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BIODIVERSITY RESEARCH

Common species have lower taxonomic diversity

Evidence from the urban floras of Brussels and Rome

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ABSTRACT

The species pool hypothesis claims that the large-scale regional species pool is the chief parameter in determining small-scale species richness through filtering of species that can persist within a community on the basis of their tolerance of the abiotic environment. Accordingly, different environmental conditions give rise to different species assemblages. From a taxonomic perspective, under the assumption of trait conservatism, co-occurring species that experience similar environmental conditions are likely to be more taxonomically similar than ecologically distant species. The next step consists in understanding how commonness and rarity of individual species produce the observed taxonomic diversity. In this paper, the importance of environmental filtering in regulating the taxonomic structure of rare and common plant species in the urban floras of Brussels (Belgium) and Rome (Italy) is tested. First, we computed the taxonomic diversity of the rare and common species of Brussels and Rome based on the branching topology of the Linnaean taxonomic trees. Next, using a randomization procedure, we determined whether the taxonomic diversity of the rare species was significantly higher than the diversity of the common species. Results show that, for both urban floras, common species that shape the community matrix and experience similar environmental conditions have a taxonomic diversity that is significantly lower than that of the rare species that represent a relatively incidental set of species of more 'disperse' origin. Finally, from a conservation/management perspective our results imply that, given their high taxonomic heterogeneity, the protection of rare species is a central issue for preserving high levels of diversity in urban areas.

Keywords
Core-satellite species model, dominant-subordinate-transient species model, randomization, species pool hypothesis, taxonomic relatedness, urban ecology.

INTRODUCTION

One of the fundamental objectives of ecology is the search for the general mechanisms that control the spatio-temporal pattern of species coexistence. On longer temporal scales, historical contingency and phylogenetic processes of species diversification play a major role (Ricklefs, 1987; Hugueny *et al.*, 1997; Svenning & Skov, 2004). At smaller temporal scales, several hypotheses have emphasized the crucial importance of local mechanisms avoiding competitive displacement. One group of theories (equilibrium theories) considers the environment as stable and recognizes niche-partitioning mechanisms and local environmental heterogeneity created by individual plants as the determinants of species diversity (Tilman & Pacala, 1993; Bever, 1994; Tilman, 1994; Bonanomi *et al.*, 2005). Another group of theories focuses on non-equilibrium coexistence dynamics (Huston, 1994) related to disturbance (Connell, 1978; Sousa, 1984) and fluctuations of environmental conditions (Chesson, 2000). Reviews in Palmer (1994), Huston (1999), and Wright (2002).

More recently, the species pool hypothesis has been proposed as one of the possible explanations for the local species richness of plant communities (Weiher & Keddy, 1995; Pärtel *et al.*, 1996; Zobel, 1997). The species pool hypothesis claims that the large-scale regional species pool is the chief parameter in determining small-scale species richness through filtering of species that can persist within a community on the basis of their tolerance of the abiotic environment. In a sense, the species pool hypothesis can be considered a coarse-scale analogue of niche partitioning mechanisms.

For instance, in stable environmental conditions, a local community can be considered to be a subset of potential

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community members that constitute the regional species pool (Kraft *et al.*, 2007). How many and which species actually segregate into habitats is controlled by environmental filtering that governs the reaction of species to biotic and abiotic factors (Zobel, 1997; Weiher & Howe, 2003). As a consequence of this filtering process, different environmental conditions give rise to different species assemblages.

From a taxonomic perspective, patterns of community structure can be interpreted using a simple logical framework (Webb *et al.*, 2002; Kraft *et al.*, 2007). When traits of interest are phylogenetically conserved (see Wiens & Graham, 2005), a clumped taxonomic distribution in which co-occurring species are more related than expected by chance indicates that phenotypic attraction (habitat filtering) dominates over repulsion (competitive exclusion). Conversely, when traits of interest are phylogenetically convergent, phenotypic repulsion that limits the ecological similarity of co-occurring species should generate phylogenetic overdispersion (co-occurring species are less related than expected by chance).

