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Quantifying the taxonomic diversity in real species communities

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Abstract

We analyze several *florae* (collections of plant species populating specific areas) in different geographic and climatic regions. For every list of species we produce a taxonomic classification tree and we consider its statistical properties. We find that regardless of the geographical location, the climate and the environment all species collections have universal statistical properties that we show to be also robust in time. We then compare observed data sets with simulated communities obtained by randomly sampling a large pool of species from all over the world. We find differences in the behavior of the statistical properties of the corresponding taxonomic trees. Our results suggest that it is possible to distinguish quantitatively real species assemblages from random collections and thus demonstrate the existence of correlations between species.

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1. Introduction

The search for patterns in the species composition across ecological communities and for the processes that cause these patterns is a central goal of ecology. The starting point is the general

assumption that an ecosystem is not a simple random collection of species. A great variety of evolution models suggest that an ecosystem is shaped by a number of evolutionary mechanisms such as speciation, competition and selection that differentiate it from a random system. Several approaches try to show evidence for these differences, even if slight. Our contribution to these efforts focuses on the study of the structure of the taxonomic classification of plants species. Though modern systematic biologists consider it more reliable and less arbitrary to describe relationships between species via phylogenetic trees [1, 2] (hierarchical structures following the steps of evolution from ancestral species to modern ones), the usual taxonomic classification is still widely used. Introduced in the 18th century by the Swedish naturalist Carl von Linné, taxonomy is based on morphological and physiological observations and it groups all species in a set of different hierarchical levels very similar to a genealogical tree. Thus, with the aim of comparing our results to the literature in this field we restrict our analysis to the traditional Linnean taxonomy. Nonetheless, due to the positive relationship between the phylogenetic closeness of two taxa and their morphological similarity [3], the taxonomic tree of a particular flora still contains information on the processes that shape it. Any classification group in the taxonomic tree is generally called a *taxon*. The distribution of the number of subtaxa per taxon at one specific taxonomic level has widely been studied starting with the work of Willis [4] and Yule [5]. Willis observed that the distribution of the number n_g of genera containing a number n_s of species in the set of all flowering plants is a power law of the kind $n_g \propto n_s^{-\gamma}$ with an exponent $\gamma = -1.5$. Two years later Yule proposed a branching process model to explain this distribution. Since then, the shape of taxonomic abundance distributions has been the object of a large number of studies. (For general reviews in the field see [6–8] and references therein. For details on the connection between phylogenesis and community ecology see Webb *et al* [9].) Burlando [8] extended these results to other pairs of taxonomic levels and observed similar behaviors for the distribution of the number n_t of taxa with n_{st} subtaxa. Models have been proposed in order to reproduce this behavior [10–13].

In this paper, we study the topological properties of taxonomic trees with the specific aim of shedding some light on the possible qualitative and quantitative differences between real ecosystems and random species assemblages. Two main points distinguish our approach from those already present in the literature. First, instead of considering single taxonomic levels (as in the case of Willis [4] and Burlando [8]), we present results obtained from the study of the statistical properties of the entire taxonomic tree as an all. Second, unlike previous studies that focused on specific taxonomic groups, such as Fabaceae, Poaceae or Brassicaceae, we analyze floras resulting from plants collected in the same ecosystem or at least in a specific geographic and climatic area. These plants do not necessarily belong to the same taxonomic group. They represent species that actually coexist, sharing the same environment and same ecological conditions.

2. Data and methods

2.1. Taxonomic data sets and graph representation

We studied 22 different floras with different geographical and climatic properties from all around the world. The size of the single data sets spreads from about 100 to 40 000 species. All species considered in different floras belong to the phylum of vascular plants (earthly plants with a lymphatic system). Most data sets have been kindly made available by the Department of Plant Ecology of the University of Rome ‘La Sapienza’. Data sets on the Flora of Lazio and Flora of Rome have been transcribed respectively from Anzalone [14] and Celesti Grapow

et al [15]. For data sets on the Flora of the Coliseum in Rome through centuries we referred to Caneva *et al* [16].

