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ORIGINAL ARTICLE

Limited evidence of local phylogenetic clustering in the urban flora of Brussels

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Abstract
As species functioning is not randomly distributed with respect to phylogeny, we should expect that species assemblages, which are subject to the same environmental filters, often possess a clustered phylogenetic structure. This locally clustered phylogenetic structure is usually detected with randomization tests. In this paper we apply a test of community phylogenetic clustering that takes into account the non-random distribution of species frequency across the phylogeny of the urban flora of Brussels (Belgium). Our results provide only moderate support to the idea that a locally clustered phylogenetic structure is central to the coarse-scale patterns of species co-occurrence of this urban area. The abiotic drivers that promote a locally clustered phylogeny in cities like Brussels are also shortly discussed.

Keywords: *Built up area, habitat filters, indicator species, null model, randomization tests, regional species pool, species richness*

Introduction

The search for a general mechanism that regulates the assemblage of local communities from the available species pool is a fundamental objective of ecology. At small spatial scales such assembly has been typically associated with local processes that promote limiting similarity; at scales encompassing large environmental heterogeneity community assembly is driven mainly by abiotic controls (habitat filters) that select for species with similar environmental requirements, reflected by a shared set of functional traits (Weiher & Keddy 1995; Kraft & Ackerly 2010).

Under the assumption that closely related species are more functionally similar than more distant ones, habitat filtering is likely to promote a phylogenetically aggregated assemblage in which co-occurring species are more related than expected by chance (Webb et al. 2002; Cavender-Bares et al. 2009). Therefore, whenever the species phylogenetic dispersion within a local assemblage reflects its functional dispersion, integrating phylogenetic information into the analysis of community diversity can help reveal how local communities are assembled (Webb et al. 2002; Diez et al. 2008; Cavender-Bares et al. 2009; Kraft & Ackerly 2010). In some cases, phylogenetic differences among species may mirror ecosystem functioning better than measuring traits directly (Cadotte et al. 2009), although, in presence of strong evolutionary convergence, information on species functioning cannot be directly predicted by the underlying phylogeny (Nipperess et al. 2010; Pausas & Verdu 2010).

Information about the impact of habitat filters on community composition is usually obtained from randomization tests of species distribution against null models (Hardy 2008; Thompson et al. 2010). In his seminal paper on phylogenetic community ecology, Webb (2000) considered a higher degree of phylogenetic clustering in local communities as compared to the available regional species pool as a

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clear fingerprint of habitat filtering (for a thorough review on this topic, see Vamosi et al. 2009). However, defining an adequate null model for the specific hypothesis to be tested is not obvious because slightly different randomization procedures may imply considerably different null hypotheses and the selection of inadequate null models may lead to misleading conclusions on the ecological hypothesis tested (Gotelli 2000). For instance, it has been recently hypothesized that environmental filters also act on the regional species pool, reducing the probabilities of certain species to persist in given environmental conditions. As shown by Ricotta et al. (2012b), the effects of strong abiotic drivers lead to a non-random distribution of species frequencies in the regional pool with common species being significantly less phylogenetically distinct than rare species. This is because common species that shape the community matrix and experience similar environmental conditions are likely to be more phylogenetically related than less frequent species (Ricotta et al. 2008).

This imbalance in the distribution of species frequencies is not without consequences. As shown by Hardy (2008), when species frequencies are non-randomly distributed in the regional phylogeny, traditional tests of phylogenetic clustering within local communities become overly liberal (i.e. the test has an increased rate of false positives). Therefore, when testing for phylogenetic clustering in local assemblages, we need to consider the non-random distribution of species frequencies in the regional phylogeny. In this paper, we apply a test of phylogenetic clustering within local communities, which takes into account the potential phylogenetic imbalance in the regional distribution of species frequencies. Applying this test on data from the urban flora of Brussels (Belgium) sampled within a systematic grid of 159 square cells of 1 km^2 in size, we show that the presence of a locally clustered phylogenetic structure appears less ubiquitous than commonly thought. The ecological drivers that structure plant species composition within the cells that show a locally clustered phylogeny are also shortly discussed.

