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Exploring taxonomic filtering in urban environments

Ricotta, Carlo; DiNepi, Micol; Guglietta, Daniela* & Celesti-Grapow, Laura

Department of Plant Biology, University of Rome 'La Sapienza', Piazzale Aldo Moro 5, 00185 Rome, Italy;
**Corresponding author; Tel. +39 0649912408; Fax +39 064457540; E-mail danielaguglietta@gmail.com*

Abstract

Question: Several mechanisms have been proposed that control the spatio-temporal pattern of species coexistence. Among others, the species pool hypothesis states that the large-scale species pool is an important factor in controlling small-scale species richness through filtering of species that can persist within a species assemblage on the basis of their tolerance of the abiotic environment. Because of the process of environmental filtering, co-occurring species that experience similar environmental conditions are likely to be more taxonomically similar than ecologically distant species. This is because, due to the conservatism of many species traits during evolutionary diversification, the ability of species to colonize the same ecological space is thought to depend at least partially on their taxonomic similarity. The question for this study is: Under the assumption of trait conservatism, does environmental filtering lead to nonrandom species assemblages with respect to their taxonomic structure?

Methods: The significance of taxonomic filtering in regulating species coexistence is tested using data from 15 local species assemblages from the urban flora of Rome (Italy). To find out whether the taxonomic structure of the selected 'local' species assemblages was significantly different from random, we used a Monte Carlo simulation in which for each local species assemblage, the actual taxonomic diversity was compared to the taxonomic diversity of 1000 virtual species lists of the same size extracted at random from a larger 'regional' species pool.

Results: We found that in most cases the local species assemblages have a higher degree of taxonomic similarity than would be expected by chance showing a phenomenon of 'species condensation' in a small number of higher-level taxa.

Conclusions: Our observations support the species pool hypothesis and imply that environmental filtering is an important mechanism in shaping the taxonomic structure of species assemblages. Therefore, the incorporation of taxonomic diversity into landscape and community ecology may be beneficial for a better understanding of the processes that regulate species coexistence.

Keywords: Rome; Species co-occurrence; Taxonomic relatedness; Urban flora.

Abbreviations: G.R.A. = Grande Raccordo Anulare; S/G ratio = Species/Genus ratio

Nomenclature: Conti et al. 2005.

Introduction

The search for general mechanisms that regulate the diversity of species assemblages is a fundamental objective of ecology. Several theories have been proposed to explain the spatio-temporal pattern of species coexistence. On longer temporal scales, historical contingency plays a major role (Ricklefs 1987; Ricklefs & Schluter 1993; Hugueny et al. 1997; Svenning & Skov 2004). In 'ecological time', two broad classes of processes have been put forward: at small spatial scales, species coexistence has been associated with local processes reducing competition, such as spatio-temporal heterogeneity, or environmental stress. Reviews are found in Palmer (1994), Huston (1999), and Wright (2002). At larger spatial scales, the importance of regional species pools has been taken into account (Weiher & Keddy 1995; Pärtel et al. 1996; Zobel 1997). The species pool hypothesis claims that the large-scale 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. Though the relative influence of these different small-scale and large-scale mechanisms has been the subject of debate, nonetheless they ultimately regulate the coexistence and diversity of species assemblages.

Even though a connection between taxonomy and community ecology dates back to Darwin (1859; see Webb et al. 2002), integration of evolutionary biology and community ecology remains in its infancy. Due to the conservatism of many species traits during evolutionary diversification, a positive relationship between the species taxonomic relatedness and their ecological similarity is expected. As a result, because of the process of environmental filtering, co-occurring species that experience similar environmental conditions are likely to be more taxonomically similar than ecologically distant species. In this paper, the importance of taxonomic filtering in regulating species co-occurrence is tested using data from 15 local species assemblages from the urban flora of Rome (Italy).

Measures of taxonomic diversity

The positive relationship between species taxonomic relatedness and ecological similarity has been traditionally analysed using species-to-genus (S/G) ratios and similar subtaxon/taxon ratios (Järvinen 1982; Gotelli 2001; Gotelli & Colwell 2001). A low S/G ratio was traditionally explained as a product of strong competition among congeneric species, which should lead to the regional extinction of all but a few species in a genus (Elton 1946). Apparently, this hypothesis was in good agreement with the widespread observation that S/G ratios were usually smaller for island biota than for mainland biota (Elton 1946).

