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Maximal species richness: an empirical approach for evaluating woody plant forest biodiversity

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Abstract

Different approaches have been used to determine reference values for species richness, usually as an estimate of potential biodiversity. But, there are practical and theoretical problems with the measurement and concept of potential biodiversity. Here we propose an empirical statistical approach to estimate maximum richness for woody plants. Using a large forest inventory data set from Catalonia (NE Spain), we analyse relationships between richness and nine environmental and structural variables. We selected three of the nine variables (annual potential evapotranspiration, canopy cover and undergrowth cover) to model relationships with maximal average species richness for multiple sites and ranges of environmental conditions. We then used linear regression to compare the lowest maximal average species richness predicted by the models for each site with observed values for a different set of plots. We use empirical information from plots, while most usual approaches are based on potential species distribution. Therefore, our method provides more integrative information of the effects of natural drivers and management practices.

Keywords: Species richness; Forest inventories; Forest conservation; Potential biodiversity

1. Introduction

Biodiversity in a given area is usually evaluated through surveys quantifying species richness of different taxonomic groups. However, this kind of approach, if performed only once, lacks temporal perspective. If there were available at least two successive surveys for species richness, checklists would be obvious tools for monitoring the effects of past management (Droege et al., 1998). Only when processes explaining the changes between both surveys are known, can this kind of information support management decisions.

A different approach is to evaluate the current state of conservation by comparing observed biodiversity to a reference value. This could be done by estimating potential richness using environmental and biotic characteristics of the area studied. However, there are many difficulties associated with choosing a reliable procedure, because relationships between richness and environmental and biotic factors often are largely unknown. The usual way to determine potential richness is to use the habitat associations of each species to estimate its potential distribution over a territory for which a map of habitats is available. Habitats map can be generated by

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merging GIS-based maps of biotope inventories, land uses, climatic, biological or geological variables, etc. Distribution maps for multiple species can then be overlapped to obtain an estimate of the potential species richness for each point (map of species richness) and predict potential species distributions (i.e. Beard et al., 1999; Lenton et al., 2000). This approach is employed frequently in gap analysis (Scott et al., 1995, 1996; Prins and Olff, 1998; Skov and Borchsenius, 1997; Crist, 2000, see also relevant documents in the web, for the National Gap Analysis Program, http://www.gap.uidaho.edu; for the California Gap Analysis Project, http://www.icess.ucsb.edu/annual-report/report_97-98/ressum98.html). An alternative approach, also based on individual species maps, has been followed to assess the biodiversity potential in the European ecosystems defined by CORINE biotopes. This approach used an expert model (LARCH-EUROPE) that produced spatial cohesion maps of the habitats (Foppen and Chardon, 1998).

The limitations of approaches based on individual species are obvious. For example, errors are multiplied when using many data layers (Flather et al., 1997). Overestimations of potential richness may also be included by rough resolution in habitat definition (Smith and Catanzaro, 1996). For example, a species can be considered as associated with a riparian habitat but many types of riparian habitats may exist and perhaps the species is not associated with all of them. Distinguishing a low number of habitat types should result in a higher estimate of potential richness values for any patch. Another problem arises when predicting the occurrence species that are rare or subjected to metapopulation dynamics. Potential species richness will be overestimated if we assume that every species occurs in any suitable habitat (Krohn, 1996).

In addition, the estimation of species richness must take into account the patch size, since small patches typically sustain lower number of species than large patches. However, the predicted occupancy will be sensitive to the type of function describing the probability of a species occurrence in relation to patch size (Veech, 2000).

In order to avoid so many speculative assumptions about the hypothetical distributions of species, we propose the use of empirical, statistically calculated, maximal species richness as a reference value for estimating the current state of woody plant forest biodiversity under different environmental conditions. In this paper, we use a simple statistical procedure to analyse a large forest inventory data set. We selected those plots with larger richness values to estimate maximal richness of woody plants in relation to the most relevant environmental and vegetation structure variables. Then, we compare maximal and observed values and we discuss the differences between them.