On the other hand, if the traits of interest are convergent, phenotypic attraction should generate phylogenetically overdispersed communities, while competition or limiting similarity should produce random (or possibly clustered) patterns of relatedness (Kraft *et al.*, 2007).

Webb (2000) compared the phylogenetic diversity of trees in each of 28 plots in a Bornean rain forest with the diversity expected if species were drawn randomly from the species pool. He found that the species in plots were more phylogenetically related than expected by chance. Ricotta *et al.* (2008) tested the importance of taxonomic filtering in regulating species co-occurrence using data from 15 local species assemblages from the urban flora of Rome, Italy. Their results indicate that in most cases the local species assemblages have a higher degree of taxonomic similarity than species assemblages randomly put together from a larger species pool. To the contrary, co-occurring species of Floridian oak species (Cavender-Bares *et al.*, 2004), Californian *Ceanothus* species (Ackerly *et al.*, 2006), and South African sedges (Slingsby & Verboom, 2006) are phylogenetically overdispersed.

The next move consists of understanding how commonness and rarity of individual species produce the overall taxonomic diversity that is observed (Lennon *et al.*, 2004). Species assemblages are composed by a continuum of species from the very rare (restricted range) to the very common (widespread). From a functional viewpoint, Gibson *et al.* (1999) linked explicitly Grime's (1998) dominant-subordinate-transient (DST) plant functional classification to the core-satellite species hypothesis (CSS), a null metapopulation model proposed by Hanski (1982, 1991) to explain the relationship between species local abundance and regional distribution.

According to Grime (1998), immediate control on ecosystem processes, like water balance and nutrient cycling, depends primarily on the relative contribution of dominant (i.e. locally abundant) species to biomass production, whereas transient species may represent a potential source of colonizers following disturbance. On the other hand, the CSS hypothesis describes the relationship between the species local abundance and their regional distribution allowing the identification of two relatively crisp groups: 'core' species, that are locally abundant and regionally common, and 'satellite' species, that are sparse and occur at only a few sites. Gibson *et al.* (1999) note that core and satellite species are equivalent to Grime's dominant and transient species, explicitly relating the occurrence of core and satellite species to different roles in ecosystems.

In this paper, the importance of coarse-scale environmental filtering in regulating the taxonomic structure of rare and common species in the urban floras of Brussels (Belgium) and Rome (Italy) is tested. Our working hypothesis is that, under the assumption of trait conservatism, if common species are better associated to the dominant environmental conditions of the study site, they should experience a phenomenon of 'taxonomic condensation' in a smaller number of higher-level taxa than rare, mostly incidental species. At the same time, due to their higher taxonomic/functional heterogeneity, the preservation of rare species will be crucial for maintaining high levels of biotic diversity in urban environments.

STUDY AREA

The study areas are the cities of Brussels and Rome. The city of Brussels covers an area of 161 km^2 and is characterized by a temperate climate with mean annual temperature of 9.9 °C and mean annual rainfall of 798 mm. There are approximately 1 million inhabitants in Brussels and, from a structural point of view, it appears as a succession of four concentric zones, from its business and historical centre to the outlying suburbs (IBGE-BIM, 1995): (1) the core is dominated by commercial and administrative activities with a limited residential function; (2) the districts, constructed in the last century, are densely built-up; (3) the periphery, less densely built-up; and (4) the suburbs that can be considered as the peak demographic growth zone. This part of the city still keeps relatively rural enclosures (Godefroid & Koedam, 2007).

For sampling the urban flora, a systematic grid covering the whole city of Brussels was used. The study area included 159 grid cells of 1 km^2 that are included in the administrative limits of the city for at least 75%. Within each of these 1 km^2-cells, all presences of plant species were recorded for 3 years (1992–94) from March to October, wherever they occurred within the administrative limits of the city. In order to avoid undersampling because of the seasonal variation, each 1 km^2-cell was surveyed twice along the growing season (early spring and summer or early autumn). This census recorded 671 spontaneously occurring seed species within the sampling grid (Godefroid, 2001).