The problem is that any subtaxon/taxon ratio is sample-size dependent (Gotelli & Colwell 2001; Marignani et al. 2004). For instance, as larger areas are sampled, more species will be recorded. The same pattern is generally true for higher taxonomic ranks, such as genera or families, albeit generic or familial richness do not rise as quickly with area as species richness. Consequently, subtaxon/taxon ratios are an increasing function of area. As emphasized by Gotelli & Colwell (2001), this monotonic behaviour is inevitable for any two taxonomic ranks since the higher taxonomic rank has fewer members than the lower taxonomic rank.

Sample size dependence in taxonomic ratios was first demonstrated for plant species assemblages by Maillefer (1929), who used draws of species from a deck of shuffled cards to compute the expected generic richness in small assemblages. One year later, Pólya (1930) analytically derived the mathematical expectation of the S/G ratio and proved its sample size dependence. In this view, recent re-examinations of S/G ratios in light of a correct null model that takes into account their sample size dependence suggest that islands species assemblages generally host more congeneric species than expected by chance (see Simberloff 1970). This tendency of congeners to coexist conflicts with the predictions of competition theory, revealing instead the ecological affinity of taxonomically related species (Gotelli & Colwell 2001; Enquist et al. 2002).

An alternative approach to subtaxon/taxon ratios consists in deriving summary statistics that quantify the overall taxonomic relatedness of a species assemblage based on the branching topology of the taxonomic tree (Izsák & Papp 1995; Ricotta 2002, 2004; Warwick & Clarke 1995, 2001).

To compute the overall taxonomic relatedness of a species assemblage, 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). Next, the overall taxonomic diversity (i.e. an inverse measure of taxonomic relatedness) of the assemblage is computed simply as the mean of all pairwise species distances (Fig. 1).

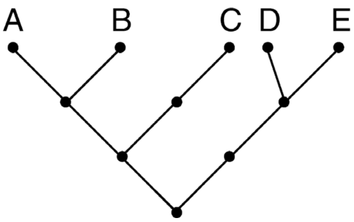
Unlike subtaxon/taxon ratios in which the analysis is limited to two taxonomic ranks, this latter measure of taxonomic diversity takes into account the entire structure of the taxonomic tree. Here, using the branching pattern of the taxonomic tree, we explored whether species taxonomic diversity is related to some extent to the overall ecological similarity of species coexisting in the same biotic space.

Study area

To identify the importance of taxonomic filtering in determining the diversity of species assemblages, we use a data set on the urban flora of Rome (Italy).

The city of Rome covers an area of ca. 300 km^2 delimited by the course of the Grande Raccordo Anulare (G.R.A.), a 68.2 km-long peri-urban circular highway which acts as an external physical and psychological barrier against urban expansion (Sanfilippo 1993). According to Blasi (1994), the bioclimate is Mesomediterranean with summer drought and an average annual temperature of 15.1 °C. Average annual rainfall is 839 mm with a main maximum in autumn and a secondary maximum in winter.

The urban landscape is extremely complex and stratified as in any area of long-standing settlement. The superimposition of different historical periods spanning more than 2700 years, from the ancient Roman remains in the city center to the modern buildings of the suburbs, severely affects the urban distribution of vegetated areas and plant species richness.



$$\Delta = \begin{array}{cccccc} A & B & C & D & E & \\ 0 & 2 & 4 & 6 & 6 & A \\ 2 & 0 & 4 & 6 & 6 & B \\ 4 & 4 & 0 & 6 & 6 & C \\ 6 & 6 & 6 & 0 & 2 & D \\ 6 & 6 & 6 & 2 & 0 & E \end{array}$$

Fig. 1. Illustration of an artificial taxonomic tree composed of five species, A, B, C, D, and E, and four nested taxonomic ranks (see Ricotta 2004). First, the pairwise species distances are computed as the number of segments separating two species in the taxonomic tree. All species distances are summarized in the species distance matrix Δ. Next, a measure of the overall taxonomic diversity of the species assemblage is computed simply as the mean of all non-zero pairwise species distances in Δ. In the above example overall taxonomic diversity equals 4.8.

The semi-natural vegetation of Rome is dominated by a mosaic of pastures and fallow lands (Celesti-Grapow & Fanelli 1993). Cultivated areas are most common in the suburbs and along the bank of the Tiber and Aniene Rivers and include fields, small orchards, vineyards and vegetable gardens. Numerous residual forest patches are scattered in the western part of the city. These forests host a number of rare species, such as *Ilex aquifolium* and *Galanthus nivalis*. Among the trees, oaks are dominant, including *Quercus suber, Q. ilex, Q. pubescens, Q. cerris, Q. frainetto,* and *Q. robur*. Other common woody species are: *Acer campestre, Fraxinus ornus, Corylus avellana, Crataegus monogyna* and *Viburnum tinus*.