Materials and methods

Study area and sampling

Brussels covers an area of 161 km^2 in the centre of Belgium and hosts approximately 1 million inhabitants. The city has developed in the relatively broad Senne valley. The altitude varies between 15 and 120 m a.s.l. Soils are in general silty and sandy-silty. The valley bottoms comprise silty alluvium derived from erosion. Various wetlands, which have never been altered, still have interesting gley soils. The soil of the vast area of forest (it occupies 10% of the city) has not been disturbed for 10,000 years. All these soils are prone to compaction and erosion due to recreation activities. They are also often disturbed by the deposition of rubble, rubbish and various other kinds of exogenous substrates. Brussels is characterized by a temperate, mild and humid climate, resulting from two influences: the maritime climate of Flanders and the continental climate of the Ardennes. As a result the winters are mild, there is little difference between the seasons and the rainfall is relatively evenly spread throughout the years. The mean annual temperature is 9.9°C; mean annual precipitation is 835 mm. The period without frost lasts 194 days. The vegetation period (when temperature >10°C) is 172 days.

From a structural viewpoint, Brussels is composed of four concentric zones that significantly affect urban plant species distribution: (i) the core, which is dominated by commercial and administrative activities, (ii) the densely built-up residential districts built in the last century, (iii) a less densely built-up periphery and (iv) the suburbs that can be considered as the peak demographic growth zone, although they still keep a significant amount of rural enclosures (Godefroid & Koedam 2007). Brussels has six distinctive features that differentiate it from other big cities (Godefroid 2011): (1) a substantial part of the biggest forest of North Belgium (1660 ha out of 4400 ha of the famous Sonian Forest); (2) about a hundred small woodlands and parks; (3) numerous water bodies; (4) various wastelands; (5) a canal and a harbor and (6) numerous protected semi-natural areas.

The flora of the whole city was surveyed from 1992 to 1994 using a systematic grid composed of 159 grid cells of 1 km^2 that fall within the administrative limits of the city for at least 75% of their area. Within each of these cells, all spontaneous seed plants were recorded with the exception of those species that were obviously planted or garden escaped. Except private gardens, the whole city area has been prospected, including managed areas (e.g. parks and lawns; Godefroid 2001). 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 as this phylogenetically distant species may bias the results considerably.

Phylogenetic tree construction

For the 670 angiosperm species of Brussels we constructed a time-calibrated phylogenetic tree using

the Phylomatic software (Webb & Donoghue 2005), a freely available tool for the construction of phylogenetic relationships among taxa. According to Faith (1992), branch lengths may be interpreted in terms of number of features, where a feature means an evolutionarily conserved trait. When the edges of the evolutionary tree are measured by supposed molecular changes, as in a cladistic analysis, branch lengths are directly related to feature richness. On the other hand, using a time-calibrated tree as a reference, the distances are temporal rather than evolutionary. In this case, it is generally assumed that feature richness is a direct function of branch length (Nipperess et al. 2010).

Although the phylogenetic tree constructed by Phylomatic contains many polytomies below the family level, to the best of our knowledge, it is the sole operational tool that enables ecologists to reconstruct a meaningful time-calibrated community phylogeny for large and taxonomically heterogeneous species assemblages. Accordingly, we consider it an acceptable, even though suboptimal, tool for the integration of phylogenetic data into studies of community diversity (see Ricotta et al. 2012a). In addition, all analyses in this paper are based on the same phylogenetic tree; therefore they are cross-interpretable and internally unbiased. Overall, the accuracy of the many studies on phylogenetic community ecology will increase with the availability of more resolved plant phylogenies.

Testing for a locally clustered phylogenetic structure of species

We defined the 670 species of the Brussels flora as the available regional species pool, from which the communities in each grid cell were assembled. To test for local phylogenetic clustering in the 159 grid cells of the Brussels flora, we first calculated the phylogenetic diversity of each cell as the mean pairwise phylogenetic distance between all species sampled within the cell. The phylogenetic distance between two species is the total branch length separating those species along the phylogenetic tree. For a time-calibrated ultrametric tree, this will be twice the time since divergence from the most recent common ancestor.

We next compared the phylogenetic diversity of each cell with the diversity expected if species were drawn randomly and without replacement from the available species pool. We used two null distributions of expected diversity values. In the first null model, the random communities were constructed keeping the probability of selecting a given species from the urban species pool equal for each species (null model R1). However, previous work of Ricotta et al. (2008, 2012b, figure 1) showed that the distribution of species frequencies among the urban phylogeny are non-randomly distributed with the species of high phylogenetic distinctiveness (i.e. a measure of the species mean phylogenetic distance from the other species in the assemblage; Warwick & Clarke 2001) being on average less abundant than species of low phylogenetic distinctiveness.

