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Regeneration traits are structuring phylogenetic diversity in cork oak (*Quercus suber*) woodlands

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Abstract

Question: What factors determine the deviations from the relationship between species richness (which considers species as independent entities) and phylogenetic diversity (PD) (which considers species relatedness)? What are the implications for community composition and phylogenetic structure?

Location: Los Alcornocales Natural Park (36°03′–36°45′N and 5°20′–5°45′W), in southern Iberian Peninsula (Spain).

Methods: We recorded all woody species and geographical features on 94 (20 m × 20 m) plots of cork oak woodlands. Disturbance information was obtained from the Park records; precipitation was estimated from local maps. PD was computed as the minimum total length of all the phylogenetic branches spanning the set of species on each site. Then, PD was regressed against species richness to test to what extent the unexplained variance in this relationship could be accounted for by environmental variables and disturbances, and against the representation of species with different regeneration strategies.

Results: Species richness and PD are strongly related; however, the remaining variability can be explained by: (1) precipitation and disturbance, and (2) the proportion of seeder species. Thus, the PD both of areas with low precipitation and high disturbance, and of areas with a high representation of seeder species, is lower than what would be expected from the species richness.

Conclusions: Regeneration traits are important in structuring plant community composition; specifically, they contribute to shaping biodiversity in Mediterranean ecosystems. Species richness tends to overestimate biodiversity in highly disturbed systems.

Keywords: Biodiversity; Disturbance; Phylodiversity; Phylogenetic Community Structure; Resprouters; Seeders.

Nomenclature: Valdés et al. (1987).

Introduction

One of the most important topics in ecology is understanding biodiversity. And the most traditional and widely used index of biodiversity is species richness (Huston 1994; Rosenzweig 1995; Pausas & Austin 2001). This measure assumes that all species are equal no matter how similar they are to one another. With the recent advances in molecular data and phylogenetic techniques, phylogenetic diversity (PD) is becoming more widely used for biodiversity assessments (Forest et al. 2007; Helmus et al. 2007). As PD includes the evolutionary divergence information for species assemblages, the factors determining the differences between this information and the species diversity on a given site are related to the historical processes structuring the PD. In high-disturbance-prone systems, such as Mediterranean plant communities, the presence of regeneration traits may determine the persistence of the species, thus contributing to the biodiversity structure. Consequently, we hypothesize that the different plant regeneration strategies are responsible for assembling Mediterranean communities (Verdú & Pausas 2007), and thus they should explain the difference between species richness and PD.

In Mediterranean flora the two main plant traits for regenerating after disturbance are: post-fire resprouting (R) and post-fire seeding (P) (Bond & van Wilgen 1996; Pausas et al. 2004). Species with only the P trait (R − P+, obligate seeder species) regenerate after disturbance only from seeds stored in the seed bank; species with only the R trait (R+P −, obligate resprouter species) regenerate after disturbance from vegetative buds. Some species may have both traits (R+P+, facultative species), thus regenerating facultatively from seeds or vegetative buds. It has been suggested that disturbance favours the P+strategy (Bond & Van Wilgen 1996; Pausas et al. 2004; Lloret et al. 2005; Pausas & Bradstock 2007) leading to an over-representation of seeder species on high-disturbance sites (Pausas & Verdú 2005, 2008; Verdú & Pausas 2007). Because seed traits, including dormancy, are heritable (Baskin et al. 2000) and taxonomically aggregated (i.e. they are common at a given taxonomic level), seeder species tend to be phylogenetically aggregated (i.e. with a common ancestry; Verdú & Pausas 2007). As examples of this aggregation, many Cistaceas and Fabaceae species are seeders (Thanos et al. 1992; Herranz et al. 1998, 1999). Indeed, the loss of the resprouting character has been related to diversification (Cowling & Pressey 2001; Verdaguer & Ojeda 2005) and thus to a greater increase in richness than in PD. Consequently, we predict that PD (i.e. considering the relatedness of the species) should be lower in relation to species richness (i.e. phylogenetic clustering; Webb et al. 2002) where seeders are dominant. In addition, because seeder species are more drought tolerant than resprouters (Paula & Pausas 2006; Pratt et al. 2007), we also predict that PD should be lower in relation to species richness in the driest parts of the landscape.