In all data sets we consider a taxonomic classification tree made up of nine levels: species, genus, family, order, subclass, class, sub-phylum, phylum and sub-kingdom. All species are classified according to the nomenclature by Cronquist [17–20]. We adopt a graph representation of the taxonomic tree. We assign a vertex for each taxon and an edge is drawn between two vertices i, j if the corresponding subtaxon j belongs to the taxon i . At the highest level, all species are eventually grouped in the same taxon; this implies that the resulting topology is that of a particular type of graph called a ‘tree’, i.e. a connected graph without loops in which any vertex can be reached starting from a specific node named root or source.

2.2. Random subsets

To compare the results obtained for the data sets with a null hypothesis we consider random species collections. We start from a pool of about 100 000 species from all around the world (a fraction of all vascular plants in the world) that contains all the species in the considered data sets. Each data set represents a subset of the pool corresponding to species collections with specific geographic and climatic properties. From this pool we extract different random collections of species with sizes comparable to those of the real species assemblages. If we want to generate a randomized version of an ecosystem of 100 species we simply select 100 species from the entire pool of 100 000 species with uniform probability. Note that only the taxa corresponding to the species level are included in the pool. The random extraction is carried on only at the lower level of the taxonomic tree. The entire taxonomic classification from the genus up to the phylum is known for each element in the pool. The taxonomic tree corresponding to the random collection is thus recreated by clustering together the extracted species that happen to belong to the same genus and by iterating this clustering procedure until we have reconstructed the nine-level taxonomic tree of every random collection. We then consider the frequency distribution of the degree of these trees.

3. Results

For every data set we represented the entire taxonomic classification as a nine-level tree graph (see the data and methods section for details). We computed the frequency distribution of the degree, defined as the probability to have k subtaxa for every taxon in all the tree, regardless the specific taxonomic level to which the different taxa actually belong. We observed a universal broad distribution, independent upon the geographic and climatic features of the different species assemblages (figure 1).

In all data sets, the initial slope of the frequency distribution (small values of the degree $1 < k < 20$) is in the range (1.9–2.7) and it decreases with the size of the system (number of species in the data set). For $k > 20$ the distribution shows a clear bending that becomes more and more evident as the size of the system increases. We are not interested here in fitting the taxa distribution with any specific function. As we will see in the following, we rather want to show that the properties of this distribution are different if we consider random species collections instead of real floras. Interestingly, we found that this result is robust in time. An example of this robustness is given by the analysis of six species collections representing the flora inside the Coliseum in Rome at six different historical periods from the year 1643 to 2001 [16]. We observed that the behavior of the frequency distribution of the degree holds through temporal evolution of the system.