Despite the intense degradation of the riparian habitats there are still patches of urban riparian woods along the banks of the Tiber and Aniene Rivers principally composed of *Salix alba, Populus alba, P. nigra* and *Alnus glutinosa*. Significant nuclei of natural vegetation are also present in the most densely populated areas of the city center, usually in the urban parks and archaeological sites.

To explore the coarse-scale spatial distribution of urban plant species richness, the area within the G.R.A. was spatially organized in a grid composed of 190 rectangular cells of roughly 1.2 km by 1.4 km (for more details on the sampling protocol, see Menichetti et al. 1987). Within each cell, all spontaneous spermatophytes were recorded (Celesti-Grapow 1995). According to this census, there are 46 473 records on the spatial distribution of 1083 spontaneous species within the sampling grid (Fig. 2). Lower-order taxa, such as subspecies, were not considered in this work. We also excluded species from the analysis which were only known from historical records (i.e. for which spatially explicit records within the sampling grid are lacking).

While this may appear inconsistent with the heavy degradation of urban environments, cities generally offer a great variety of habitats to natural flora and fauna

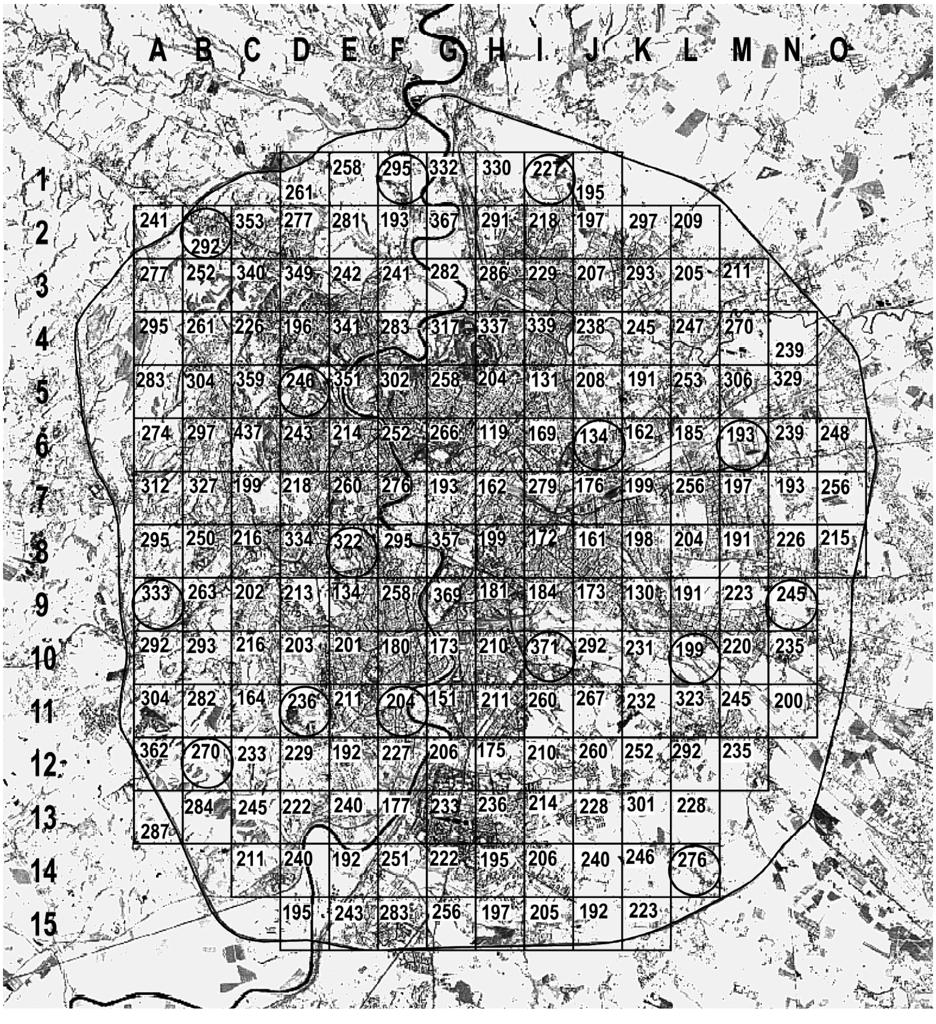


Fig. 2. Seed plant (spermatophyte) species richness distribution in the city of Rome. Labels are number of species per unit cell. The 15 circled cells were selected for taxonomic diversity analysis.

and constitute important nuclei for the immigration and naturalization of non-native species (Henke & Sukopp 1986; Ricotta et al. 2001; Deutschewitz et al. 2003; Kühn et al. 2004; Celesti-Grapow et al. 2006).