Cork oak forests are an emblematic Mediterranean ecosystem of the western Mediterranean Basin (Pausas et al. 2009). They have been used for centuries to obtain acorns (for human and animal consumption) and to produce cork. These woodlands are still in use, especially for cork production, and shrub clearing to facilitate cork extraction and reduce fire risk is a common practice. Understanding the structure of this ecosystem biodiversity is especially important in Los Alcornocales Natural Park (southern Spain), the largest existing protected Cork oak forest (Aronson et al. 2009). Given its complex disturbance history, the Cork oak forest is a good system to evaluate whether disturbance and regeneration strategies are structuring its biodiversity. Specifically, we aim to test whether having seed traits that allow populations to persist through disturbances lowers the PD one would expect from the species richness.

In this framework, we carried out field sampling to quantify woody species richness in different conditions (disturbance and climate) in the Los Alcornocales Natural Park. Using available phylogenies, we computed PD for each site. We then tested whether the unexplained variance in the relationship between PD and species richness could be explained by climate and disturbance factors, and by the representation of the different regeneration strategies (seeding and resprouting).

Methods

Study area

We studied the Cork oak forests from Los Alcornocales Natural Park (36°03′–36°45′N and 5°20′–5°45′W; 167 767 ha), located just north of the Straits of Gibraltar, in the southern Iberian peninsula (Spain; Fig. 1). This Park harbours the largest cork oak forest in the Iberian Peninsula and is probably the best conserved in the whole dis-

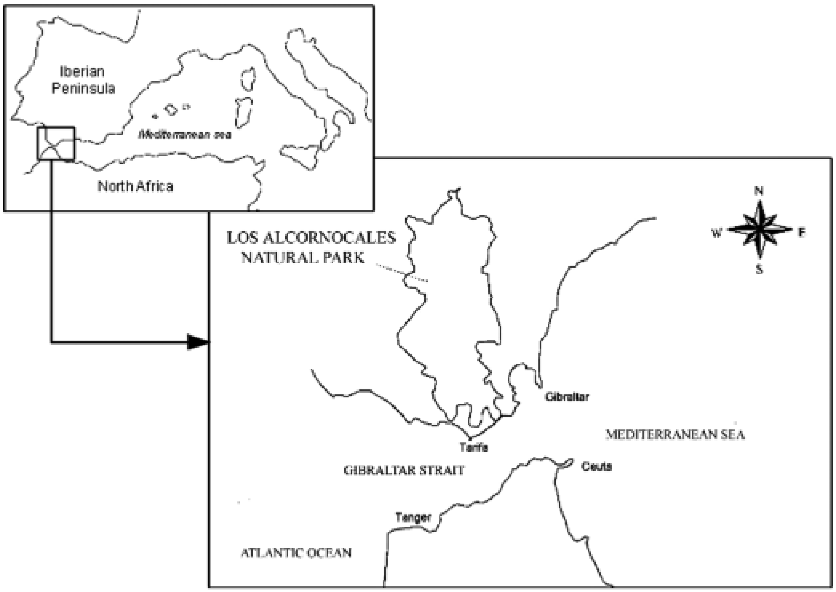

Fig. 1. Location of Los Alcornocales Natural Park, on the Iberian side of the Strait of Gibraltar.

tribution area of the species (western Mediterranean basin; Aronson et al. 2009). The landscape is defined by a series of mostly north-south oriented mountain ranges with a maximum altitude of 1092 m. Soils are acidic and poor in nutrients, and originated from Oligocene-Miocene sandstones. The temperatures are mild and highly predictable: annual average = 15.7°C; average maximum = 34.3°C; average minimum = 2.78°C (CMA 2004). Total annual precipitation varies between 700 and 2000 mm, with most occurring between September and May. In the study area, altitude and rainfall are positively correlated (altitude and rainfall: $r = 0.79$, $P = 0.012$, based on nine meteorological stations with more than 17 years of data).

