders, etc.), non-randomness in the species distribution of abundances is more evident for abundant species than for rarer ones.

Discussion

Species differ in their ecological requirements, thus being able to colonize different habitats. At the scale of our analysis where plant-to-plant competitive interactions become irrelevant, such ecological differentiation among species emphasizes the role of environmental constraints that filter the species that can persist within a given habitat on the basis of their tolerance of the abiotic environment (Cavender-Bares et al. 2009). In this paper, we hypothesize that these filters may produce a non-random species distribution of abundances in the regional phylogeny looking like that in Figure 1.

In principle, as highlighted by Hardy (2008) this latter phylogenetic pattern could be caused by a number of biogeographical processes that occur outside the focal species assemblage. However, in our case, the observed relationship of low species phylogenetic distinctiveness at increasing species occupancy frequencies speaks in favor of abiotic controls that tend to limit the species' tolerance to environmental constraints within certain limits. In this view, urban environments constitute an appropriate biological model for testing the effects of environmental filtering on the species phylogenetic structure (Ricotta et al. 2009, 2010). Compared to their rural surroundings, urban areas have higher air temperatures, a high proportion of surface runoff that increases the aridity of most urban habitats, and a high alkalinity of soils, which are usually affected by adjacent concrete and other lime-based materials (Sukopp 2004, Godefroid and Koedam 2007, Godefroid et al. 2007). As a consequence, urban flora is

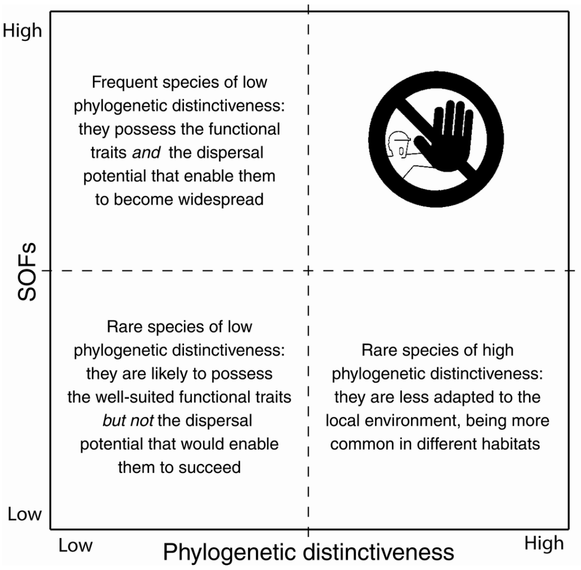

Figure 2. Simple schematic framework to relate the distribution of species abundances to their phylogenetic distinctiveness. Both axes are on arbitrary scales. According to our data, species with high phylogenetic distinctiveness and high SOF values (i.e., the species in the upper-right portion of the graph) are quite uncommon (see Fig. 1).

mainly composed of closely related species that are functionally similar and able to deal with urbanization (Knapp et al. 2008). For the specific case of Brussels, the strong environmental drivers on the species spatial distribution were already investigated by Godefroid (2001), Godefroid et al. (2007) and Godefroid and Koedam (2007), and the reader is addressed to these papers for additional details.

In this framework, although our results are limited to the urban flora of Brussels, we believe that the observed nonrandom species distribution of SOFs in the regional phylogeny with common species being significantly less phylogenetically distinct than rare species, could represent an emergent pattern of any plant assemblage that is shaped by more or less intense environmental filtering mechanisms. The hypothetical schematic framework of Fig. 2 can be used to propose a temptative description of the biological mechanisms that drive the distribution of species abundances as a function of their phylogenetic distinctiveness. Under the assumption of phylogenetic signal, ecological similarity between species is related to phylogenetic relatedness, such that the species that share the functional traits that enable them to succeed in a given habitat are more likely to be phylogenetically close to each other. Accordingly, most of the common species that shape the urban matrix have quite low values of phylogenetic distinctiveness.

To the contrary, rarer species of low SOF values represent a highly heterogeneous set of species of more diverse origin. Some of them (the lower-left portion of Figure 2) could be highly adapted to the environmental conditions of urban habitats; they might just lack the dispersal potential that promote the spread of the more common species. Some other species (the lower-right portion of Fig. 2) like e.g., the Nymphaeales, which are often aquatic species, may be less adapted to the local environment, being more common in habitats that are subject to different abiotic conditions (Grime 1998). This might explain the lack of significance for the relationships between phylogenetic distinctiveness and SOFs at low quantile values (i.e., for $\tau < 0.50$). As suggested by Grime (1998), the high phylogenetic distinctiveness of rare species implies a high chance that, in the case of changing environmental conditions (e.g., habitat disturbance), there will already be a sufficient number of species with variable functional traits, some of which may be capable of exploiting the new conditions. Likewise, from a conservation viewpoint, given their high taxonomic heterogeneity, the protection of rare species is a central issue for preserving high levels of (urban) diversity.

To conclude, this paper is part of a growing body of evidence demonstrating the complex interactions between environmental conditions and evolutionary relationships among co-occurring species. In this view, we hope our findings will give some insight into the role of rare and common species in regulating species co-occurrence and their driving factors.

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