The city of Rome covers an area of approximately 300 km^2. The climate is Mediterranean, with average annual temperature of 15.1 °C and average annual rainfall of 839 mm. The urban landscape is highly complex and varied, both in terms of physiography and land use (Ricotta *et al.*, 2001; Blasi *et al.*, 2005).

The city of Rome has a population of 2.5 million inhabitants and is still in a phase of marked urban expansion, mainly towards the eastern and south-eastern sectors of the city where the topography is more favourable. Conversely, the western and north-western sectors contain numerous residual forest patches. Significant nuclei of natural vegetation are also present in the main urban parks and archaeological sites (Celesti-Grapow *et al.*, 2006).

The flora of Rome was comprehensively surveyed from 1985 to 1994 (Celesti-Grapow, 1995). All spontaneous plants were recorded within a grid composed of 190 rectangular cells of 1.6 km^2 in size (the detailed sampling protocol is described in Menichetti *et al.*, 1987). In recent years, the species inventory has been constantly updated and currently totals 1083 spontaneously occurring seed species with at least one spatially explicit record within the sampling grid. Occasional species were not included in the present species inventories.

METHODS

Definition of rare and common species

The present study is addressed at describing how relatively rare and common species contribute to the taxonomic diversity of a given species assemblage. Though a number of different definitions of commonness and rarity can be found in the ecological literature (for a review see Gaston, 1994), in this paper our definition of rare and common species is based solely on their occupancy frequency in the sampled grid cells of both urban floras.

In this view, the occupancy frequency distributions of the seed plants of Brussels and Rome are both unimodal with a satellite mode (*sensu* McGeoch & Gaston, 2002; Fig. 1). Accordingly, for defining species of very restricted and very widespread range, we did not use the terms 'core' and 'satellite' species that are generally related to the U-shaped distribution typical of Hanski's (1982) CSS model. Instead, out of the many possible names (see Olff & Bakker, 1998), we used the more neutral terms 'rare' and 'common' species.

First, in accordance with Pärtel *et al.* (2001), we defined common species as those occurring in more than 75% of sampled quadrats and rare species as those occurring in up to 25% of quadrats. Though these limitations are obviously subjective, the selected thresholds allowed the inclusion of a large number of species from both urban species pools, maintaining the rare and common species still well distinct (Pärtel *et al.*, 2001). The threshold of 25% is consistent with the limit of rare species used in many other papers (see Kunin & Gaston, 1997).

