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Short communication

More rich means more diverse: Extending the 'environmental heterogeneity hypothesis' to taxonomic diversity

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ABSTRACT

It is widely appreciated that increasing environmental heterogeneity is one of the chief determinants of high species richness. An additional outcome that arises from the relationship between environmental heterogeneity and species richness is that species richer areas are usually taxonomically more diverse than species poor areas. For instance, due to the larger niche availability, species that coexist in heterogeneous environments experience a less severe effect of clustering in their functional traits giving rise to assemblages that are more functionally diverse than in more homogeneous areas. On the other hand, due to the conservatism of many species traits during evolutionary change, the ability of species to colonize the same ecological space is thought to depend at least partially on their taxonomic similarity, such that a positive relationship between the species taxonomic relatedness and their trait similarity is expected. In this paper, we tested the relationship between species richness and taxonomic diversity with 11 florae collected in Latium (Central Italy). The significance of the observed association was then verified with a null model assuming a random distribution of species across the landscape.

1. Introduction

A widely recognized consequence of the relationship between species and the environment is that one expects to find more species in areas of high environmental heterogeneity (Kerr and Packer, 1997; Fraser, 1998; Ewers et al., 2005; Dufour et al., 2006). The relationship between environmental heterogeneity and species richness is one of the strongest determinants of the species–area relationships. For instance, most environmental variables possess some degree of spatial autocorrelation and exhibit distance decay (e.g. Burrough, 1981; Palmer, 1990), meaning that heterogeneity in the environment increases as a function of spatial scale (see also Hobbs, 1988). Therefore, especially at landscape/regional scale, the species–area relationship should be largely determined by environmental heterogeneity (Rosenzweig, 1995; Whittaker, 1998).

A second, less obvious, consequence to be expected from the connection between environmental heterogeneity and species richness is that species richer areas are on average taxonomically more diverse than species poor areas. This is because, under the assumption of trait conservatism during evolutionary diversification, a positive relationship between the species taxonomic relatedness and their ecological similarity is expected such that co-occurring species that experience similar environmental conditions are likely to be more taxonomically similar than ecologically distant species. This simple expectation has been verified in a number of systems as diverse as tropical rainforests (Webb, 2000) and urban ecosystems (Ricotta et al., 2008a). On the other hand, due to the larger niche availability, species that coexist in heterogeneous environments experience a less severe effect of taxonomic clustering giving rise to more diverse assemblages. In this paper, the relationship between species richness and taxonomic diversity is tested using data from 11 florae collected in Latium (Central Italy). The observed richness-diversity association was then compared to the results of an adequate null model assuming a random distribution of species across the landscape.

2. Data and methods

We tested the validity of the relationship between species richness and taxonomic diversity using published data from 11 different seed plant florae of Latium. The data set (see Table 1) covers very different environments ranging from mountain regions to coastal zones and from urban areas of high human impact to areas of relatively low human pressure.

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Table 1
Location, species richness and bibliographic source of the 11 florae analyzed in this study.

Location	Species richness	Source
Ausoni Mountains	1412	Lucchese, F., Lattanzi, E., 2000. Atlante della Flora dei Monti Ausoni. Regione Lazio, Roma
Castel di Guido	502	Bartolucci, F., De Lorenzis, A., Cecere, J.G., 2004. La Flora vascolare. I quaderni dell'Oasi Castel di Guido, vol. 1. LIPU, Roma
Castelli Romani Regional Park	994	Bassani, P. Unpublished data
Circeo National Park	1169	Anzalone, B., Lattanzi, E., Lucchese, F., Padula, M., 1997. Flora vascolare del Parco Nazionale del Circeo (Lazio). Webbia 51, 251–341
Flora of Colosseum	236	Celesti-Grapow, L., Caneva, G., Pacini, A., 2001. La Flora del Colosseo (Roma). Webbia 56, 321–342
Monte Testaccio	167	Pavesi, A., Leporatti, M.L., 1999. La Flora vascolare del Monte Testaccio in Roma (Lazio). Informatore Botanico Italiano 30, 25–36
Monte Rufeno Natural Reserve	982	Scoppola, A., 2000. Flora vascolare della Riserva Naturale Monte Rufeno (Viterbo, Italia centrale). Webbia 54, 207–270
Prenestini Mountains	920	Guarrera, P., Lattanzi, E., 1992. La Flora dei M. Prenestini (Lazio), con osservazioni sulle piante officinali. Annali di Botanica, 48 (S7) 33–75
Flora of Rome	1083	Celesti-Grapow, L. 1995. Atlante della flora di Roma. ARGOS Ed., Roma
Selva del Lamone	822	Scoppola, A., Lattanzi, E., Anzalone, B., 1996. La Flora del Lamone (Alto Viterbese). Annali di Botanica 52 (S11) 169–238
Veio Regional Park	752	De Sanctis, M., Attorre, F., Bruno, F., 2003. Contributo alla conoscenza della flora veientana (Roma). Informatore Botanico Italiano 35, 343–366

