Epiphytic bryophytes of *Quercus* forests in Central and North inland Iberian Peninsula

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Abstract. Diversity patterns are governed by a complex network of interacting factors. Studies directed to disentangle the most important factors affecting diversity have frequently shown divergent results, which has encouraged a rewarding debate about the relative importance of each factor. Scale dependency has been identified as a direct cause of at least part of such divergences. However, studies with spatially-explicit measurements at different scales are costly and therefore they are relatively scarce despite their importance. Here, we present a database to disentangle the cross-scale variation in the importance of factors affecting the diversity of epiphytic bryophyte communities in *Quercus* dominated forests (*Quercus ilex* L., *Quercus pyrenaica* Willd. and *Quercus faginea* Lam.) in the North-western region of the Iberian Peninsula. We provide species-per-site abundance information with more than 9000 entries and an environmental table containing 20 *in situ* measured variables at three different scales (forest, stand, and sample). The database will help to advance the research of cross-scale effects of diversity patterns while at the same time providing valuable information on the distribution of a poorly known group of organisms.

Keywords. Bryophyte, climate, database, epiphyte, forest, Mediterranean, scale dependency

Introduction

The whys and wherefores of the distribution of biodiversity in space have long intrigued ecologists (Elton 1946, Hutchinson 1959), and are still the source of debate (see e.g. Kraft et al. 2011). Currently we hold much knowledge on the causes of biodiversity gradients. For example, current climate is known to constrain species richness patterns (Hawkins et al. 2003), at least to some extent (see Hortal et al. 2011). However, there is a lack of consensus on many aspects of the relationships between biodiversity and a number of other factors, and the underlying mechanisms driving diversity patterns are still under discussion (see for example, current debate on the relationship between net productivity and diversity in Gillman et al. 2015). In addition, the relative importance of each factor has also been the subject of continuous debate (Ricklefs 2008, Brooker et al. 2009). Allegedly, at least part of the controversy is relat-ed to the scale dependency of diversity patterns (Willis and Whittaker 2002). Although the importance of cross-scale effects has been long recognized, only recently has it become a key question in biodiversity studies (Whittaker et al. 2001, Hortal et al. 2010, Guisan and Rahbek 2011). However, acquiring standardized data at multiple scales is usually cost-intensive, so the number of studies dealing with cross-scale changes in the drivers of diversity is relatively scarce. Therefore, there is an urgent need for reliable, spatially-explicit data that provides information on the variations of diversity across scales.

The relative significance of the factors affecting diversity patterns and the scale at which they become apparent depends on the ecology and life history of the taxa under consideration (Whittaker et al. 2001). Recently there has been an increase in the taxonomic scope covered by biodiversity studies that has begun to clarify the

relationship between biodiversity patterns and the life history traits of the organisms under study (Diniz-Filho et al. 2010, Heino 2011, Santos and Quicke 2011, Aranda et al. 2013, Patiño et al. 2014). However, an important gap of knowledge still remains (e.g. Fontaneto and Hortal 2013). As for many other small-sized, inconspicuous taxa, knowledge on the diversity patterns of bryophytes is scarce (Medina et al. 2011). Interestingly, they have unique characteristics that make them an ideal study system to test hypotheses related to changes in the factors affecting biodiversity across scales. Because of their small size and their ability to be in thermic and hydric equilibrium with the environment they are thought to be strongly dependent on the immediate (micro-scale) environment, whereas at the same time they are also known to depend on general meso-climatic conditions. Within bryophytes, epiphytes in Mediterranean forests are particularly well suited to analyse cross-scale relationships because they grow in a set of nested island-like systems: at the landscape-scale forests are isolated patches in an unsuitable matrix while at the smallest scale trees are islands in a mostly unsuitable area (see Medina et al. 2014).