This phylogenetic imbalance in the species frequencies will potentially reduce the power of traditional tests of community phylogenetic clustering in rejecting the null hypothesis when the null hypothesis is improbable enough to be rejected. Therefore, we also used a second null model that accounts for the species rarity and commonness *sensu* Ricotta et al. (2008, 2012b). In R2, the probability of selecting a given species from the available pool is proportional to its frequency in the 159 grid cells (i.e. to the number of cells in which the species is present; null model R2). Accordingly, common species have higher probabilities to be included in the random species assemblages than rare species of low occupancy frequencies in the sampling grid. The same null model R2 was also used by Kraft and Ackerly (2010) for testing for habitat filtering in an Amazonian forest and by Thompson et al. (2010) for testing for limiting similarity in a roadside plant community in England, while Hardy (2008) proposed instead to permute "species with similar abundances among the tips of the phylogenetic tree". However, this procedure raises the problem of asking when are species abundances similar to each other, and this question is not necessarily easy to answer (see Ricotta et al. 2008).

For constructing both null distributions of expected phylogenetic diversity, 999 random species assemblages were generated for each cell by keeping the number of species of each random assemblage equal to the actual species richness of the corresponding cell. All randomizations were performed using the program "TreeCreeper" freely available for download at http://www.ecoap.unina.it/doc/publications.htm. *P*-values (one-tailed test) were then computed as the proportion of random values that was as low or lower than the actual phylogenetic diversity of each cell.

A critical point of this procedure is that when testing for interactions between a local species pool (i.e. the species in single 1-km^2 cells) and the corresponding regional species pool (i.e. the whole urban flora, which is the hypothetical reservoir of species that are potentially able to colonize the local community), it is of crucial importance to determine the number of species in the regional pool accurately (Dupré 2000). A number of authors (e.g. Dupré 2000; Gerhold et al. 2008) calculated the size of the regional species pool for a local community as the number of species in the regional flora that share the ecological niche position of the species constituting

the local community based on similar values of the Ellenberg ecological indicators (see Ellenberg et al. 1991). However, this way of estimating the size of the regional species pool may give rise to a circular reasoning: we cannot investigate the impact of local environmental constraints on community assembly if the species of the regional pool are selected based on their ecological affinity to the local community. For this reason, we think it is more prudent to include the entire urban flora in the regional species pool as was done by Ricotta et al. (2008), although this definition of the regional pool implicitly assumes the same ability for all species to gain access to local sites (i.e. according to this definition we assume all species in the urban flora have the same dispersal ability), which is not always the case. Differences in the proportion of built-up area and species richness between the cells that show significant local phylogenetic clustering according to null model R2 and the remaining cells were investigated with a traditional Student's *t*-test. We also used a randomization test in which, for each variable, the difference between the mean values of the two groups of cells is tested against a null model of random attribution of all cells to both groups.

Finally, to explore which species are typically found in those cells, we used indicator species analysis (see Dufrêne & Legendre 1997). Here, indicator species are defined as those species that are more common in the cells with a locally clustered phylogeny than expected from a random null model in which all cells have equal probability to host each species, irrespective of the species ecological characters. Accordingly, the number of presences of all species in the selected cells was compared with the corresponding null distributions obtained from 999 permutations of the species presences within the cells. Only those species having a frequency higher than 5% in the whole sampling grid have been used for this analysis.

Results

When testing for local phylogenetic clustering without constraints on the species rarity and commonness (i.e. with null model R1), our results show that in 124 cells out of 159 the expected phylogenetic diversity is significantly larger than the one computed from the actual species assemblage ($p < 0.05$). That is, on average, species in local communities are recognized as phylogenetically closer to each other than in random assemblages, rejecting the null hypothesis that the species composition of local communities is a random subset of the regional species pool. By contrast, when the same test is run keeping the probability of selecting a given species proportional to its occurrence in the sampling grid (null model R2), the null hypothesis that the local phylogeny is a random subset of the regional phylogeny is rejected 60 times out of 159 ($p < 0.05$).