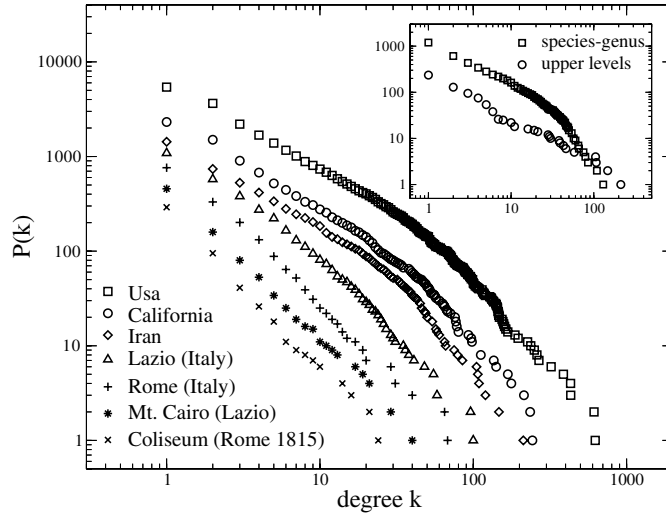


Figure 1. Frequency distribution of the degree for some of the considered species collections (we show here the cumulative distribution which represents the distribution of the number of taxa containing more than k subtaxa). The distribution is universal through different assemblages. We observe a clear bending around $k = 20$ which becomes more evident as the size of the system increases from about 250 (*bottom*) to about 33 000 (*top*). Since higher taxa definition is somewhat arbitrary we show what is the effect of those on the statistics of the whole tree. *Inset:* we make a comparison between the frequency distribution of the degree for the entire tree of the Flora of Iran (outside the inset) and the contribution of the species–genus levels and of the rest of the tree from the family up to the phylum of the same data set.

To gain insight into the behavior of the frequency distribution of the degree and in the presence of the bending, we split the taxonomic tree into two parts. We compared the contributions given separately to the frequency distribution of the entire tree by the nodes belonging to the genus level and those belonging to all other levels. Figure 1 (inset) shows the difference between the frequency distribution of the number of genera containing k species and that of the number of all upper taxa, from the family level up to the phylum containing k subtaxa. The first one is mainly responsible for the shape of the final distribution at small values of the degree and shows a very strong bending for $k > 20$. The contribution of the second one is relevant for the smoothing of the bending at larger values of the degree.

Another remarkable universal feature across taxonomic levels emerges from the study of the topology. If we label each taxonomic level by L , we can define n_L as the number of taxa at level L . In order to understand the organization of taxonomic levels, we defined $n_g = n_2, n_f = n_3$ and $n_o = n_4$, respectively as the number of genera ($L = 2$), families ($L = 3$) and orders ($L = 4$) in our species assemblages, and we measured the relationship between these numbers and the number $n_s = n_1$ of species ($L = 1$) in each data set. The resulting distributions are well fitted by power-law functions with exponents less than 1 (figure 2). As expected [10], the number of higher taxa rises at a slower rate than species richness. But what is more surprising is that for these taxonomic levels the number n_{L+1} versus n_L scales as a power law:

$$n_{L+1} \propto n_L^\alpha, \tag{1}$$

with universal exponent $\alpha = 0.61$ independent upon L . This property can be understood from the main panel in figure 2 by noting that $n_2 \propto n_1^\alpha$ with $\alpha = 0.61$ is the scaling between n_g

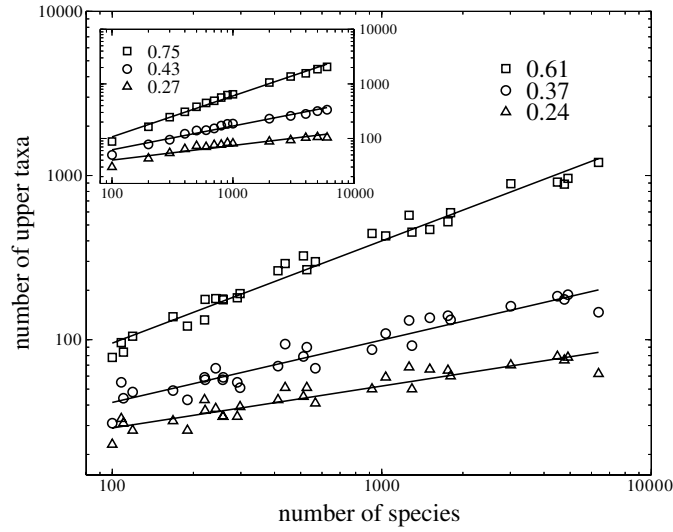


Figure 2. Relationship between the numbers n_g (squares), n_f (circles) and n_o (triangles), respectively the number of genera, families and orders in our species assemblages, and the number of species n_s . The resulting distributions are well fitted by power-law functions with exponents less than 1 showing that the number of higher taxa rises at a slower rate than species richness [10]. Moreover, the number n_{L+1} of taxa at level $L + 1$ versus the number n_L of taxa at level L is as a power law with universal exponent $\alpha = 0.61$. *Inset:* the same relationship as in the case of random collections of species (results obtained as an average over 100 random collections for each value of n_s). Three exponents are greater than that in the real case suggesting that real species assemblages show a greater taxonomic similarity than random ones. Moreover, in this case the scaling exponent between n_{L+1} and n_L is not universal.