Sampling

To sample a broad spectrum of cork oak forests in the study area, a stratified sampling was performed based on a previous classification of the cork oak land properties in the Park (Coca 2007). Fourteen representative properties were selected, ranging from 150 to 650 m a.s.l. Each land property was divided into homogeneous areas from the point of view of management and physiognomic features, yielding a total of 32 land units. In each land unit, we randomly selected three (rarely two or four) 20 m × 20 m plots (a total of 94 plots) to account for the additional variability within the land units (e.g. slope, aspect and soil characteristics). On each of these plots all the rooted woody species as well as the geographical features (aspect, location, and altitude) were recorded.

Data analysis

A plot was considered disturbed if it had been heavily cleared (usually with the use of machinery and affecting the soil) at least once since 1960 (the earliest year with reliable disturbance history information). The precipitation regime was estimated from local maps (UTE 1990) and classified in two categories: low (<1300 mm) and high (>1300 mm). As previous analyses with more precipitation categories showed very similar results, we used only two categories for the sake of simplicity.

We computed not only woody plant species richness but also the richness of species presenting the different post-disturbance regeneration traits (resprouting and seeding). Regeneration traits for each species were assigned on the basis of field experience and from a trait database (Paula et al. 2009; Fig. 2). To compute the PD for each site we first assembled a phylogenetic tree with branch lengths (million years) for the species in all plots with the help of the Phylomatic software implemented in PHYLOCOM 3.41 (Webb et al. 2007) and using the angiosperm megatree version R20050610.new (Fig. 2). Then, from this tree, and for each site, the minimum total length of all the phylogenetic branches to span the set of species on the site (Faith 1992) was computed using APE software (Paradis et al. 2004).

First, PD was regressed against species richness; then, we used this relationship as a null model and tested to what extent the remaining variance could be explained by: (1) environmental variables (precipitation and aspect) and disturbance (yes/no), and (2) the representation of the species with different regeneration strategies. To evaluate whether some of the unexplained variance can be attributed to spatial factors, the land units (nested in land property) were added to the model. To visualize the influence of the studied variables in explaining PD, the residuals from the PD-species richness regression were plotted against the significant variables. A binomial GLM model evaluated with a χ^2 test was used test the different representations of seeder species in relation to precipitation and disturbance.

Results

The total number of woody species on the sampled plots was 69, and ranged from 7 to 30 species per plot (plot size = 400 m^2). Obligate seeders (R − P+) ranged from being absent to representing up to 35% of the total species (mean = 18%); obligate resprouters (R+P −) ranged from 50% to 96% (mean = 71%); and facultative species (R+P+) ranged from absent to up to 17% of the species (mean = 6%).

Both PD and species richness were strongly related ($r = 0.91$, $F_{1,92} = 467.7$, $P < 0.0001$). After including species richness in a regression model, the proportion of species of any of the four regeneration groups (tested independently) explained a significant proportion of the unexplained variance (Table 1). The relation was negative both with the proportion of obligate seeder species (R − P+), and with the proportion of all seeders (R − P+ and R+P+). Conversely, the relation was positive with the resprouters (all resprouters or obligate resprouters; Table 1). Thus, seeder species (P+) contribute to reduce PD from the values expected from the species richness (Fig. 3), while resprouting species increase PD.