2. Description of the study area

This study is based on data collected across the 31 000(km^2 region of Catalonia, Spain, located beside the Mediterranean Sea in the northeast of the Iberian Peninsula. Grasslands, shrublands and forests cover approximately 60% of the region, but old and dense human occupation has often led to a high degree of fragmentation in its natural systems. Most of the area has a Mediterranean climate, with mild winter temperatures and a significant summer drought which is the main cause of frequent and severe wildfires. However, the region also includes some mountainous areas (that reach altitudes around 3000(m in the Pyrenees) with a cold winter climate. This physiography creates topoclimatic gradients from Mediterranean-type biomes to temperate (winter deciduous forests and shrublands), subalpine (boreal-like conifer forests), and alpine (mountain grasslands) biomes. There also is a gradient due to increasing continentality and decreasing moisture from the coast to the central plains, where shrub subdesertic types of vegetation are dominant. The vegetation of the area, as it occurs all through the entire Mediterranean Basin, has been deeply influenced by human activities and management (Thirgood, 1981). Our study was limited within this region to nearly monospecific forest-types, including evergreen oak (*Quercus ilex*, *Q. suber*) and pine (*P. halepensis*, *P. pinea*) Mediterranean forests, deciduous forests (*Quercus humilis*, *Q. petraea*, *Q. robur*, *Fagus sylvatica*, *Castanea sativa*), middle mountain pine forests (*P. sylvestris*, *P. nigra* ssp. *saltzmanii*) and mountain conifers (*P. uncinata*, *Abies alba*).

3. Methods

Forestry data were obtained from the *SIBosC* data set that includes the results from field sampling in

10 644 circular 10(m radius plots (IEFC; Gracia et al., 1992). The plots were randomly located on the forest areas. In one-fifth of the plots a complete list of woody underground species was recorded. For this study we used a subset of 1387 plots selected under the following criteria: (1) plots must have the record of all woody plant species found in the plot and (2) they must have >80% of the total BA assigned to a single dominant tree species. The reason for this second condition was to reduce heterogeneity due to management practices: because most forests in the region are managed to promote single species dominancy, mixed forests can be considered as cases with a non-standard management for the region and we preferred do not include them in work:

Radiation (kJ(m^{-2} per day), based on field measurements, and derived by the RADIAC program (Gracia, 1990).

Slope (°), measured in the field.

Altitude (m), measured in the field.

Canopy cover, derived from field measurements. Individual tree canopies were considered elliptic and their cover was estimated by measuring the maximum and minimum diameters. Thus, the canopies of different trees could overlap and canopy cover could be >100%.

Undergrowth cover, derived from field measurements of interception along transects, ranging from 0 to 100%.

Mean annual temperature (°C), obtained from the Catalonia climatic maps (CCM), which were been built by interpolating point meteorological data combined with data from a digital elevation model. These had a final resolution of 45(m (Ninyerola et al., 2000).

Mean annual precipitation (mm per year), also obtained from the CCM.

Annual potential evapotranspiration (E_T, mm per year), obtained from the sum of monthly E_T values, which were calculated with the Thornthwaite formula, using the temperatures provided by the CCM.

Annual actual evapotranspiration (E_A, mm per year), obtained from a model developed in the same study area by Piñol et al. (1991), and based on the formula:

$$E_A = \frac{(\text{precipitation} \times E_T)^{(1/k)}}{(1 + (\text{precipitation}/E_T)^k)^{(1/k^2)}},$$

where $k = 2$ is an empirical factor obtained from some catchments located in the study area.

The dependent variable that we considered in each plot was the number of woody plant species, which hereafter we will refer to as species richness.

We built a correlation matrix with all nine environmental variables and richness (Table 1). Because the large sample minimised the possibility of spurious correlations, we directly used the r-values to decide which variables were eventually included in the analysis. Specifically, we excluded those variables that showed $|r| < 0.1$ when correlated to species richness. This value was selected as an arbitrary threshold of significant covariation between species richness and environmental variables. As a

Table 1
Matrix containing correlation of richness and all other variables initially included in the study