and n_s , while $n_3 \propto n_2^\alpha \propto (n_1^\alpha)^\alpha \propto n_1^\beta$ with $\beta = \alpha^2 = 0.37$ is the scaling between n_f and n_s , and finally $n_4 \propto n_3^\alpha \propto ((n_1^\alpha)^\alpha)^\alpha \propto n_1^\gamma$ with $\gamma = 0.23$ (very close to the fitted value 0.24) is the scaling between n_o and n_s . This remarkable universality, on which we comment later, has never been documented before in the literature to the best of our knowledge.

We compared our floras to a null model of random collections of species in order to test and quantify the significance of these universal results. We considered a pool of about 100 000 species from all around the world (containing also all the species in the considered data sets) and we randomly extracted different collections with sizes comparable to those of the real species assemblages. We reconstructed the taxonomic tree of these random collections and studied the frequency distribution of the degree (see the data and methods section for details). In figure 3 we compare the degree distribution of a real species assemblage to that corresponding to a random collection of the same size.

Finally, we studied the frequency distribution of the number $n_s(g)$ of species in each genus g , normalized by its average $\langle n(g) \rangle$ and we compared results for a species assemblage and a random collection of species. Starting again from our pool of about 100 000 species, we considered a large number of different random distributions of a number of species, corresponding to the size of the real list studied, among the different genera present in the pool. At the end, we obtained a mean occupation number $\langle n(g) \rangle$ for each genus. We then considered a real species assemblage and a single random collection of species of the same size and we measured the degree $n_s(g)$ of each genus in both cases. We computed the frequency distribution of the ratio $n_s(g)/\langle n(g) \rangle$ and we compared a real species distribution

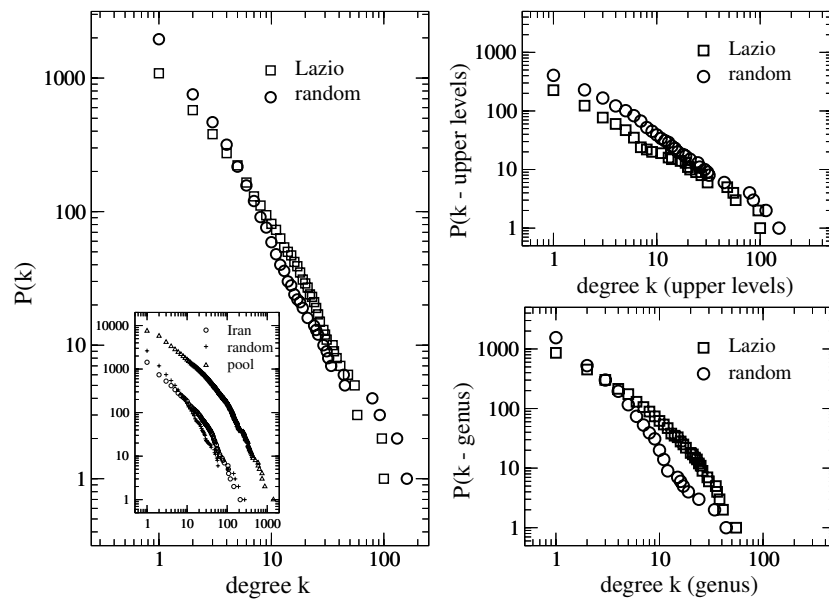


Figure 3. Frequency distribution of the degree for the Flora of Lazio and for a random collection of species of the same size, about 3000 species. *Inset:* the same comparison in the case of the Flora of Iran; the frequency distribution of the entire pool of 100 000 is also shown. *Right:* the comparison between the specific distributions in the case of the species–genus levels (*bottom*) and of the rest of the tree (*top*) is shown. The random data are always obtained as a mean over 100 realizations (random sampling of the big pool of species).

of species among genera with a random one. The two distributions are shown in figure 4 (with a comparison between the Flora of Lazio and a random collection of the same size; similar results hold for every real species assemblage).