Methods

Out of the 190 cells that constitute the sampling grid, 15 units were randomly selected. To minimize spatial autocorrelation, we imposed an additional restriction to the sampling procedure: once one cell is randomly selected, its eight nearest-neighbours are automatically excluded from the next sampling iteration. As a result, subsequent taxonomic analysis is prevented to run on adjacent cells (see Fig. 2).

For each species assemblage in the 15 sampled cells, we computed the S/G ratio and the proposed measure of overall taxonomic diversity using the procedure shown in Fig. 1. To determine whether the taxonomic structure of the selected species assemblages was significantly different from random, we constructed the following Monte Carlo simulation: for each species assemblage, the actual overall taxonomic diversity was compared to a distribution of similarly calculated values from 1000 virtual species lists obtained by reassigning species randomly and without replacement from the entire urban species pool composed of 1083 spontaneous spermatophytes. Throughout the simulation, the number of species of each random assemblage was held equal to the actual species richness of the corresponding cell (see Enquist et al. 2002). *P*-values (one-tailed test) were computed as the proportion of Monte Carlo-derived values that were as low or lower than the actual taxonomic diversity.

For the calculation we used the following taxonomic levels: species, genus, family, order, subclass, class, subphylum, and phylum; the taxonomy refers to Judd et al. (1999). In addition, to investigate which taxonomic level contributes most in regulating species co-occurrence, we performed a 'leave-one-level-out statistic' on the following taxonomic levels: species, genus, family and order. For instance, we run the above Monte Carlo simulation four additional times, each time leaving out one taxonomic level in the computation of the taxonomic diversity.

Finally, to compare the potential effects of taxonomic filtering at different scales, we introduced a second, finer spatial scale for analysis. Using the same Monte Carlo simulation, we related the species lists of the 15 sampled cells to their direct neighbourhood with the analyzed cell in the center. For example, the species assemblage of cell D5 was compared with the pooled species assemblages of cells C4, C5, C6, D4, D5, D6, E4, E5 and E6, while the species assemblage of cell A9 was related to the species assemblage obtained by pooling cells A8, A9, A10, B8, B9 and B10 (see Fig. 2).

Table 1. Species richness, genus richness, S/G ratios and taxonomic diversity of the flora of Rome and the 15 local species assemblages analyzed. The *P*-values (one-tailed test) obtained by comparing the taxonomic diversity of the local species assemblages with an equal-sized random sample of the 'regional' species pool are shown in the last two columns. In the sixth column, the whole flora of Rome is used as regional species pool; in the last column, the species lists of the 15 sampled cells are compared to their direct neighborhood with the analysed cell in the center. For both simulations the null hypothesis is that the species composition of local assemblages is a random sample of a given regional species pool. NS = not significant at the 0.05 level.

					P-values	
Cell code	Species richness	Genus richness	S/G ratio	Taxonomic diversity	Coarse-scale analysis	Fine-scale analysis
A9	333	217	1.535	9.827	$P = 0.039$	P = 0.361 NS
B2	292	210	1.390	9.702	$P < 0.001$	$P = 0.001$
B12	270	188	1.436	9.757	$P = 0.012$	$P = 0.135$ NS
D5	246	184	1.337	9.740	$P = 0.003$	$P = 0.002$
D11	236	179	1.318	9.823	$P = 0.080$ NS	$P = 0.596$ NS
E8	322	220	1.464	9.728	$P = 0.003$	$P = 0.004$
F1	295	209	1.411	9.687	$P < 0.001$	$P = 0.008$
F11	204	150	1.360	9.678	$P < 0.001$	$P = 0.064$ NS
I1	227	160	1.419	9.542	$P < 0.001$	$P < 0.001$
I10	371	250	1.484	9.780	$P = 0.013$	$P = 0.472$ NS
J6	134	110	1.218	9.588	$P = 0.002$	$P = 0.031$
L10	199	144	1.382	9.621	$P = 0.003$	$P = 0.095$ NS
L14	276	197	1.401	9.748	$P = 0.007$	$P = 0.296$ NS
M6	193	138	1.399	9.545	$P < 0.001$	$P = 0.034$
N9	245	165	1.485	9.551	$P < 0.001$	$P = 0.011$
Rome	1083	492	2.201	9.930	– –	– –

Results

As shown in Table 1, all cells sampled have a S/G ratio that is lower than that of the entire urban species pool, leading to the (wrong) conclusion that local species assemblages would be more taxonomically diverse than the whole regional species pool.