	Richness	Radiation	Altitude	Slope	Undergrowth cover	Canopy cover	Temperature	Precipitation	Annual E_T	Annual E_A
Richness	1.000									
Radiation	0.079	1.000								
Altitude	−0.535	−0.269	1.000							
Slope	−0.081	−0.518	0.271	1.000						
Undergrowth cover	0.507	0.008	−0.374	0.067	1.000					
Canopy cover	−0.188	−0.202	0.138	0.199	−0.147	1.000				
Temperature	0.530	0.290	−0.984	−0.276	0.381	−0.143	1.000			
Precipitation	−0.423	−0.213	0.753	0.318	−0.225	0.299	−0.787	1.000		
Annual E_T	0.456	0.273	−0.892	−0.278	0.360	−0.210	0.925	−0.774	1.000	
Annual E_A	0.522	0.297	−0.968	−0.271	0.396	−0.139	0.977	−0.692	0.934	1.000

consequence, radiation and slope were rejected. From the remaining environmental variables, we selected annual E_A as representative of abiotic factors because it showed high correlation with all the other topoclimatic variables (altitude, mean annual temperature, mean annual rainfall, and annual E_T) and it functionally integrated the effect of these variables on vegetation. We selected canopy cover and undergrowth cover as representatives of vegetation structure and management history. These two variables also showed a low correlation value between them. Therefore, further statistical analysis considered one dependent variable (richness) and three independent variables (annual E_A, canopy cover and undergrowth cover). We then selected the plots with the highest values of richness for the respective environmental variables. This process usually led to the selection of different localities for each variable. That is because the selected plots for a given environmental variable were not always selected for the other variables and, as a result, environmental variables could not be analysed in a single model, thus precluding the use of multivariate analysis.

E_A and undergrowth cover had some degree of correlation ($r = 0.396$). To minimise confounding effects of such correlation on the analyses, we developed two models for assessing the relationship between richness and E_A: one considering only plots with undergrowth cover less than 62% and the other using plots with higher undergrowth cover. This threshold allowed a balance of the number of plots belonging to the two undergrowth groups. For the same reason, we built two models to analyse the relationship between richness and undergrowth: one for plots with E_A values $\leq$840(mm, and another for plots with values >840(mm. Because canopy cover exhibited low correlation with E_A ($r = -0.139$) and with undergrowth cover ($r = -0.147$), a single model to predict richness from canopy cover was developed. The number of intervals was decided after several trials as a compromise to ensure a broad range of environmental conditions and enough number of plots within each interval.

We split the range of values of annual E_A and canopy cover in eight intervals, and the range of values of the undergrowth cover in nine intervals. Then, from the plots included in each interval we selected 20% of plots with the highest richness values. This percentage ensured enough number of plots to perform further analysis. Next, we developed functions of maximum richness for each independent variable by fitting second-degree polynomial relationships between mean richness (of the highest 20%) per interval and the mean interval values of each environmental factor for each interval. These functions were developed using a subset of 1061 plots, which represents approximately 75% of plots (76.5% more precisely). We then used the functions to estimate maximal richness for the remaining 326 plots. This approach allowed us to predict maximal richness in the region under different environmental conditions. The use of the upper richness values allowed us to investigate the maximal richness reached in the region under different environmental conditions. Our predicted maximal richness values were not the result of hypothetical distribution ranges for each species (as the potential richness estimations described Section 1) but values estimated from empirical field surveys at the stand level.

As a final step, we assumed that richness at a given locality was limited by one of the three environmental factors. Consequently, maximal richness for a given locality was predicted as the lowest of the three values obtained from the different functions. We applied this procedure to the remaining 326 plots, which were not used to build the models, obtaining a maximal richness value for each plot. We evaluated the relationship between maximal and observed richness for the same 326 plots using linear regression.

Calculations were made using R environment available at http://www.r-project.org. Correlations were calculated with Pearson's correlation coefficient.

4. Results

The five models relating maximal species richness to the three variables (canopy cover, undergrowth cover and E_A) are shown in Fig. 1. In Fig. 1A, maximal richness declined when canopy cover increased, ranging from 12 to 13 species per plot when canopy cover was <150% to 8 species per plot for 300% cover.