Here we present data designed to disentangle the cross-scale variation in the importance of the factors affecting the diversity of epiphytic bryophytes. To do so we surveyed epiphytic bryophyte communities in *Quercus* dominated forest (*Quercus ilex* L., *Quercus pyrenaica* Willd. and Q*uercus faginea* Lam.) at three different scales

(forest, stand, and sample), using a standard protocol to avoid including eventual variations in community structure within each individual tree. More precisely, we describe the sampling strategy and the obtained output, providing spatially-explicit data on species composition and environmental conditions at the three scales of analysis.

Materials and Methods

Study Area

The surveys spanned North and Centre Inland Spain, encompassing an area of *ca.* 150,000 km^2 (Fig. 1). This region covers a wide climatic gradient with large variations in precipitation and temperature regimes. In the north of the study area (Fig. 1) climate is predominantly Atlantic with a characteristic humid to very humid summer and relatively mild temperatures. The rest of the territory hosts several variants of the Mediterranean climate that can be separated into three different regions (Mediterranean, Continental and Mediterranean-Atlantic) that show large differences in the temperature regime, season of maximum precipitations and intensity of summer drought. The study area covers a small part of the area under Atlantic climate and the continental region within the area under Mediterranean climate. Within the continental region there is also an important climatic variation. The westernmost zone of the study area in the border with Portugal is within the mild continental zone (Fig. 1). Due to the influence of the Atlantic Ocean, this zone shows rainy winters with infrequent snows and less than 40 frost days, that become even less towards the south. The inner part of the study (continental zone, Fig. 1) area has wider temperature variations, with most precipitations occurring during spring or autumn.

Within the continental zone the study area shows three well-differentiated units that stand out because of their singular climatic conditions. The northern plateau (Fig. 1) is an elevated plain surrounded by mountains. Its distinctive characteristics include cold winters (with locations that bear up to 170 frost days in the easternmost facade) and warm summers. Precipitations are low (less than 500 mm per year in most of this zone)
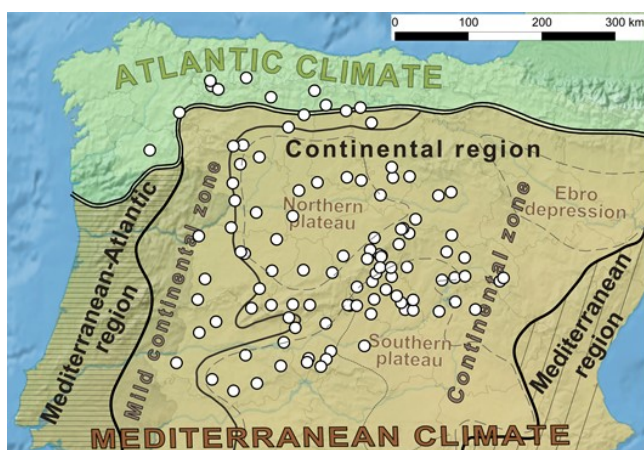

Figure 1. Map depicting the climatic regions of the study area, modified after Tullot (2000). White dots show the location of the sampled forests.

and despite the ample daily temperature variations dew is relatively uncommon due to the low air humidity. The southern plateau (Fig. 1) is less isolated and has a higher topographic complexity, thus harbouring more heterogeneous conditions. Overall the southern plateau has warmer winters and hotter summers but, most importantly, this region is characterized by a longer and drier summer drought, especially in the western half of the plateau that bears the hardest conditions. The third unit is comprised by mountainous areas surrounding the plateaus (Fig. 1). Overall, these mountain ranges represent wet and relatively cold areas. However, they harbour a highly diverse mosaic of climatic conditions due to their topographic complexity, where the relief and orientation play a paramount role shaping temperature and precipitation regimes.

Survey design

The selection of the sites to be surveyed was directed to obtain a good representation of the climatic and spatial variability of the study area. We based the selection procedure on a *p-median* Environmental Distance protocol (Hortal and Lobo 2005), designed to maximize the environmental variability covered by the surveys, taking also into account previously-known localities (see N. G. Medina et al. 2013 for a complete description of the selection method).