By contrast, at the larger spatial scale of analysis, in all simulations but one, the resulting taxonomic diversity is larger than the one computed for the real data with a significance level of 0.05 (Table 1). That is, on average, pairwise species distances in real assemblages are shorter than in assemblages randomly put together from a larger species pool, rejecting the null hypothesis that the species composition of local assemblages is a random sample of a given regional species pool.

Notice that, analysing all cells that compose the sampling grid (i.e., without considering spatial autocorrelation), for 170 cells out of 190, the actual taxonomic diversity is lower than that obtained from the Monte Carlo simulations ($P = 0.05$; one-tailed test). By contrast, none of the 190 cells has a taxonomic diversity that is significantly larger than that obtained from the average of all Monte Carlo simulations (data not shown here).

At the finer spatial scale (i.e. in which the 15 local species assemblages are compared to their direct neighbourhood), the results obtained are less clear than at the coarser scale. For instance, the null hypothesis is rejected 8 times out of 15 (Table 1). Nonetheless, even in this case, none of the analyzed cells has a taxonomic diversity that is significantly larger than that obtained from the average of all Monte Carlo simulations.

The results of the leave-one-level-out statistics are shown in Table 2. Leaving one taxonomic level out in the computation of the taxonomic diversity decreases to some extent the number of times the null hypothesis is rejected. For instance, leaving out the species level, the null hypothesis is rejected 4 times out of 15; by contrast, leaving out the genus level does not change the results of our analysis.

In this view, the outcomes of the 'leave-one-level-out statistic' were evaluated as follows: first, for each taxonomic level in Table 2, we summed up the number of Monte Carlo-derived values in each cell that were as low as or lower than the actual taxonomic diversity. Next, we ranked the four taxonomic levels according to the obtained values, i.e., species = 685, family = 501, order = 406, and genus = 205.

The reasoning behind this procedure is that if in the calculation of taxonomic diversity we leave out a level that is important in regulating taxonomic filtering, then the number of Monte Carlo-derived values that are as low or lower than the actual taxonomic diversity will increase more than if we leave out a less important taxonomic level.

Table 2. Results of the leave-one-level-out statistics on the following taxonomic levels: species, genus, family and order. For each taxonomic level that is excluded from the simulation, the corresponding taxonomic diversities (TD) and the *P*-values (one-tailed test) of the 15 sampled cells are shown. NS = not significant at the 0.05 level.

Cell	Species		Genus		Family		Order	
code	TD	*P* values	TD	*P* values	TD	*P* values	TD	*P* values
A09	7.874	$P = 0.215$ NS	7.838	$P = 0.047$	7.976	$P = 0.147$ NS	8.004	$P = 0.132$ NS
B02	7.717	$P = 0.012$	7.709	$P < 0.001$	7.836	$P = 0.001$	7.868	$P < 0.001$
B12	7.798	$P = 0.051$ NS	7.766	$P = 0.013$	7.892	$P = 0.032$	7.919	$P = 0.021$
D05	7.775	$P = 0.041$	7.747	$P = 0.007$	7.887	$P = 0.039$	7.909	$P = 0.020$
D11	7.818	$P = 0.087$ NS	7.830	$P = 0.071$ NS	7.965	$P = 0.150$ NS	7.985	$P = 0.122$ NS
E08	7.649	$P < 0.001$	7.735	$P = 0.001$	7.862	$P = 0.009$	7.895	$P = 0.002$
F01	7.754	$P = 0.019$	7.696	$P < 0.001$	7.820	$P < 0.001$	7.849	$P = 0.002$
F11	7.758	$P = 0.045$	7.687	$P = 0.002$	7.826	$P = 0.012$	7.854	$P = 0.006$
I01	7.593	$P < 0.001$	7.554	$P < 0.001$	7.726	$P = 0.001$	7.752	$P < 0.001$
I10	7.835	$P = 0.097$ NS	7.808	$P = 0.020$	7.931	$P = 0.035$	7.961	$P = 0.023$
J06	7.593	$P = 0.003$	7.595	$P = 0.003$	7.780	$P = 0.008$	7.803	$P = 0.008$
L10	7.683	$P = 0.007$	7.631	$P = 0.002$	7.785	$P = 0.003$	7.813	$P = 0.005$
L14	7.790	$P = 0.042$	7.756	$P = 0.005$	7.891	$P = 0.020$	7.921	$P = 0.029$
M06	7.561	$P < 0.001$	7.555	$P < 0.001$	7.714	$P < 0.001$	7.742	$P < 0.001$
N09	7.619	$P = 0.003$	7.565	$P < 0.001$	7.722	$P < 0.001$	7.751	$P < 0.001$
Rome	7.945	– –	7.941	– –	8.039	– –	8.073	– –

Discussion

The consistency of our results with previous studies on S/G ratios (Simberloff 1970; Enquist et al. 2002) and on the branching structure of phylogenetic trees (Webb 2000) reinforces the assumption that taxonomic clustering is a common outcome of the mechanisms that regulate species coexistence and diversity.