The shape of the two functions describing the relationship between maximal richness and E_A, which were derived separately for plots where undergrowth cover was below or above 62%, were almost identical

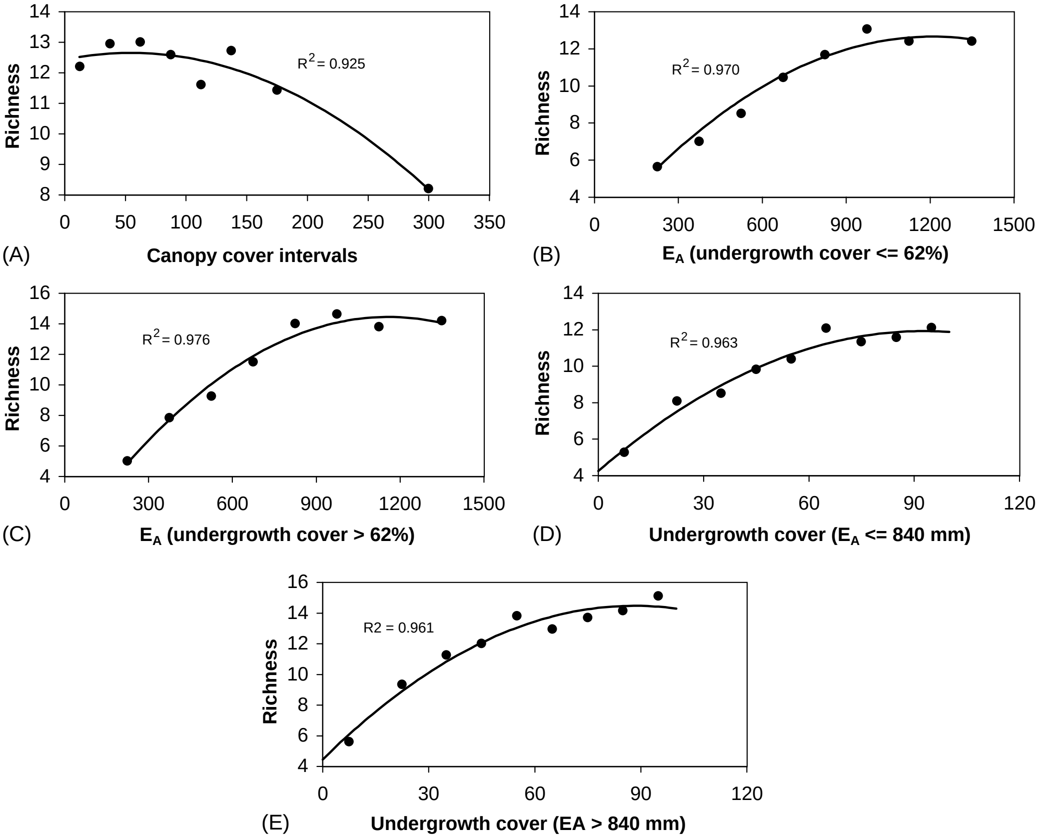

Fig. 1. Fitted polynomial functions between mean richness (obtained from the 20% of the plots with the highest richness) and mean interval canopy cover (A), annual actual evapotranspiration (B and C), and undergrowth cover (D and E). The fitted function and the coefficient of determination (R^2) for each model are given within the figure for each case.

(Fig. 1B and C). There was a difference of approximately one species in all intervals of E_A, which suggests a small additive effect of undergrowth cover. Thus, both functions were considered when estimating potential richness for the 326 test plots. The relationship between maximal richness and E_A was a positive parabolic one; maximal richness increased in a quasi-linear fashion from approximately 5 to 12–14 species, whereas E_A increased from 200 to 800(mm. Richness remained stable once E_A reached 1400(mm.

The two remaining functions (Fig. 1D and E) describing the relationship between maximal richness and undergrowth cover were derived separately for plots where E_A was, respectively, below or above 840(mm. Both functions were very similar and again, there was a slight additive effect (now from E_A). Thus, we used both functions to assess potential richness of the test plots. This relationship was a positive parabolic one; maximal richness steeply increased from 4 to 11–13 species when undergrowth cover increased from 0 to 60%. Maximum richness peaked and remained level at 11–15 species. Due to the method used to measure undergrowth cover, there were no values >100%.