We sampled 107 forests. Forty of these forests had previous information on species composition and abundance at the forest scale (Lara 1993, Albertos et al. 2005, Cortés 2005), while the remaining 67 forests were sampled during the current survey and therefore have detailed information on species composition and abundance at the three scales of analysis (forest, stand, and sample; see below).

Sampling method

Environmental characteristics were recorded at three scales of analysis in all the 107 forests. The strategy followed to sample the three scales of analysis is summarized in Fig. 2. We first examined aerial photographs and traversed the forest to locate and select three stands separated by at
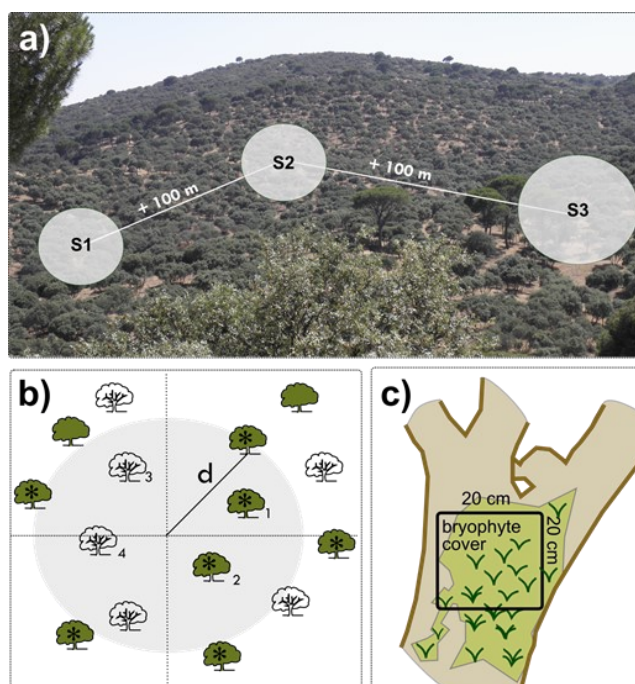

Figure 2. Scheme summarizing the sampling strategy at the three scales of analysis. a) S1, S2 and S3 refer to the three stands surveyed in each locality. b) The numbers indicate the trees were the environmental measures at the tree scale were taken, whereas *d* is the diameter to the sixth closest tree to the centre. Green coloured trees represent trees colonized by bryophytes and stars indicate sampled trees. c) The black quadrat depicts the sampling area in each tree.

least 100 m that had homogeneous conditions and were representative of the overall structure of the forest (Fig. 2a). Then we established the centre of the stand in an area more or less equidistant to the closest trees (Fig. 2b). Stand-scale characteristics were measured on the circular plot that included the six closest trees to the centre. Finally, we divided the stand into four sectors using the geographic North as reference, and made a division every 90 degrees (Fig. 2b). Micro-scale characteristics were measured on the tree that was closest to the centre in each of the four sectors.

Several sampling strategies can be used to survey epiphytic bryophyte communities. Some studies use sampling units of fixed size and sample all the trees in each unit (Király and Ódor 2010, Király et al. 2013, Ódor et al. 2013). However, this method is impractical in Mediterranean environments, especially in forests under strong anthrop-

ic influence. In these conditions, tree density is highly variable and there can be large differences in the number of trees per sampling unit. Therefore, if a quadrat of fixed size is used, some units will have just one tree –leading to a clear underestimation of epiphyte richness– while other sampling units will have an unpractically high number of samples. Because of this, our approach is based on using a fixed number of samples. This strategy is the most common approach in the study of epiphytic bryophytes in Mediterranean environments (see e.g., Lara 1993, González-Mancebo et al. 2004, Albertos et al. 2005, Garcia et al. 2005, Draper et al. 2006, Ezer et al. 2009, Mazimpaka et al. 2010).