Overall, significant phylogenetic clustering is associated with a higher proportion of built up area ($t = 2.546$, $p < 0.05$) and a lower species richness ($t = 2.644$, $p < 0.05$; Figure 1). Both randomization

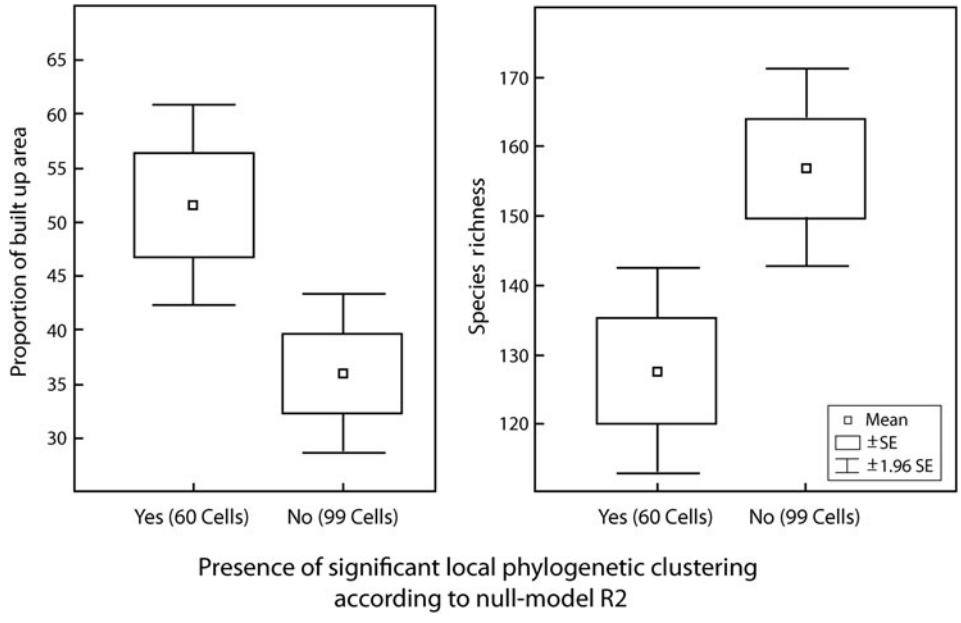

Figure 1. Box plots of the proportion of built up area and species richness in each cell for the 60 cells that show significant local phylogenetic clustering according to null model R2 (Yes) and for the remaining 99 cells (No). For built up area $t = 2.546$, $p < 0.05$; for species richness $t = 2.644$, $p < 0.05$.

Table I. Indicator species for the 60 cells that show a significantly clustered phylogeny according to null model R2.

Indicator species	Number of presences in the whole sampling grid	Expected number of presences in the selected cells	Actual number of presences in the selected cells	*P*-values
Ailanthus altissima	19	7.143	11	0.046
Amaranthus retroflexus	12	4.461	10	0.002
Armoracia rusticana	13	4.852	9	0.015
Asparagus officinalis	17	6.467	11	0.022
Ballota nigra	29	11.062	20	0.002
Berteroa incana	18	6.844	14	0.003
Bromus tectorum	11	4.127	8	0.013
Chenopodium album	121	45.668	54	0.002
Conyza canadensis	132	49.819	59	0.001
Daucus carota	107	40.414	51	0.001
Diplotaxis tenuifolia	21	8.007	13	0.012
Echinochloa crus-galli	48	17.945	24	0.022
Echium vulgare	10	3.812	7	0.038
Galinsoga ciliata	116	43.598	51	0.003
Galinsoga parviflora	34	12.856	18	0.036
Herniaria glabra	10	3.73	8	0.009
Lactuca serriola	89	33.363	46	0.001
Lathyrus latifolius	31	11.701	17	0.024
Lepidium ruderale	57	21.437	29	0.013
Lepidium virginicum	20	7.606	13	0.009
Matricaria maritima	120	45.251	51	0.022
Melilotus albus	80	30.111	42	0.001
Melilotus officinalis	39	14.798	20	0.041
Mercurialis annua	120	45.182	56	0.001
Oenothera parviflora	47	17.791	26	0.001
Papaver rhoeas	58	21.84	28	0.031
Pastinaca sativa	11	4.149	8	0.015
Picris hieracioides	58	21.847	33	0.001
Polygonum aviculare	140	52.898	58	0.009
Polygonum persicaria	131	49.524	56	0.006
Reseda lutea	30	11.42	17	0.010
Reseda luteola	20	7.537	13	0.008
Sagina procumbens	134	50.571	57	0.003
Senecio inaequidens	27	10.158	21	0.001
Senecio viscosus	47	17.794	29	0.001
Senecio vulgaris	144	54.452	60	0.001
Silene latifolia	41	15.64	22	0.023
Sisymbrium altissimum	19	7.191	12	0.014
Solanum nigrum	96	36.358	51	0.001
Sonchus oleraceus	131	49.492	56	0.004
Tragopogon pratensis	32	11.992	17	0.033
Verbascum thapsus	24	8.972	14	0.019
Vicia villosa	9	3.406	7	0.018
Viola arvensis	20	7.59	12	0.027

