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TREECREEPER: SOFTWARE FOR TESTING FOR HABITAT FILTERING IN LOCAL COMMUNITIES

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Abstract – In this paper we introduce a program for testing for habitat filtering in local communities compared to a regional species pool. Based on phylogenetic or functional species data, the program first calculates the mean species dissimilarity in the local community. Next, it compares this value with a null distribution of expected values obtained drawing species randomly and without replacement from the regional species pool.

Keywords: Local species pool, Mean species dissimilarity, Null model, Randomization process, Regional species pool, Species clustering

Introduction

Several theories have been proposed to explain the processes that drive species coexistence. Among others, the species pool hypothesis states that the large-scale species pool is the chief parameter in driving local-scale community assembly through filtering of species that can persist within a community on the basis of their tolerance of the abiotic environment. If species traits are preserved to some extent during evolutionary diversification such that closely related species are more functionally similar than more distant ones, co-occurring species that experience similar environmental conditions are likely to be more phylogenetically similar than expected by chance (Cavender-Bares et al., 2009). Therefore, a high degree of phylogenetic and/or functional clustering in local communities as compared to the available regional species pool is usually assumed as a fingerprint of habitat filtering.

Here, the regional species pool is defined as the total number of species in a target landscape or region. From a biological viewpoint, the regional pool represents the reservoir of species that are potentially able to survive and reproduce within a given portion of biotic space, thus determining the small-scale species richness within local communities (Dupré, 2000). The presence of a locally clustered phylogenetic or functional species composition is usually detected with randomization tests (see Vamosi et al., 2009) in which multiple local communities are compared within the context of a larger regional species pool that is composed of all species within the local communities. However, such tests should be applied with care because relying on inadequate null models can lead to significant effects on the ecological hypothesis being tested. It has been recently shown by Hardy (2008) that failing to account for the species rarity and commonness when testing for habitat filtering in local communities may increase the rate of type I errors (or false positives). Therefore, to avoid inflated rates of type I errors, we need to consider the species occurrences in the regional phylogeny. The present paper thus describes a computer program, TreeCreeper, developed for testing for habitat filtering in local communities that accounts for the species rarity and commonness in the regional species pool. How this is done will be clear in the next section, when we discuss the randomization options offered by the program.

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PROGRAM DESCRIPTION

TreeCreeper is designed to perform tests for habitat filtering in local communities based on phylogenetic or functional species data. Given a phylogenetic or functional symmetric dissimilarity matrix between species and a species × site matrix with the Boolean presence/absence scores of each species in the N communities (or plots, quadrats, assemblages, etc.), the program first calculates the mean dissimilarity between all species in each community (i.e. the mean value of all pairwise species dissimilarities in the sub-diagonal half of the input dissimilarity matrix). The observed mean species dissimilarity is then compared with the dissimilarity expected if the same number of species were drawn randomly and without replacement from the available (i.e. regional) species pool, which consists of all species in the species × site matrix.

Two different randomization methods are available for generating a null distribution of expected mean dissimilarities. The first method uses only species presences and absences. With this method the random communities are constructed assuming that each species has an equal probability of selection, irrespective of the species occurrences in the species × site matrix. With the second method, a species probability of occurring in a random community is proportional to the species occurrence in the species × site matrix (see Kraft & Ackerly, 2010; Thompson et al., 2010), or to any other user-defined probability distribution.

The number of randomized values that are higher/lower than the observed mean dissimilarity indicates whether the observed value is improbable enough to reject the null hypothesis that there is no phylogenetic or functional over- or underdispersion in the data. If the local community is significantly underdispersed than the null distribution drawn from the regional species pool (i.e. if the observed mean dissimilarity is significantly lower than the random expectation), then the evidence is considered consistent with the hypothesis that abiotic filters helped structure the local community. On the other hand, if a local community is found to be significantly overdispersed compared to the null distribution drawn from the regional species pool (i.e. if the observed mean dissimilarity is significantly higher than the random expectation), then it is likely that the local community has been structured by competition processes (see Webb et al., 2002; Cavender-Bares et al. 2009).