4. Discussion

Recently, a great variety of social, technological and biological systems have been represented as graphs. In most cases the statistical properties of such graphs are universal. The frequency distribution of the number of links per site k (i.e. the degree) is distributed according to a power law of the kind $P(k) \propto k^{-\gamma}$ with an exponent γ between 2 and 3. This result suggests the possible existence of a unique mechanism for the onset of such common features [21]. In the case of real species assemblages the frequency distribution of the degree of the corresponding taxonomic tree cannot be properly fitted by a power law but still the functional form appears to be a robust one across geography and time. Instead of trying to find the proper fit for such quantity, we concentrate on the different properties we can measure for real floras and random collections. The deviations from a power-law function actually contain the relevant information on the presence of a correlation between different species populating the same area. Figure 1 shows the frequency distribution of the degree of the taxonomic tree for some of the floras considered in this study. The result is stable in time and is independent of the geographic and climatic properties of the specific data set. The characteristic shape of the distribution derives from a different behavior of the branching process across different levels of the taxonomic tree. The comparison of the degree distribution at different taxonomic levels

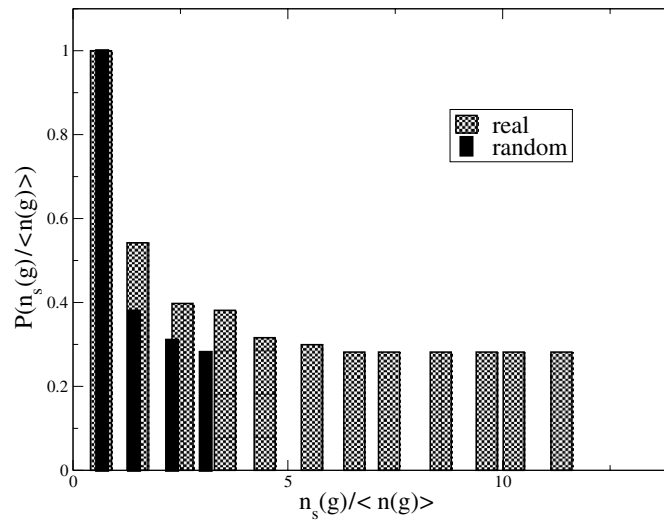


Figure 4. Distribution of the normalized number of species in each genus for a random uniform process and for a real flora (Flora of Lazio, about 3000 species). The deviations observed in real flora are one order of magnitude larger than the standard deviation (here equal to 0.54) that indicates the existence of an “attraction effect” between species leading to a smaller genus diversity. The random data are obtained by averaging over 100 realizations.

suggests that the taxonomic tree is far from being equilibrated. The origin of the bending in the distribution of the entire tree seems to lie in the distribution of the degree at the genus level, which strongly contributes to the smaller values of the degree, while the distribution of the upper levels contributes to the tail of the distribution lightening the bending. Moreover, the study of the number of higher taxa as a function of the species richness (figure 2) reveals that the number of species increases more rapidly than the number of taxa at the upper levels. This behavior propagates through the taxonomic tree: the number of families increases at a slower rate compared to the number of genera but it rises faster than the number of orders. More precisely, the number of taxa at a given level versus the number of taxa at the lower level is a universal power law with exponent $\alpha = 0.61$ which is level independent. Therefore, even if the details of the branching process differ from one level to the other, the overall taxonomic diversity measured by the number of taxa at a given level obeys a surprisingly regular scaling from the leaves to the root. This suggests that the observed scaling behavior reflects some intrinsic organization principle underlying the taxonomic structure of real ecosystems. This result is confirmed by the analysis of randomized data (see below) where this universality is destroyed.