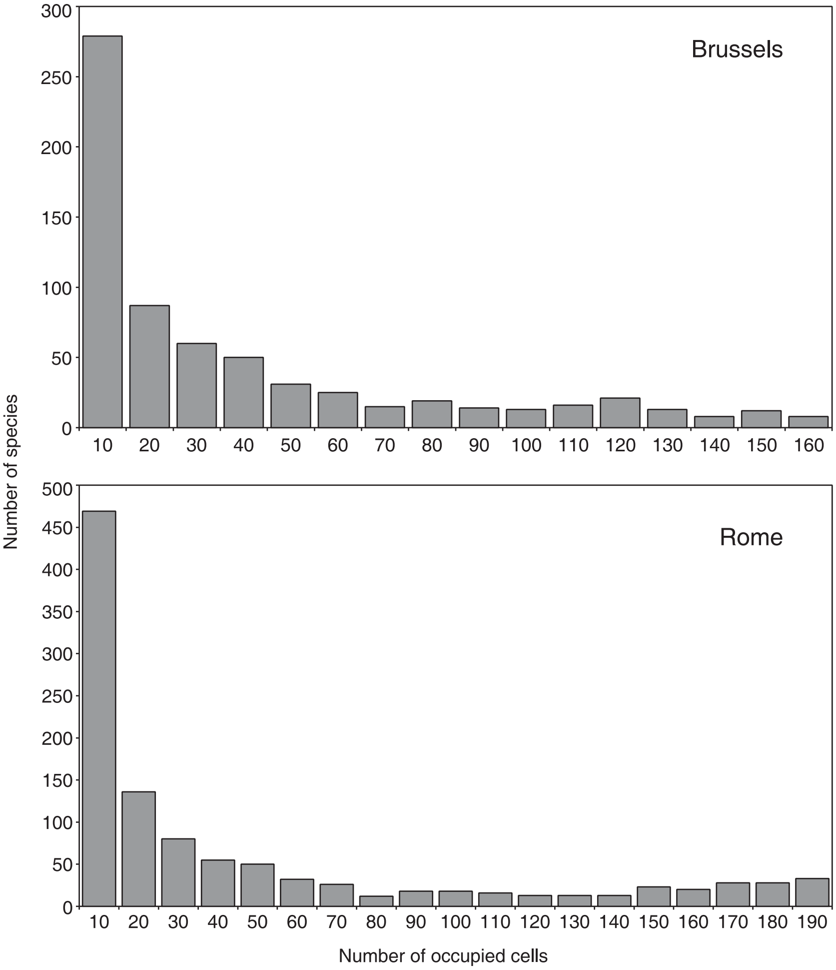

Figure 1 Frequency distribution of occupied cells for the seed plants of Brussels and Rome.

Nonetheless, due to the asymmetric distribution of species frequencies (Fig. 1) that results in a typically larger number of rare species (see Gaston, 1994; Lennon *et al.*, 2004), to determine the common species we also tested lower thresholds (i.e. more than 70% and 65% of sampled quadrats). In doing so, we progressively included more 'common' species in the taxonomic analysis. Similarly, at the opposite end of the distribution, we set the threshold to up to 20% and 15% of sampled quadrats to progressively exclude a larger fraction of 'rare' species from the analysis.

Statistical analysis

As suggested by many authors (e.g. Izsák & Papp, 1995; Warwick & Clarke, 2001; Ricotta, 2002, 2004), we computed the overall taxonomic relatedness of the rare and common species of Brussels and Rome based on the branching topology of the Linnaean taxonomic trees of both floras.

First, all pairwise species distances within a given assemblage are computed using the corresponding topological distances (i.e. the number of segments separating two species in the taxonomic dendrogram; for an example, see Fig. 2). Next, the overall taxonomic diversity (i.e. an inverse measure of taxonomic relatedness) of the assemblage is computed as the mean of all non-zero pairwise species distances (Ricotta, 2004). Webb (2000, pp. 147–148 and Fig. 1) termed this index 'net species unrelatedness' or 'mean pairwise nodal distance'.

For constructing the taxonomic trees, we used the following taxonomic levels: species, genus, family, order, subclass, class, subphylum, and phylum; the taxonomy refers to Judd *et al.* (1999).

Ideally, when computing the taxonomic relatedness of species, one should rely on phylogenetic information. For instance, a suitable phylogenetic tree is readily obtainable on the Web at: www.phylodiversity.net/phylomatic (see Webb & Donoghue, 2005).

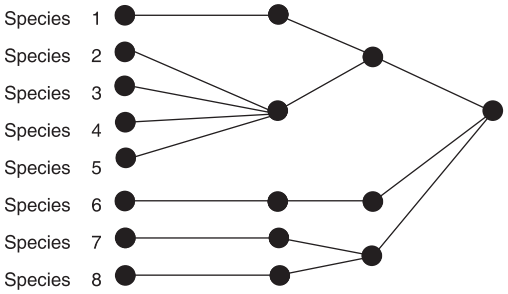

Figure 2 Example of an artificial taxonomic tree composed of eight species, and four taxonomic ranks. The pairwise species distances are the number of segments separating two species in the taxonomic tree. For example, the taxonomic distance between species 2 and species 3 is $d_{23} = 2$, while the distance between species 1 and species 6 is $d_{16} = 6$. Based on these distances, a simple measure of the overall taxonomic diversity of a given species assemblage is computed as the mean of all non-zero pairwise species distances in the assemblage.