Due to the general sample-size dependency of subtaxon/taxon ratios, S/G ratios are unable to capture the species condensation effect caused by taxonomic filtering. Conversely, the proposed measure of taxonomic diversity seems more effective in verifying the influence of the regional species pool on local species assemblages.

As concerns the scale of analysis, the Monte Carlo simulation shows that taxonomic filtering is much more evident at the coarser scale where the species richness of the regional species pool is one order of magnitude larger than the richness of the local species assemblages. At the finer scale of analysis, with a regional species pool of the same order of magnitude of the local species assemblages, the effects of taxonomic filtering are less obvious, though there is no evidence of any opposite effect of ‘species segregation’.

To explore the influence of species richness on taxonomic diversity, in Fig. 3 we plotted species richness vs. taxonomic diversity for the 15 species assemblages sampled. The scatter plot of Fig. 3 shows a slight, though significant ($R^2 = 0.419$, $P < 0.01$) positive relationship between these variables, implying a positive effect of species richness on the taxonomic diversity of local assemblages.

To clarify the causes of this positive relationship, i.e.whether this correlation is due to a mathematical flaw in the definition of the index (since taxonomic diversity is computed as the mean value of all non-zero pairwise species distances in a given assemblage, it should be basically independent of species richness), or to some causal ecological process, we generated the following random model: out of the 1083 species of the flora of Rome, we extracted at random 800 species assemblages of different species richness. We generated 8 series of 100 random species assemblages, each one containing 100, 150, 200, 250, 300, 350, 400, and 450 species. The lower and upper species richness in the random assemblages roughly corresponds to the lower and highest species richness in the 190 cells of the flora of Rome (i.e., 119 and 437 species, respectively).

The plot of species richness vs. taxonomic diversity of these 800 random assemblages (Fig. 4) proves the mathematical independence of these two variables ($R^2 = 0.004$, $P > 0.05$). Therefore, the observed positive relationship of Fig. 3 is necessarily caused by some