Notes: The table shows the number of species presences in the whole sampling grid, the number of expected presences in the selected cells (mean of 999 randomizations plus the actual value), the actual number of presences in the selected cells and the associated *p*-values (one-tailed test; $p < 0.05$). Species nomenclature follows Lambinon et al. (2004).

tests also show significant differences in species richness and the proportion of built up area between both groups ($p < 0.05$). The indicator species that are significantly associated to the cells with a locally clustered phylogeny are shown in Table I.

Discussion

Species differ in their ecological requirements necessary for the presence and maintenance of their populations (e.g. Mattana et al. 2012; Simões et al. 2012). Such ecological differentiation among species highlights the role of environmental constraints that filter the species that can persist within a given habitat and are able to grow and reproduce under the prevailing abiotic conditions (Webb et al. 2002; Thompson et al. 2010). Nonetheless, our results provide only moderate support for the idea that abiotic constraints are central to the local assembly of this urban plant community. For instance, once species have passed through a coarse-scale habitat filter (i.e. they are able to survive in urban

environments) in 99 cells out of 159, species appear to be assembled into local communities at random.

However, in the remaining 60 cells we observe a clustered phylogenetic structure in response to locally specific environmental constraints. That is, in more than one third of the sampling grid, locally intense abiotic drivers lead to an increased level of phenotypic attraction for which locally co-occurring species are more phylogenetically related than expected from a random null model in which the effects of the non-random distribution of species frequencies in the whole urban phylogeny are already included. Failing to account for differences in the species commonness severely biases our results. As expected, in our Brussels example, null model R1 will inevitably lead to overly liberal results. This is because, if during the randomization process all species have the same a priori selection probability, rare species with low occupancy frequencies and high phylogenetic distinctiveness are more likely to be selected than common species, thus increasing the rate of Type I error (Hardy 2008).

As shown by our results, there is a positive relationship between the presence of a locally clustered phylogeny and the proportion of build up area. According to Godefroid (2001) and Godefroid and Koedam (2007), in Brussels densely built up areas are associated with higher temperatures (as inferred by the Ellenberg temperature index), a high proportion of surface runoff that increases the aridity of such areas and a high alkalinity of soils, which are usually enriched with construction rubble (mainly concrete and other lime-based materials; Sukopp 2004). Therefore, due to high levels of disturbance and stress, together with a generalized lack of open grounds, like private gardens, parks or small remnants of more natural vegetation, densely built-up areas are usually associated to reduced species richness (Kent et al. 1999). As a result, the indicator species in Table I, like *Conyza canadensis*, *Mercurialis annua*, *Polygonum aviculare*, *P. persicaria*, *Sagina procumbens*, *Senecio vulgaris* or *Sonchus oleraceus* to mention just the most abundant ones, usually belong to the ecological group of urbanophile species (species having a strong affinity towards urban areas; Politi Bertoncini et al. 2012). Most of these species share traits that allow them to survive in highly disturbed and fragmented urban environments, like competitiveness, ruderalness, annual life cycle, mass production of propagules and efficient dispersal mechanisms (see Godefroid & Koedam 2007; Knapp et al. 2008a, 2008b).

To conclude, we can say that, because of their strong abiotic drivers, urban areas constitute an ideal biological model for testing the effects of environmental filtering on plant communities. However, when analyzing the phylogenetic structure of species assemblages, the use of adequate null models for which the statistical assumptions match the underlying biological processes is of crucial importance for getting meaningful insight into the mechanisms that shape community assembly and their driving factors. Also, while many studies consider urban areas as homogeneous units, the urban matrix represents a highly variable multidimensional system and various types of built-up areas have different effects on environmental conditions, ecological processes and local species pools (Roy et al. 1999). Therefore, we hope our findings will shed some insight into the complex interactions between environmental conditions and evolutionary relationships among co-occurring urban plant species.

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