The initial model (PD against species richness) was also significantly improved by including precipitation regime and disturbance (Table 2). Aspect

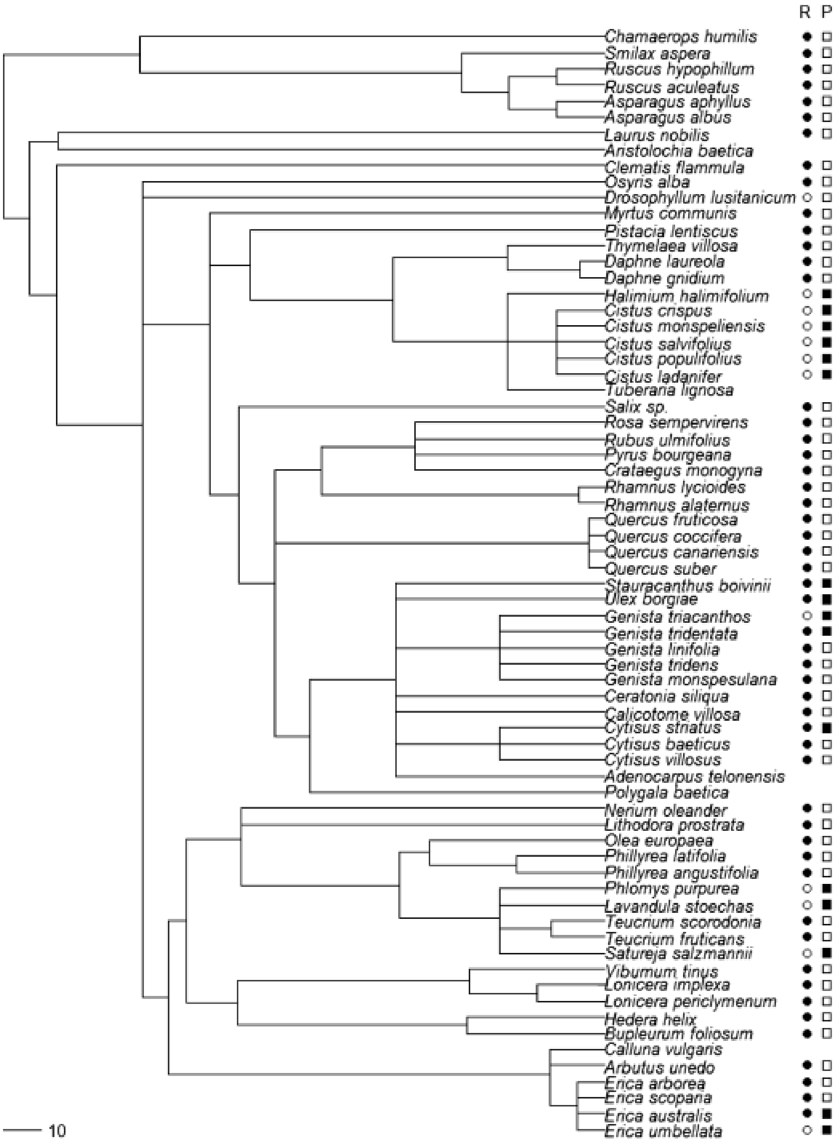

Fig. 2. Phylogenetic tree and the species' post-fire regeneration traits considered (R, resprouting ability, circles; P, post-fire seeding, squares). Branch lengths are in millions of years. Filled symbols indicate species having the ability regenerate post-fire by means of resprouting (circles) and/or by germinating (squares); empty symbols indicate species that lack the corresponding regeneration ability. For some species we were unsure of their regeneration strategy (no symbols) either because no information was available or because there was conflicting information; these cases are not considered in the analysis.

was not significant once the other two variables were in the model. Differences in land units also explained a significant proportion of the variance, indicating the importance of other unknown parameters. The fact that precipitation showed a positive relation suggests that sites with higher rainfall have higher PD than what would be predicted from species richness (Fig. 4). In contrast, disturbance showed a negative relationship, that is, disturbed sites have lower PD in relation to their richness (Fig. 4).

The proportion of P+species was significantly higher on the disturbed sites than on the undisturbed sites (32% vs. 23%; binomial GLM, χ^2 test, $df = 92$, $P = 0.008$), and under the lowest precipitation (low = 27% vs high = 19%; binomial GLM, χ^2 test, $df = 92$, $P = 0.025$).