Fig. 2 shows the relationship between observed richness in the 326 test plots and the lowest of the three maximal values that we estimated for the same plots using the five fitted models. The upper line is the expected linear relationship if all the plots had reached their potential richness value (i.e. a straight line with slope 1 and passing through the point (0, 0)). The lower line is the fitted regression between the pre-

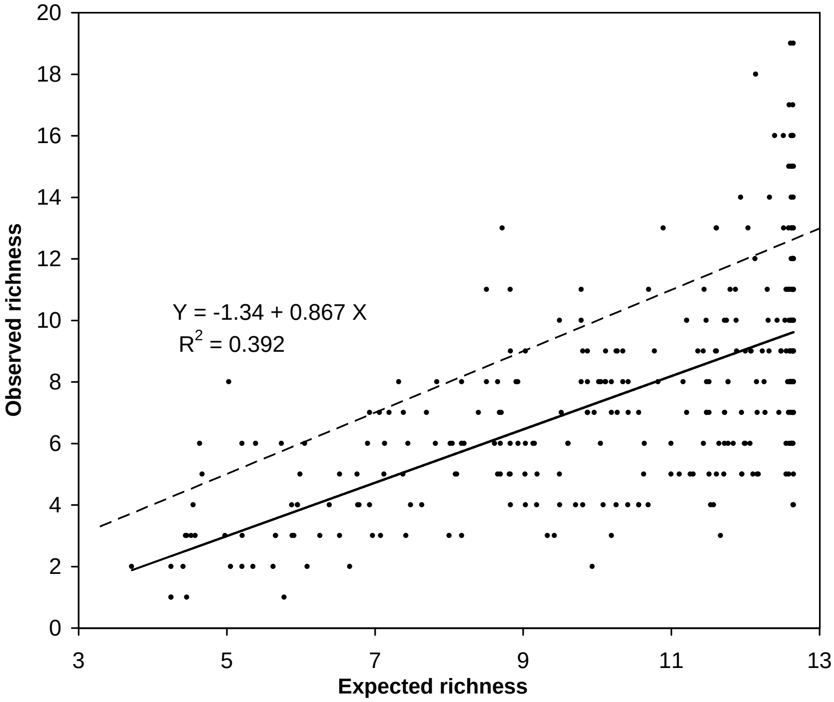

Fig. 2. Scatterplot showing the relationship between the expected and the observed richness for the 326 plots used to test the fitted functions. The continuous line is a simple linear regression fitted to the points of the graph. The coefficients of the regression model and the determination coefficient (R^2) are given in a small box. The dotted line shows the relation to be found if plots had reached their maximal richness (i.e. a line with slope = 1).

dicted and observed values. Clearly, most of the test plots did not achieve their estimated maximal; measured values were frequently lower than maximal, but around 10% of the plots was over the estimated maximal richness. The distance between the two lines is approximately 2–3 species, and, on average, observed values were within 50–75% of the expected maximal values.

5. Discussion

Many factors can influence woody plant species richness, but most can be grouped into two categories: climate and vegetation structure. Climate is often the primary factor influencing plant richness (Adams and Woodward, 1989; O'Brien, 1998; Ohman and Spies, 1998). E_A and temperature are highly correlated and E_A also is related to water budget and radiation. Therefore, E_A can integrate climate conditions as it occurs in our data, where E_A is highly correlated with these variables and has been used in relating diversity to climate (Waring and Running, 1998; Latham and Ricklefs, 1993). A number of studies (Currie and Paquin, 1987; O'Brien, 1998; O'Brien et al., 1998) have found a strong correlation between E_A and tree or woody plant diversity, which has led to a formulation of a general species–energy theory (O'Brien, 1998). This theory predicts that diversity would increase in environments with higher E_A (but see Hoffman et al., 1994). Soil fertility or disturbance history also may be important, but the current structure and composition of the vegetation in part reflect their effects. Unfortunately, soil and management variables were not available for this study.