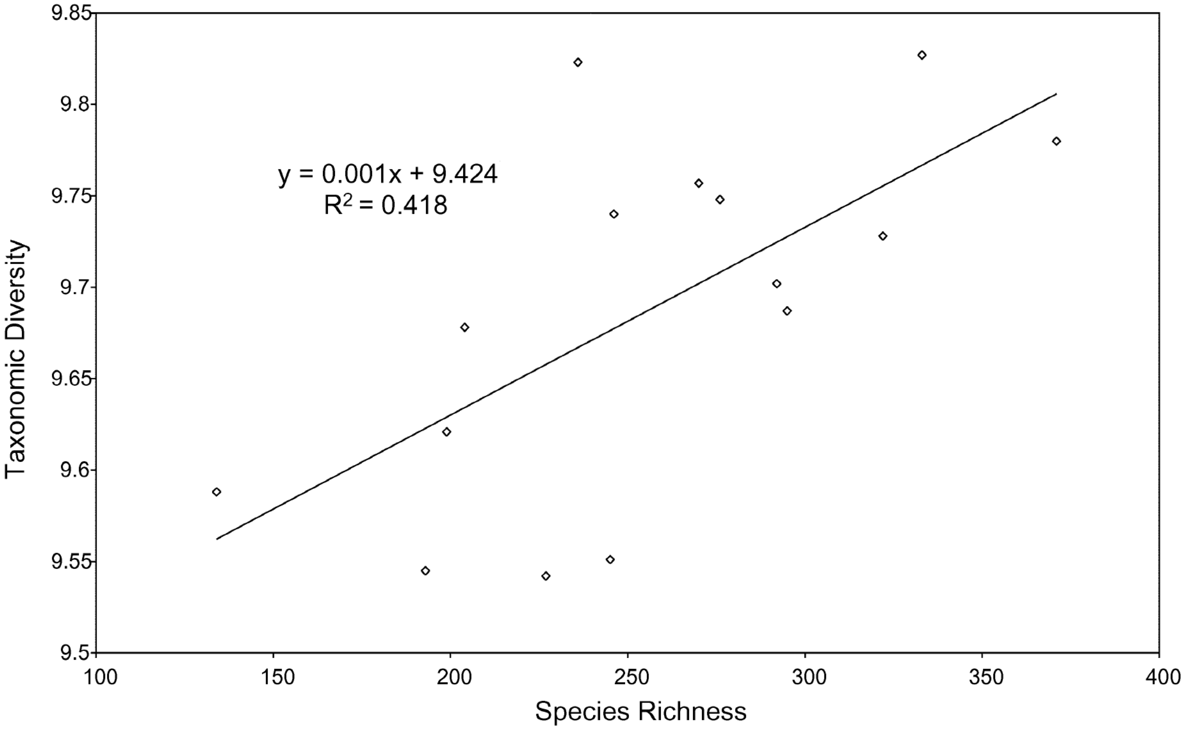


Fig. 3. Scatter plot of taxonomic diversity vs. species richness for the 15 species assemblages analysed. The slope of the regression line is significant at the $P < 0.01$ level.

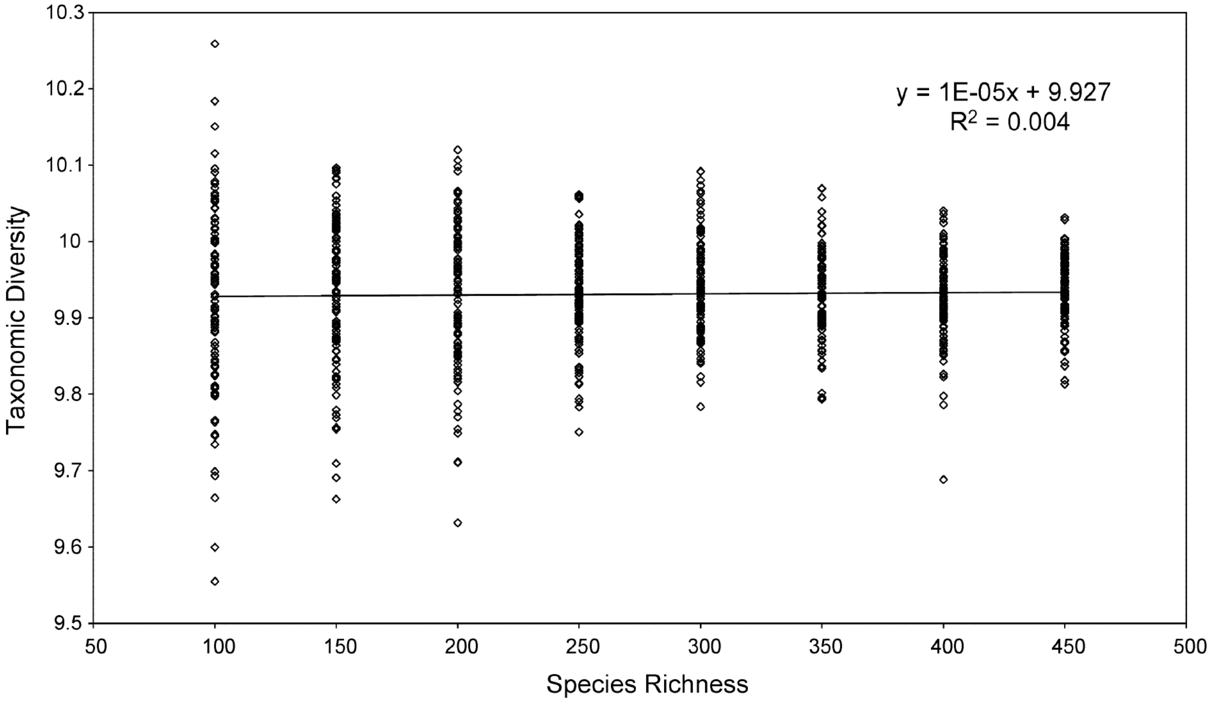


Fig. 4. Scatter plot of taxonomic diversity vs. species richness for the 800 species assemblages of varying species richness drawn at random from the whole flora of Rome. The slope of the regression line is not significant at the $P < 0.05$ level.

ecological mechanism linking species richness to taxonomic diversity.

For instance, several studies show that, due to the larger niche availability, species richness is increased by environmental heterogeneity (see e.g. Dufour et al. 2006; Pausas et al. 2003). For the same reason, environmental heterogeneity also increases the taxonomic diversity of the local species pool. For instance, local species assemblages that persist in heterogeneous environments experience a less severe effect of taxonomic filtering than species assemblages that colonize more homogeneous environments. Accordingly, whenever the species pool hypothesis plays a role in regulating local species coexistence, high species richness should imply high taxonomic diversity.