Based on phylogenetic trees, the calculation of mean taxonomic relatedness among species could either rely on topology (see Crozier, 1997) or on the much greater information content of branch-length metrics. However, applying a topological approach to phylogenetic trees, we face an important limitation: the cladogram structure is known to be altered as a function of the species included. As a consequence, the species richness of a clade will influence its branching structure, and thus the level of relatedness of two species in that clade. This can lead to the paradoxical situation that two species drawn randomly from a species-rich clade are likely to appear more distant than two species from a less species-rich clade, even if the ages of the most basal speciation event in the two clades are the same (Webb, 2000). For example, a usual outcome of the topological analysis of phylogenetic trees is that two congeneric species can appear as distant as two species that belong to the same family, but to different genera.

On the other hand, a major impediment to a more general application of phylogenetic methods based on branch lengths is that they can be used only when the phylogenies are available for all plant species being studied. By contrast, so far we do not have unambiguous fully resolved cladograms at the species level even for a small proportion of these species.

In this context, Ricotta *et al.* (2008) investigated which taxonomic level contributes most in regulating taxonomic condensation/overdispersion in the urban flora of Rome. Though the results of Ricotta *et al.* (2007) were obtained in a full systematic (i.e. Linnaean) framework, the results obtained show that the species level is the most important one in regulating taxonomic filtering, such that omitting the species level from the analysed tree results in a sensible loss of information.

For all these reasons, Crozier *et al.* (2005) suggests to use taxonomy as a reasonable surrogate for phylogeny: 'Systematists generally try to make the arrangement of species into taxa mirror the topology of an inferred evolutionary tree, and the various classificatory levels similarly reflect the systematist's judgement as to the degree of difference. Thus surrogate phylogenies can be inferred from systematic nomenclature' (Crozier *et al.*, 2005).

To determine whether the taxonomic diversity of the common species of Brussels or Rome was significantly lower than the diversity of the rare species, we did 999 Monte Carlo simulations (see Webb, 2000; Enquist *et al.*, 2002) where each time we reassigned species randomly and without replacement from the urban species pools to groups of common and rare species. Throughout the simulations, the number of species of each random assemblage was held equal to the actual number of rare (common) species.

Next, using the occupancy frequency thresholds 25–75%, 20–70%, and 15–65%, we compared the actual difference in taxonomic diversity between the rare and the common species of both floras to the differences obtained from the random assemblages. *P*-values (one-tailed test) were computed as the proportion of Monte Carlo-derived values that were higher than the actual difference in taxonomic diversity between rare and common species. To generate the null distributions of taxonomic diversity we used the software developed *ad hoc* by one of the authors (C. Ricotta).

Table 1 Number of rare and common species of Brussels and Rome at the selected occupancy frequency thresholds together with their taxonomic diversity values. Common species are defined as those occurring in more than the selected percentage thresholds of sampled quadrats, while rare species are defined as those having an occupancy frequency in the sampled quadrats up to the selected per cent thresholds.

	Threshold	Number of species	Taxonomic diversity
Brussels			
Rare species	25%	476	10.025
	20%	436	10.031
	15%	395	10.057
Common species	75%	47	9.311
	70%	59	9.367
	65%	74	9.472
	All species	671	9.939
Rome			
Rare species	25%	773	10.023
	20%	724	10.019
	15%	672	10.050
Common species	75%	132	9.563
	70%	143	9.500
	65%	158	9.576
	All species	1083	9.930

RESULTS

The number of rare and common species of Brussels and Rome at the selected occupancy frequency thresholds is shown in Table 1 together with their taxonomic diversity values, while Table 2 shows the differences in taxonomic diversity between the rare and the common species of Brussels and Rome at the selected thresholds of occurrence in sampled quadrats and their associated *P*-values.

As shown in Table 2, for both urban floras, independently of the selected threshold of occurrence in sampled quadrats, rare species assemblages have a taxonomic diversity that is significantly higher than that of common species, rejecting the null hypothesis that from a taxonomic viewpoint, common species are indistinguishable from rare species.