Our available data included only plots with nearly monospecific tree cover, which may have decreased the canopy contribution to species richness. But, this effect probably was not very relevant, because most tree species present in a plot were represented in the undergrowth. Thus, woody plant richness was largely determined by the undergrowth richness. Closed canopies reduce habitat heterogeneity within forests and suppress woody species with medium to high light requirements. As a consequence, woody plant richness can be related negatively to tree canopy cover and positively to undergrowth cover. For instance, if trees dominate in a plot, richness should be low because the number of tree species is typically moderate. Conversely, a high dominance of shrubs will often lead to higher richness. Our models support this expectation: maximal richness increased with E_A and shrub cover but decreased with tree cover.

We used the lowest of the three maximal richness values predicted by the models for each point, assuming that richness was limited by the most restrictive factor. Nevertheless, multiple factors could restrict potential richness in a specific location (instead of being a single limiting factor). However, we found little difference in the functions when we modelled annual E_A separately for different ranges of undergrowth cover and vice versa. Of course, different factors may limit different species. Thus, the combined effect of the three factors would result in a different set of species than would be produced by a single factor. But, this may not produce any systematic bias. Our approach is based on empirical observations of species richness at the stand level without consideration for species composition and they reveal the overall results of the interaction on species richness. The deviation from the linear relationship between observed and maximal richness with slope equal to one (the upper line in Fig. 2) also suggests that factors, other than the three considered in the models (i.e. management, soil fertility, etc.), may be limiting richness.

Many managers would be interested in relating current richness to a reference value in order to assess the conservation status of a site or territory, hence efforts to measure a ‘‘potential richness or potential biodiversity’’. But, there are conceptual and practical obstacles to this kind of measures (see the review by Smith and Catanzaro, 1996). For example, information about environmental conditions, species–habitat associations and species interactions may be missing. Even if such information is available, definition of potential habitat is often subjective or dependent upon the resolution of available data.

On more conceptual grounds, the use of potential values is problematic. The number of species in a community depends on niche partitioning. Very similar habitats can support different number of species, depending on the available species pool (as shown in comparisons between islands and a continent, MacArthur and Wilson, 1967). Communities also can be more or less saturated as a result of local biotic interactions (competition and predation), dispersal, and evolution (Cornell and Lawton, 1992). The concept of ‘‘saturation’’ suggest there is a maximum limit to species richness for each habitat, that is regulated by habitat properties. This is reminiscent of the metaphor introduced by Gleason (1917) (see also Pulliam, 1997) of a habitat as a glove with each finger filled with an equal number of species. However, species do not occupy previously empty fingers (niches). Rather, they build their niche in interaction with others. A niche asserted without reference to specific organisms is neither testable empirically nor a source of novel information (Goldstein, 1998). If more species are available, we can expect that each niche partition will be finer, but there is no basis to look for fixed saturation richness. Founder effects and community assembly rules also may produce different richness as a consequence of stochastic processes related to the order of arrival.

To avoid subjectivity in defining habitats or species preferences, we must use statistical approaches, based on large data sets that combine spatially explicit empirically derive information on richness, habitat and community structure. Two approaches are conceivable. One is to define habitats using a set of values for a number of variables. Then, absence–presence of species could be associated with each defined habitat. Then areas potentially occupied by each species could be predicted elsewhere. This reduces subjectivity in relating habitats and species, but may be misleading because biotic interactions, biogeographical factors, habitat size and other are not fully considered.

The second approach is the one we propose. We knew the entire range of richness values observed in a very large set of plots. These values were empirically, not theoretically derived potential values: even our richest plots could have contained more species under other conditions, e.g. different management histories. In fact, observed richness for some individual plots greatly exceeded the calculated maxima (Fig. 2) because we used averages for the 20% plots with the highest richness, not the maxima. A potential improvement to our approach, which could be easily accomplished using GIS, would be to discount for the effect of habitat sizes.

In conclusion, statistically obtained maximal richness of woody species appears more useful for predicting diversity distribution patterns, diversity hotspots, and biodiversity status than potential richness obtained from hypothetical individual species distributions. Although our approach can be used only as a heuristic tool to detect zones with anomalous (high or low) richness values, local deviations from maximal averages can be individually analysed. This procedure, however, might never become a substitute for the knowledge about species composition at each site and its dynamics.

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