According to many authors (e.g. Izsák and Papp, 1995; Webb, 2000; Ricotta et al., 2008b), we computed the taxonomic diversity of each flora based on the branching topology of the corresponding taxonomic tree. Nonetheless, with all the shortcomings of taxonomic diversity measures obtained from phylogenetic data (see Ricotta et al., 2008b), we used Linnaean taxonomy as a reasonable surrogate for phylogeny, as suggested by Crozier et al. (2005): "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 judgment as to the degree of difference. Thus surrogate phylogenies can be inferred from systematic nomenclature".

First, all pairwise species distances within a given flora were calculated using the corresponding topological distances (i.e. the number of nodes separating two species across the Linnaean dendrogram). According to Prinzing et al. (2001) such nodal distances correspond to a certain degree to ecological and niche distances between lineages. The overall taxonomic diversity of the flora was then computed as the mean of all non-zero pairwise species distances. 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). To explore the influence of species richness on taxonomic diversity, for all florae in Table 1, we calculated the linear regression of taxonomic diversity on species richness.

In principle, since taxonomic diversity is an intensive measure computed as the mean value of all non-zero pairwise species distances in a given flora, it should be independent of species richness. Nonetheless, to correctly test theoretical assumptions on the effects of species richness on taxonomic diversity (i.e. whether the observed correlation is due to statistical artifacts or to some causal ecological process), observational data on the diversity–richness relationships must be compared to an appropriate null expectation. To determine whether the observed relationship between taxonomic diversity and species richness was significantly different from random, we compared the slope s and the correlation coefficient R found for the least-squares regression of the actual data to a distribution of similarly calculated values from 999 randomizations; in each randomization we generated 11 virtual florae reassigning species randomly with replacement from a 'pooled species list' (2063 species) obtained assembling all species found in the 11 florae analyzed. Throughout the randomizations, the number of species of the virtual florae was held equal to the actual species richness found in the real florae (see Ricotta et al., 2008a). P-Values (one-tailed test) were computed as the proportion of randomized values that were as high or higher than the slope and the correlation coefficient obtained from the actual data. A second randomization test was then applied according to the same procedure, but resampling the species from the larger regional flora of Latium (Conti et al., 2005; 3042 species) instead of using the pooled species list from the selected study areas.

3. Results

In Fig. 1 the scatter plot of taxonomic diversity versus species richness shows a positive relationship between these variables ($R = 0.858$, $s = 0.024$), while the correlation coefficients and the slopes of the 999 least-squares regressions obtained under both null models of randomly assembled florae were both significantly lower than the observed values, implying a direct effect of species richness on the taxonomic diversity of local assemblages (see Table 2). Values of R varied from 0.905 to −0.900 for the null model obtained resampling the whole flora of Latium with a significance level $P = 0.004$ (i.e. only three values out of the 999 randomizations were found to be higher or as high as the actual coefficient of correlation), while resampling the pooled species list of 2063 species produced null values of R between 0.891 and −0.873 ($P = 0.003$). As regards the slope, for both null models the most extreme level of significance possible $P = 0.001$ (i.e. 1 in 1000) is obtained meaning that, for our data, the regression between species richness and taxonomic diversity is significantly steeper than expected by a random null model. Finally, as shown in Table 2, for both null models, the mean values of R and s are very close to zero implying no relationships between species richness and taxonomic diversity if species assemblages are generated randomly.

4. Discussion

According to Gotelli and Graves (1996), a null model operates as a standard statistical null hypothesis for detecting pattern that would be expected in the absence of a particular ecological mechanism. Hence, the use of an appropriate null model helps the researcher in keeping the effect of actual ecological driving forces separate from statistical artifacts. By randomizing the species composition of the florae analyzed keeping their richness constant, our null model allowed us to highlight the relationship between the richness and the taxonomic diversity of seed plants assemblages, thus extending the potential influence of habitat heterogeneity well beyond the expected effects on species richness.