Finally, to determine which taxonomic level contributes most to 'species condensation', the results of Table 2 show that the species level is the most important one in regulating taxonomic filtering, while, interestingly, the genus level is the least important one. This result reinforces the above observation that S/G ratios are not necessarily the most adequate tool for exploring the effects of taxonomic filtering.

Overall, our observations indicate that species assemblages are taxonomically structured. Nonetheless, the mechanisms that induce the taxonomic attraction and repulsion are not universal, but depend upon the scale involved (Webb et al. 2002). At regional to continental scales, taxonomic sorting is mainly determined by biogeographic processes like speciation and migration. At intermediate scales, species segregate into habitats based on the strength of environmental filtering. As during evolutionary change species traits tend to be preserved within a taxon, the species capabilities of colonizing a given piece of physical space with a certain set of environmental conditions will depend to some degree on their underlying taxonomic similarity.

By contrast, at the smallest scales, individual-based interactions play a major role, and taxonomic clustering/segregation is determined by the relative strength of mechanisms that promote long-term species coexistence versus competitive displacement.

Due to the coarse grain of our data, the results obtained support the species pool hypothesis and imply that, at the scale of our study, environmental filtering is an important determinant of the spatial pattern of taxonomic diversity. While this poses the problem of defining the source pool (Zobel 1997; Dupré 2000), the incorporation of taxonomic information may bring new light to the study of the processes that regulate the coexistence of species in the same ecological space.

For instance, the regional species pool determines the species that are potentially allowed to colonize a given piece of space. 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. Nonetheless, even species that pass this first filter can be filtered out by competitive displacement such that small-scale species coexistence is maintained by local mechanisms avoiding neighbourhood exclusion. These mechanisms include local environmental heterogeneity created by individual plants (Tilman & Pacala 1993; Bever 1994; Bonanomi et al. 2005), equilibrium mechanisms through niche partitioning (Tilman 1994), and non-equilibrium coexistence dynamics (Huston 1994) related to disturbance (Connell 1978; Sousa 1984) and fluctuations of environmental conditions (Chesson 2000).

In this framework, experimental evidence shows that, at finer spatial scales, these mechanisms may become more important than taxonomic filtering in regulating species coexistence, such that coexisting species are more phylogenetically (Cavender-Bares et al. 2004), or functionally (Stubbs & Wilson 2004) dissimilar than expected from a random model.

Nonetheless, in most of these models, all species are considered as equivalent units with independent functional traits, while the way in which differences between species affect species coexistence can be very complex, and this is hardly captured by measures such as species richness that do not contain any information about individual species. Therefore, diversity measures that incorporate taxonomic distances between species may contribute to a deeper understanding of the intra- and interspecific interactions that allow coexistence in multi-species systems at different scales (see Webb 2000).

Finally, we conclude with a cautionary remark: the proposed index uses taxonomic information, and not phylogenetic data, although the latter are in principle preferable. For instance, traditional Linnaean classification generally represents overall similarity rather than the possession of common derived characters. Besides, in combining different taxa into a (super)taxon of higher hierarchical level, we are implicitly assuming some kind of equivalence between taxa at the same hierarchical level. For example, we are assuming that a genus in the *Fabaceae* and a genus in the *Papaveraceae* represent the same 'taxonomic information' in the nested hierarchy (Dale 1998), whereas taxonomic ranks may differ greatly in age and species richness among different lineages. It is sufficient to look at the recent revision of the genus *Eucalyptus* (Hill & Johnson 1995) or at the 242 micro-species of *Hieracium* listed in the Norwegian flora (Lid 1952) to recognize these problems.

Nonetheless, despite the limitations of using the Linnaean taxonomy as a measure of species distances, our results demonstrate the potential of this simple method for quantifying the taxonomic structure of species assemblages.

Alternatively, the taxonomic relatedness of species could easily be derived in a full phylogenetic context, by replacing taxonomic trees by proper phylogenetic trees (review in Crozier 1997). However, a major obstacle in using a phylogenetic approach is that there are no phylogenies available for all plant species being studied and that phylogenization of most interesting species is unlikely to occur within the next several years.

Also, applying a topological approach to phylogenetic trees, we encounter two major drawbacks (see Webb 2000). First, the structure of the phylogenetic tree is unstable and depends on the species included, such that the number of nodes between two taxa is determined by the particular reference phylogeny used. As a result, the measures obtained can only be used to compare assemblages whose species are a subset of the species in the reference phylogeny. Second, the species richness of a clade will influence its branching structure such that two species drawn at random from a species-rich clade are likely to appear more topologically distant than two species from a species-poor clade. For all these reasons, it is probably more realistic to remain within a Linnaean taxonomic framework, at least at present.

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