Running the program will bring up the main window (Figure 1) containing the different options for the processing routine. The different items are described in detail in the user's manual together with the format of the source data that must be in a comma-separated values (CSV) file. The manual can be downloaded along with the executable from the Web site of the Department of Forestry and Environmental Sciences of the University of Naples 'Federico II', URL: *http://www.ecoap.unina.it/doc/publications.htm,* or from *http://www.worldinabox.eu/TreeCreeper.* Example files are also included.

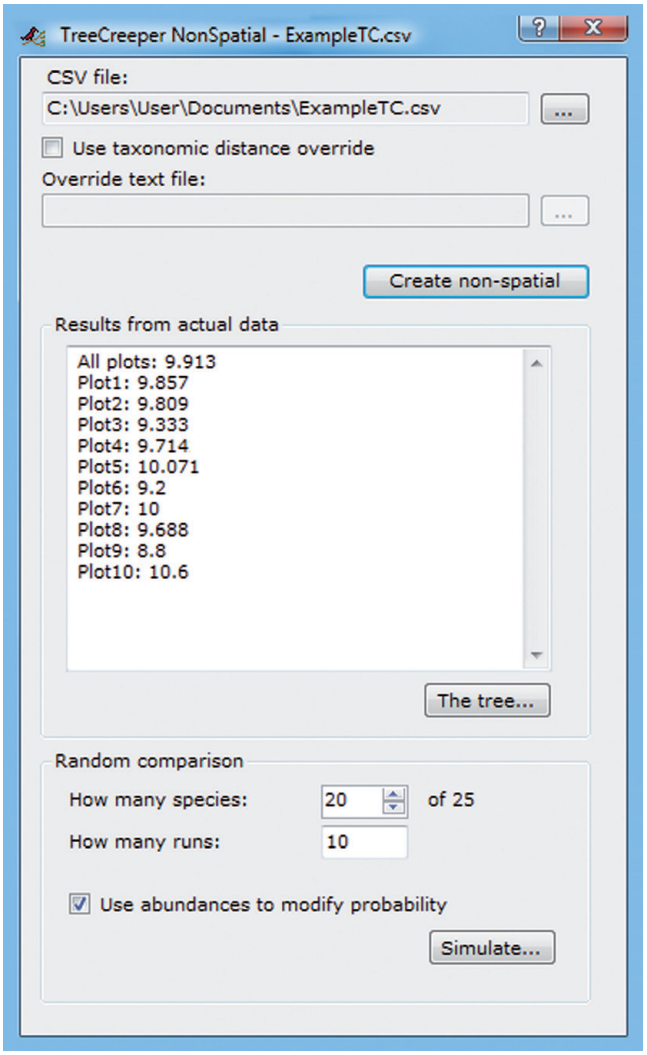

Figure 1. Overlook of the program starting window showing the different options for the processing routine.

As a default option, TreeCreeper calculates the mean taxonomic distance of a species list based on a classical Linnaean taxonomic hierarchy in which taxa are assigned to taxonomic categories, like species, genus, family, etc. In this case, the taxonomic distance distance between two species is calculated as the number of nodes connecting both species along the taxonomic tree. Specifically, if two species belong to the same genus, their distance is 2 (there are two nodes separating both species); if two species belong to different genera but the same family, their distance is 4, and so forth. Besides using taxonomic distances, any other symmetric pairwise species dissimilarity can be used. For example,

TreeCreeper allows calculating the mean phylogenetic distance of a species assemblage using the pairwise phylogenetic distances obtained from the 'phydist' routine of the program Phylocom (Webb et al., 2008).
Once the user has specified the input files to base the analysis on, the testing procedure is composed of two steps: the program first calculates the mean dissimilarity for each community and for all available species in the regional species pool. These values are listed in the results box of Figure 1. Next, to test whether the observed mean dissimilarities are clustered or overdispersed compared to a random expectation, the random comparison allows you to pick random sub-selections from the regional species pool using one of the available randomization methods. TreeCreeper allows you to select the number of species to draw at random and without replacement from the regional pool and the number of runs. The mean dissimilarity values of all random assemblages are listed in a separate results box. TreeCreeper has been designed to be intuitive, thereby making the program easy to use. The program flexibility in the user's selection of input data and randomization options may help ecologists revealing the processes governing the assembly and coexistence of species. TreeCreeper is freely available, providing that it is not for commercial use and that every published material derived from it refers to the program. Comments (favorable and otherwise!) and bug reports can be e-mailed to the authors.

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