In principle, it would be possible to repeat the same analysis selecting the occupancy frequency thresholds of rare and common species such that the difference in taxonomic diversity between rare and common species is maximized. However, as the controlling parameter of this general procedure is continuous, maximization would always require a complete screening of possible occupancy frequency thresholds of which the selected values are only special cases. That is, absolute optima could not be found easily and maximization of taxonomic differences would greatly complicate the calculations.

DISCUSSION

Overall, our analysis shows that the distinction between rare and common species at the selected occupancy frequency thresholds is taxonomically sustained. For instance, we found that common species have a lower taxonomic diversity as compared to the taxonomic diversity of rare species.

Table 2 Difference in taxonomic diversity between the rare and the common species of Brussels and Rome at different thresholds of occurrence in sampled quadrats (i.e. 25–75%, 20–70%, and 15–65% presences in sampled quadrats for the rare and common species, respectively). All diversity values are significant at the 0.01 level. *P*-values (one-tailed test; 999 randomizations) were computed as the proportion of Monte Carlo-derived values that were higher than the actual difference in taxonomic diversity between rare and common species. The null hypothesis is that from a taxonomic viewpoint, common species are indistinguishable from rare species. Common species are defined as those occurring in more than the selected per cent thresholds of sampled quadrats, while rare species are defined as those having an occupancy frequency in the sampled quadrats up to the selected percentage thresholds.

	Occupancy frequency thresholds	Taxonomic difference	*P*-values
Brussels	25–75%	0.714	$P = 0.001$
	20–70%	0.664	$P = 0.001$
	15–65%	0.585	$P = 0.003$
Rome	25–75%	0.460	$P = 0.001$
	20–70%	0.519	$P = 0.001$
	15–65%	0.474	$P = 0.001$

This observation supports the assumption that environmental filtering is an important mechanism in regulating the coexistence of species assemblages. Accordingly, while the CSS model provides an explicit spatial framework for Grime's DST classification, environmental filtering completes the picture and offers a mechanistic background for assigning different taxonomic/functional properties to rare and common species. In this view, looking at the species pool hypothesis from the perspective of the species commonness and rarity, we may equate our common species to a local species pool that is filtered out from among the entire urban species pool based on the species adaptation to the dominant environmental conditions.

From a taxonomic perspective, if during evolutionary change species traits tend to be preserved within a taxon, the species capabilities of colonizing the same ecological space with a certain set of environmental conditions will depend, to some degree, on their underlying taxonomic similarity. As a result, common species that shape the community matrix and experience similar environmental conditions are likely to be more taxonomically similar than rare species.

Pärtel *et al.* (2001) suggest that the different capability of habitat exploitation of rare and common species of dry alvar grassland stands in Estonia resides in their different degree of adaptation to local environmental conditions. Common species are generally better suited to the abiotic environment of the study site due to the relative homogeneity in their morphological and functional traits; by contrast, rare species are a relatively incidental set of species that are more variable in their functional traits compared with the common species. Brown (1995) suggests that locally rare species may be common in habitats that are subject to different abiotic conditions, while Grime (1998) observes that rare (transient species in the DST classification) are often juveniles of dominants at other sites (see also Lennon *et al.*, 1997).

Accordingly, due to their more 'disperse' origin along with their lager environmental heterogeneity, rare species are, on average, more taxonomically dissimilar than expected by chance. Consequently, due to their high taxonomic and possibly functional variability, a high diversity of rare species implies a high probability that, in the case of 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 (Grime, 1998).

This aspect requires particular attention when setting up conservation strategies for urban areas: the preservation and restoration of local rare habitats and their connections with the surrounding natural areas require special attention if the trend towards homogenization due to the extinction of rare species following urbanization is to be avoided (e.g. Kühn & Klotz, 2006). For example, in Rome, the permanence of these connections with diaspore pools in the surroundings is one of the main reasons to explain the high urban species richness (Celesti-Grapow *et al.*, 2006). Here, a promising approach is to educate the urban public, raising the awareness of city residents on the importance of remnants of native habitats (McKinney, 2006).