Twenty samples were collected in each forest, which is known to be enough to obtain an adequate representation of the diversity of epiphytic bryophytes in Mediterranean environments (Lara 1993, Albertos et al. 2005, Mazimpaka et al. 2010, Medina et al. 2010, 2014). We collected seven samples in the first two stands and six in the last one. The proportion of trees colonized by bryophytes varied from all or most tree trunks in some forests, to less than 10% in others. In the cases were the proportion of colonized trees was low, we established a stopping rule to avoid overlapping areas across stands. Thus we stopped searching for trees after visiting 100 trees in a forest (35 visited trees in the first two stands and 30 trees in the last one).

For each sampled tree trunk we took samples at a height between 1.20 m and 2.00 m above the ground (Fig. 2c). Such height avoids an excessive influence of the colonization of soil bryophytes while providing relatively similar conditions of humidity across the forest, thus ensuring that the sampled communities are mainly composed of typically epiphytic bryophytes and that the samples are comparable. Each sample consisted of a quadrat of 400 cm^2 in the side of the tree with the highest bryophyte cover. At each quadrat, bryophyte cover was estimated visually and then all bryophytes within the quadrat were collected. All species were identified based on specialized literature (Pedrotti 2001, Casas et al. 2006, 2009, Guerra et al. 2006, 2010, 2014, Brugués et al. 2007).

Nomenclature follows Ros et al. (2007) for liverworts and Ros et al. (2013) for mosses, except for *Orthotrichum comosum*, which was described after this latter checklist (R. Medina et al. 2013). Vascular plants are named according to Castroviejo (1986).

Data description

The database consists of a compressed file in RAR format and two separate CSV files and a text file. The compressed file (*SpDistr,* Supplementary Material S1) includes the distribution maps of the species found in the study area in a PNG format and a description of the most common distribution types that can be found in the study area in a text file (*DistrType*). The first CSV file contains data on species occurrences and their abundance (*spabun*, Supplementary Material S2*),* the other CSV file includes the rest of the variables (*var*, Supplementary Material S3) and the text file describes the data type and units of the columns in the *var* file. In both CSV files the first column (*Loc*) indicates the locality number, the second one (*Stand*) indicates the number of stand (S0 for the data coming from previous surveys where species occurrences were recorded only at the forest and sample scales and S1, S2 or S3 refer to the first, second and third stand of the data acquired in this study), and the third one (*Sample*) identifies each sample with a unique code. Missing data are encoded as NA (Not Available). In the species database, the remaining columns depict the abundances of the 88 species of bryophytes found during the surveys, measured as the percentage of the 400 cm^2 sample occupied by the species.

In the environmental database the first column after *Sample* (*Source*) identifies the origin of the data (0 = the present study, 1 = data collected by Lara (1993), 2 = Albertos (2001), and 3 = Cortés (2005). The next columns refer to the variables as described below:

Data at the forest scale: The database includes several geographic references of the localities including Province (*Prov*) and Town (*Town*), as well as the geographic coordinates (*CoordX* and *CoordY,* datum WGS84). This information is followed by a date column (*Date*) and topographic

data gathered in the field: altitude (*Alt*) was measured with a GPS*,* aspect (*Aspect*) was measured with a compass (stands in flat surfaces are coded as "F" to avoid confusion with North aspect, 0 degrees) and slope (*Slope*) was visually estimated. The database also includes information on the type of forest (*ForTyp*), a categorical variable with three levels: QI for the forests dominated by *Quercus ilex*, QF for the forests dominated by *Q. faginea*, and QP for the forests dominated by *Q. pyrenaica*. Finally at the forest scale we included a variable related to forests and landscape structure (forest history*, ForH*) that is available only for *Quercus ilex* dominated forests and accounts for changes in forest structure in the last 57 years. To classify the forests we compared aerial photographs taken nowadays to the ones taken in a flight from the 1956 to 1957 American flight. We grouped the forests into three categories: (1) "forested" if the forest has a similar structure to that observed in 1956-57, (2) "degraded" if the forest was more open or degraded in 1956- 57 than nowadays, and (3) "strongly degraded" if the forest was very opened or presented a shrub-like structure in 1956-57.