Discussion

Because PD and species richness are strongly related ($r = 0.91$), our results initially suggest that the role of PD in the biodiversity assessment of our study system will be limited (Rodrigues & Gaston

Table 1. ANOVA table showing the change in explained variance from the initial model (phylogenetic diversity against species richness) to the model including the proportion of species of each regeneration strategy (each strategy added independently). Regression coefficients (slope) are also included for the four models. *F*, *F*-test; *P*, associated *P* value; Res. Df, residual degree of freedom; RSS, residual sum of squares.

	Res. Df	RSS	Sum. Sq.	*F*	*P*	Coeff.
Initial model (PD∼species richness)	92	1 201 072				
Obligate seeders (R − P+)	91	847 589	353 483	37.95	< 0.0001	− 753.69
All seeders (R − P+and R+P+)	91	820 518	380 553	42.21	< 0.0001	− 557.48
Obligate resprouters (R+P −)	91	882 675	318 397	32.83	< 0.0001	475.69
All resprouters (R+P − and R+P+)	91	948 258	252 814	24.26	< 0.0001	554.77

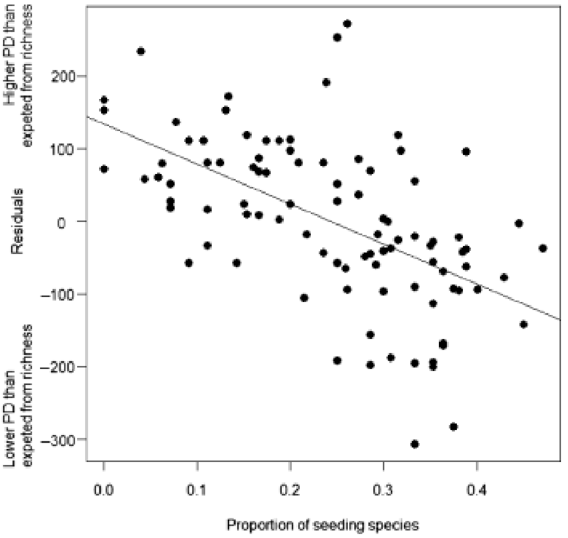

Fig. 3. The relationship between the residuals from the phylogenetic diversity–species richness regression, and the proportion of post-disturbance seeding species (P+; $R = -0.560$, $P < 0.0001$). Negative residuals indicate lower phylogenetic diversity than expected from species richness values, that is, a tendency for phylogenetic clustering.

Table 2. ANOVA table showing the change in explained variance from the initial model (phylogenetic diversity against species richness) to the model including the significant environmental variables (variables added sequentially). *F*, *F*-test; *P*, associated *P* value; Res. Df, residual degree of freedom; RSS, residual sum of squares.

	Res. Df	RSS	Sum. Sq.	*F*	*P*
Initial model (PD∼species richness)	92	1 201 072			
Precipitation	91	1 106 953	94 119	12.45	0.0008
+Disturbance	90	1 051 645	55 308	7.31	0.0088
+Land Unit (nested in Property)	60	453 457	598 188	2.64	0.0007