We also measured the mean degree of the genera for different sizes of the data sets and we found that it increases with size. In bigger assemblages the number of genera obviously increases but with an exponent smaller than 1, meaning that a greater number of species are distributed among a proportionally smaller number of taxa. The combination of these two results, together with the fact noted previously that different taxonomic levels contribute to different regions of the degree distribution, could explain why the frequency distribution of the degree of the entire tree does not change in the same way for different values of k while increasing the size of the system. Even if taxonomic classification is somewhat arbitrary, these results indicate a precise trend. There are examples of branching process models that try

to reproduce similar behaviors in the distribution of subtaxa per taxon at specific taxonomic levels [5, 13, 22]. This behavior of the degree distribution of taxonomic trees either reflects a topological property of the general structure of the taxonomic classification (i.e. the taxonomic tree of all the plants in the world follows this peculiar distribution and so does every subset) or it reflects the existence of some interaction between different species in the same environment. We now discuss the evidence that the latter hypothesis holds.

The most immediate test of the significance of the results presented above is a comparison between observed data sets and a null model of random collections of species. The frequency distribution of the degree in the real and random cases is shown in figure 3. If we consider the entire tree, we find that the initial slope of the distribution (small values of the degree $k < 10$) is different in the two cases. In figure 3 (left) we have 2.1 for the Flora of Lazio and 2.5 in the case of a random collection of the same size extracted from the entire pool (similar results with specific values of the slope hold for any of the observed data sets). Moreover, for $k > 10$ the bending, that is evident in the case of the real species assemblage, is not present in the random case. In the inset, we present the same comparison for the Flora of Iran. The third distribution given in the plot corresponds to the entire pool of about 100 000 species. Note that, unlike the random collection, the real system is able to reproduce the behavior of the pool. Once again we consider separately the distribution at the species–genus level and for the rest of the tree (figure 3 right). In the first case we have a different slope in the first part of the distribution and very soon a divergence of the two distributions (figure 3, right bottom). In the second case the distribution corresponding to the random collection of species overestimates that relative to the observed data at all values of the degree (figure 3, right top). Since the two data sets are subsets of the same pool of species and are classified according to the same taxonomic structure, these results provide a quantitative measure of the expected long-range correlations between different species in the same environment. These correlations shape the taxonomic structure of real species collections generating specific features that cannot be shared by a random subset. Differences are actually not very strong and one could object that real data sets are simply biased random collections. But fundamental ecological assumptions together with previous and further considerations in our discussion strengthen the idea that nature actually follows a non-random path in the organization of an ecosystem and that differences between real and random collections, even if slight, are to be considered as the evidence of this non-random behavior. Moreover, we have observed that an increase in the size of the big pool of species from which we extract the random collections results in stronger differences between the real data sets and the randomized one.

An even more convincing confirmation of the presence of correlations between species in the same environment comes from the comparison of the behavior of the number of superior taxa versus the number of species. In the random case the variation in the number of genera, families and orders with respect to the number of species is qualitatively similar than to that in real systems, but the values of the exponents are always greater (figure 2 inset). This result points out that species in the same environment are more taxonomically similar than random collections of species. From an ecological point of view, co-occurring species that experience similar environmental conditions are likely to be more taxonomically similar than ecologically distant species, because of the process of environmental filtering. During evolutionary diversification species traits tend to be preserved within a taxon. As a consequence of this, the species capabilities of colonizing a given piece of physical space with a certain set of environmental conditions is thought to depend to some degree on their taxonomic similarity [12]. In the random case the universality of the scaling exponent relating the number of taxa at a given level to that of taxa at the lower level is destroyed. This is easily seen because, if universality held in the random case too, the families–genera scaling

exponent (0.43) and the orders–families one (0.24) would be respectively the second and the third power of the genera–species scaling exponent (0.75) as in the case of real data. Instead we have $0.75^2 \simeq 0.56 > 0.43$ and $0.75^3 \simeq 0.42 > 0.27$. Therefore the universality displayed by real data is not accidental and appears to be a meaningful characteristic of co-evolved communities of species which is not shared by random species assemblages.