Data at the stand scale: At this scale we recorded several variables that describe forest structure. Canopy cover (*CanCov*) was defined as the proportion of the forest floor covered by the vertical projection of the canopy (Jennings et al. 1999). It was visually estimated in the field taking the surface of each stand as a reference (see stand area definition in Fig. 2b). Tree density (*TrDens*) was estimated by applying the formula:

N (trees/ha)= (10.000*5,5)/(π * d)

where *d* is the distance to the sixth closest tree to the centre of the stand (Fig. 2b). The average diameter of the trees in a stand (*ForDiam*) was calculated as the mean of the diameters at breast height of the six trees located closer to the centre of the stand. Tree species (*TrSp*) is a complex variable that details the scientific names of the tree species found in the stand followed by their importance (an estimation of the percentage of trees of each species in the stand). Additionally, we also estimated shrub cover (*ShrubCov*) as the percentage of the forest floor occupied by shrubs, as well

as their average height in meters (*ShrubHeig*). Finally, we included a variable related to the percent of trees that were colonized by bryophytes (*PerCol*).

Data at the sample (tree) scale: At this scale we measured several variables that are known to be representative of the variation of the tree scale micro-environment and at the same time have proven to be relevant for the diversity and structure of bryophyte communities. Bark roughness (*BarkRough*) was estimated as the average depth of two furrows, namely the two deepest ones at breast height in each of the two sides of the tree. The diameter (*Diam*) at breast height (1.50 m) was measured with a *DendroFlexómetro©* that uses a Biltmore scale to correct for the curvature of the tree surface. Note that this is different to the measure of the average diameter at the stand scale (*ForDiam*), as this *Diam* is based on the four trees that are closer to the centre in each of the four sectors, while the *ForDiam* is based on the six trees located closer to the centre irrespective of their orientation (Fig. 2b). Canopy depth (*CanDep*) was calculated by subtracting the total height of the tree to the height at which the crown starts. Height was calculated using a *DendroFlexómetro©* that has a Christen scale incorporated. Additionally, we measured two indicators of the amount of light that passes through the canopy (*LAI1* and *LAI2*). To calculate them we took two hemispherical photographs of the canopy at 1 m height and a distance of 50 cm from the trunk surface at the North and South faces of each tree with an Olympus SP590-UZ camera and a fisheye lens. Then we estimated the percent of sky covered by the canopy (*LAI1*) and the total amount of light that passes through the canopy (*LAI2*) with GLA software (Frazer et al. 1999). LAI2 was calculated taking into account the geographic position, cloudiness (*kt*), spectral fraction (*sf*), beam fraction (*bf*) and topography of the site. Data on *bf* for each site were extracted from PGIVS maps, and *kt* and *sf* were derived from *bf* using the formulae on GLA user manual (Frazer et al. 1999). Here note that both LAI indices refer to the mean amount of light per day taking into account all the year for the perennial species (*Quercus ilex*), while for the de-
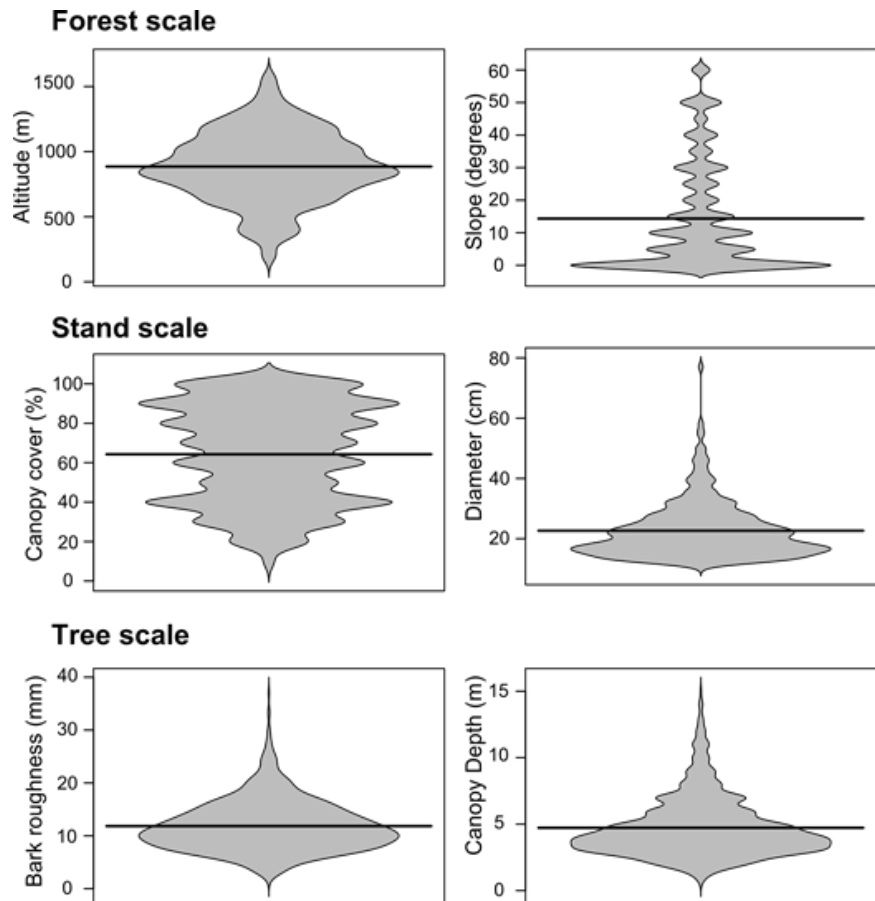
Figure 3. Beanplots of the quantitative variables in the database. We have selected two variables per scale to illustrate the variability across forests. Grey area represents the area under the density curves of the data values; the horizontal line is the average value.