2002; Proches et al. 2006; Forest et al. 2007). However, the unexplained variance after accounting for species richness can be largely explained by the amount of species with different regeneration traits. Species that have the capacity to regenerate from seeds after disturbance (P+species) reduced the PD relative to the value expected from a given species richness (phylogenetic clustering, Webb et al. 2002). Thus, the proportion of seeders plays an important role in the phylogenetic structure of communities. This is in agreement with previous studies suggesting that fire reduces mean phylogenetic distances at community level (Cavender-Bares et al. 2004; Verdú & Pausas 2007). Most seeders appeared at the onset of the Mediterranean-type climate during the late Tertiary/early Quaternary (Pausas & Verdú 2005) and are aggregated to few lineages, such as in Cistaceas and Fabaceae; thus, they have a low contribution to the PD. The higher phylogenetic clustering in fynbos with respect to the thicket forests found in South Africa by Proches et al. (2006) could also be related to the different representation of post-fire regeneration strategies in these two ecosystems. In the Mediterranean Basin, the presence of seeder species is favoured by human disturbance, although they most likely evolved in Mediterranean ecosystems in response to the evolutionary pressure exerted by fire (Bond & van Wilgen 1996; Keeley & Bond 1997; Pausas & Verdú 2005; Pausas & Keeley 2009). In the Mediterranean Basin, seeder species are favoured by fire, the heat of which breaks their dormancy (Keeley & Fotheringham 2000; Paula & Pausas 2008) and thus greatly increases their recruitment. However, their germination is not strictly tied to fire, and other human disturbances may also play a similar role. For example, a strong soil disturbance may produce mechanical scarification of seeds and thus stimulate the germination of species with physical dormancy (Baeza & Vallejo 2006). Moreover, removal of vegetation may expose the soil surface to the heat of the summer sun, which in Mediterranean conditions can reach considerable temperatures (>60°C were recorded by Díaz 1997), thus also breaking dormancy and increasing the recruitment of obligate seeders (e.g. in fuel breaks; Baeza & Roy 2008). Consequently, the difference

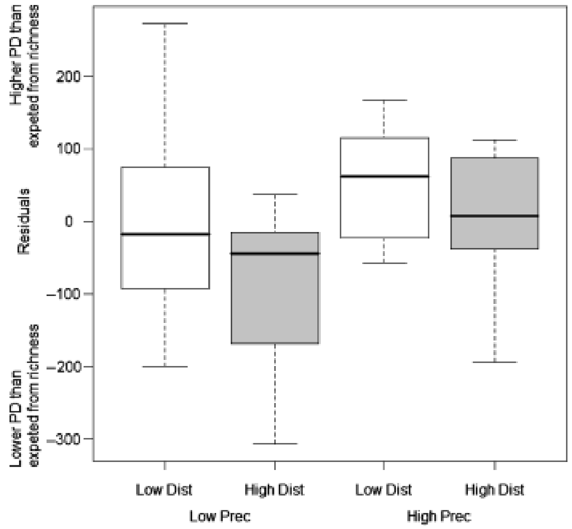

Fig. 4. Distribution of the residuals from the phylogenetic diversity–species richness regression, in relation to High/Low disturbance and High (>1300 mm)/Low (<1300 mm) precipitation. The ANOVA with the two factors (precipitation and disturbance) is significant ($P<0.05$), the interaction is not.

between PD and species richness can also be explained by the occurrence and, presumably, the frequency of disturbances. Indeed, the proportion of P+species was significantly higher on the disturbed sites than on the non-disturbed sites. Although recruitment may be stimulated after human-caused disturbance, this stimulation may not be as great as after a fire, because of the larger extent and magnitude of a fire as well as the multiple germination cues produced by a fire (heat, or chemical stimulus from smoke or charred wood; Keeley & Fotheringham 2000) compared with human-disturbances (e.g. clearing).

The difference between PD and richness was also strongly related to the precipitation regime, in the sense that lower precipitation implied lower PD. Indeed, the proportion of P+species was significantly lower under high precipitation, which in our study area corresponded to high-altitude sites. The high drought tolerance of P+species (Paula & Pausas 2006) makes them more competitive in warm and dry climates, which are in turn more fire-prone than high rainfall areas. The P+species also fit with the concept of disturbance-dependent (gap) recruiters (Keeley 1998), not only because they are more abundant on disturbed sites, but also because drier and warmer conditions result in lower productivity and thus more space for recruitment and subsequent survival and growth (Specht 1981).

In conclusion, our results support the hypothesis that the regeneration strategies of local flora are an important factor shaping composition and biodiversity in Mediterranean plant communities. These strategies have implications for biodiversity assessments, as they suggest that species richness tends not only to overestimate biodiversity in disturbed systems but also to underestimate it under low disturbance and high rainfall regimes.

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