Finally, the mean degree of the genera grows more slowly with the number of species in the random case than in the real one, confirming the idea of a greater taxonomic diversity of random species collections. A wide range of evolutionary models suggests that this correlation between species could lie on evolutionary mechanism such as speciation, selection and competition [23]. One possible explanation of the presence of power laws in taxonomy systems has been proposed in the framework of the spin-glass theory [13]. In the simplest version, a spin-glass (considered as a paradigmatic model of disordered systems) consists of randomly coupled binary variables (spin-up or spin-down) defined for every node of a regular lattice. The idea is that phenotype traits can be coupled together in a similar fashion. Some aspects of evolution could then be described by the same mathematical framework as that employed in the description of a spin-glass system. The latter is known to have equilibrium states characterized by a hierarchy of sub-equilibrium states. Ultimately, it is the intrinsic disorder (in this case the genetic codes of the various species) that naturally produces the observed scale invariance. This can also be empirically found by means of a simple statistical model [24]. It is interesting to note that, as the exponent γ of the degree distribution has a value between 2 and 3, the distribution itself has a finite average value and diverging fluctuations around this value. Biologically, this means that, even if the mean number of off-springs in a taxon can be defined, every now and then a taxon with a huge number of off-springs appears. This quantitative analysis suggests that taxonomic trees are related to the wide class of scale-free networks present in epidemics [25] as well as in protein interactions [26].

We discuss one last result in agreement with our previous considerations. We studied the distribution of species among genera. The results given in figure 4 indicate that in real assemblages, species are not randomly distributed among genera. The frequency distribution of the ratio $n_s(g)/\langle n(g) \rangle$ (degree of each genus normalized to the mean occupation number) decays very rapidly in the random case. The deviations from the observed distribution are one order of magnitude larger than the standard deviation, spotting that in real assemblages there is an effective attraction between species that leads to over-represented genera, while random species collections tend to spread among a greater number of genera (less species for each genus). This result is in good agreement with the previous assertion that real data sets are more taxonomically similar than random collections of species, and with the hypothesized existence of some universal mechanism leading species organization in nature.

In conclusion, our results confirm that a taxonomic tree is not simply an artificial classification of species, but it contains information on the processes that shape the corresponding flora. We have studied the frequency distribution of the degree for the taxonomic trees of several data sets corresponding to collections of species from different geographical and climatic environments and we have revealed the presence of universal stable properties. We have numerically characterized real species assemblages with respect to random collections spotting differences in the frequency distribution of the degree and confirming the idea that species in the same environment are characterized by greater taxonomic similarity than random ones. In particular, we have observed that genera diversity in real assemblages is usually (very) low. All these results suggest the existence of some long-range correlation between species in the same environment and they could help in the realization of a new model able to reproduce such properties. Finally, we conclude with a cautionary remark: in this paper we used traditional Linnaean classification and not phylogenetic data, although the latter may seem

preferable. In principle, the species taxonomic information could easily be derived in a full phylogenetic context, by replacing Linnaean taxonomic trees by proper phylogenetic trees. 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. Moreover, we encounter two main limitations in applying a topological approach to phylogenetic trees [12]. First, the structure of the phylogenetic tree is unstable and it depends on the species included in such a way that the number of nodes between two taxa is determined by the particular reference phylogeny used for the classification. As a result, the resulting measures 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 given taxon will influence its branching structure in the sense that two species drawn at random from a species-rich taxon are likely to appear more topologically distant than two species from a species-poor taxon. For all these reasons, it is more realistic to remain within a Linnaean taxonomic framework. We think that the results presented in this paper could thus contribute to a better understanding of the mechanisms ruling organization and biodiversity in plants ecosystems.

Acknowledgments

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