ciduous species (*Quercus pyrenaica* and *Quercus faginea*) this amount of light corresponds to the period of the year when those species remain with leaves. The total number of days was calculated based on the known phenology of these species in the Iberian Peninsula. Finally, we included two variables related to biotic characteristics: the percentage of the quadrat of 400 cm^2 that is occupied by bryophytes (*BrioCov*) and lichens (*Liq*), estimated visually in the field in both cases.

Data overview and relevance

Overall the database holds more than 9000 entries from 88 species of mosses and liverworts. Both bryophyte diversity (see distribution maps, Supplementary Material S1) and environmental characteristics (Fig. 3) vary widely among forests.

The data presented here offer the opportunity to explore several ecological questions. On the one hand, we provide spatially-explicit data at three different scales that allow exploring the hierarchies of variables that affect species diversity,

as well as the relative importance across scales of the different factors determining both richness and changes in community composition. In addition, the information included in this database makes possible to explore distribution patterns of the species at different scales and to test to what extent occurrence data are constrained by species distributions at higher levels. The database offers a plethora of environmental measures that can be used not only for bryophyte studies, but also for other studies relating forest structure with diversity. Apart from its relevance to evaluate general ecological questions, these data also expand the knowledge on the distribution of bryophytes. The database presented here is the outcome of a systematic study covering the northern plateau and part of the southern plateau of the Iberian Peninsula, an area that has been scarcely visited by bryologists. We therefore expect these data to be used for ecological studies, checklists and distributional atlases, helping to unveil the determinants of the structure of local epiphytic bryophyte communities and the distribution of bryophyte species.

Acknowledgements

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