More specifically, the most common species in the flora of Rome were *Amaranthus retroflexus*, *Aster squamatus*, *Chenopodium album*, *Conyza sumatrensis*, *Cynodon dactylon*, *Dactylis glomerata*, *Galium aparine*, *Hordeum murinum*, *Malva silvestris*, and *Poa annua*. All these species were found within all 190 grid cells sampled. The families most frequently found in Rome were Asteraceae (135 species), Poaceae (124), and Fabaceae (120). The same families were also the most abundant ones within the rare species (77 Asteraceae, 81 Poaceae, and 85 Fabaceae) and the common species (31 Asteraceae, 18 Poaceae, and 11 Fabaceae) at the 25% and 75% occupancy frequency thresholds, respectively. This is not a surprise as from a simple probabilistic viewpoint, species assemblages put together at random from a larger species pool have a greater chance of containing a high proportion of species belonging to the most common families. This effect is similar to the 'sampling effect' discussed in studies of functional biodiversity effects (e.g. Loreau & Hector, 2001; see also Leps *et al.*, 2006).

Likewise, the species most frequently found in Brussels were *Poa annua* (159 presences in the grid cells), *Stellaria media* (157), *Cirsium arvense* (157), *Plantago major* (156), and *Urtica dioica* (156), while the most frequent families were Asteraceae (76 species), Poaceae (66), and Brassicaceae (44). The high number of species in this latter family indicates the more continental character of Brussels as compared to Rome. The same families were also the most abundant ones within the rare species (49 Asteraceae, 44 Poaceae, and 35 Brassicaceae), while within the common species, the Asteraceae (13) were the only family totalling to more than four species.

As to the exotic/native origin of common and rare species, the flora of Rome contains 88 alien species (8.1% of the total flora). Of these, 14 species belong to the common species group (i.e. 10.6% out of the commonest 132 species) and 51 are rare species (6.6% out of 773). On the other hand, the flora of Brussels contains 153 alien species (22.8% of the total flora); six of these (12.7% out of 47) belong to the common species group, while 127 (26.7% out of 476) belong to the rare species.

The lower number of established alien species in Rome is mainly due to the fact that many alien species of Brussels originate from southern Europe and are thus native in Rome. Also, according to their origin in warmer regions, in Brussels alien species generally possess narrower environmental requirements as compared to Rome. For instance, the lower presence of aliens within the rare species of Rome is due to the adaptation of naturalized species (i.e. species which have established self-sustaining populations; see Richardson *et al.*, 2000; Pyšek *et al.*, 2004) to the average conditions of urban habitats, such as different degrees of man-made disturbance, which makes them generally widespread all across the city (Celesti-Grapow, 1995). By contrast, in Brussels, most aliens have high temperature requirements that can be met only in densely built-up areas where the urban heat-island effect is more pronounced (Godefroid, 2001; Godefroid & Koedam, 2007). As a result, if alien species are preferentially confined to a specific urban habitat, they cannot reach high levels of commonness.

Finally, looking at the species ecological characteristics, it emerges that in Brussels 26 species out of the 47 commonest species (i.e. 55.3%) at the 75% occupancy frequency threshold are of synanthropic origin. By contrast, in Brussels synanthropic species contribute only for 29.4% of the total of rare species at the 25% occupancy frequency threshold (140 species out of 476). The same holds for Rome, where 80.3% of the commonest species (106 out of 132) are synanthropic species, while only 48.3% of rare species (373 out of 773) are of synanthropic origin. This different contingent of synanthropic species within the common and rare species of both floras clearly shows that common species are on average better adapted to the ecological characteristics of urban environments as compared to the rarest species.

To conclude, this paper is part of a growing body of evidence demonstrating the great potential of taxonomic analysis for the study of community assembly. In this view, 'phylogenetic community ecology' *sensu* Webb *et al.* (2002) constitutes a bridge between ecological and evolutionary studies that emphasizes the complex interactions between environmental conditions and evolutionary relationships among taxa for the maintenance of species diversity. We hope our findings will contribute to a deeper understanding of the role of rare and common species in regulating the ecological functioning and taxonomic structure of multispecies systems.

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