

Epiphyte communities in Mediterranean fragmented forests: importance of the fragment size and the surrounding matrix

Juan Luis H. Cardós · Isabel Martínez ·
Victoria Calvo · Gregorio Aragón

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Abstract

Context Mediterranean forests have been fragmented intensively over time, thereby yielding small and isolated forest remnants. They host a rich variety of epiphytes, which may be affected by landscape structure. Previous studies have analyzed the influence of habitat quality on these epiphytic communities, but there is little knowledge of the effects of other fragment features.

Objectives We evaluated the impacts of forest loss and fragmentation on epiphytic communities (lichens

and bryophytes) at plot and fragment scales after controlling the variation in forest structure and management.

Methods We considered 40 fragments of dense oak forests in a human-modified landscape. We quantified their spatial attributes (size and shape), the quality of the surrounding matrix and the forest stand structure. We modeled community traits, and the presence and abundance of species at fragment and plot scales.

Results Fragment size, shape, and the quality of the surrounding matrix were key factors that affected epiphytic richness and diversity. Larger and more regularly shaped fragments hosted the richest and most diverse communities, possibly offering a larger core area and thus favoring the entry of typical forest species. A high-contrast matrix was only favorable in small fragments, probably allowing the arrival of propagules. The species-level response was highly variable.

Conclusions Landscape structure provides powerful explanations of the richness and diversity losses among epiphytes. Forest management should ensure the retention of the largest possible continuous forests. The management strategy of the matrix will depend on the conservation goal, since we observed different effects related with quality and fragment size.

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J. L. H. Cardós (✉) · I. Martínez · V. Calvo · G. Aragón
Biodiversity and Conservation Area, Department of
Biology and Geology, Physics and Inorganic Chemistry,
Experimental Sciences and Technology Superior School,
King Juan Carlos University, c/Tulipán s/n,
28933 Móstoles, Spain
e-mail: juanluish13@gmail.com

I. Martínez
e-mail: isabel.martinez@urjc.es

V. Calvo
e-mail: v.calvodonate@gmail.com

G. Aragón
e-mail: gregorio.aragon@urjc.es

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Landscape structure · Fragment shape · Species
diversity · Mediterranean oak forest · Species-area
relationship · Cyanolichens

Introduction

Mediterranean forests have been intensively fragmented over time and large proportions of the original landscapes have been transformed into croplands and grasslands in order to satisfy human needs (Thirgood 1981; Scarascia-Mugnozza et al. 2000). These fragmentation processes have yielded small and isolated forest remnants in the human-modified landscape (Saunders et al. 1991), thereby causing the decline and disappearance of numerous species linked to these habitats (Fahrig 2003).

Forest fragmentation leads to changes in the core area, shape, and spatial separation of fragments, where changes in the surrounding area of the forest fragments (matrix) and human exploitation of the remnant fragments, such as selective clearing and logging, have major effects on their habitat quality (Kupfer et al. 2006). Reductions in the core area due to fragmentation are associated with the loss of habitats for species that require interior forest conditions (Harrison and Bruna 1999). Fragments with irregular shapes undergo a greater incidence of the “edge effect” because the proportion of edge amount increases compared to more regular fragments (Laurance and Yensen 1991). In addition, the spatial separation of the fragments decreases the likely success of dispersal and reduces movements of organisms among fragments (Hanski 1998). However, the effects on the abundance and distribution of species due to changes in the size and shape of fragments might be mitigated or exacerbated by differences in the composition, structure, and management of the matrix (Murphy and Lovett-Doust 2004). For example, microclimatic variations that cause the “edge effect” will be reduced if the matrix is structurally similar to the forest fragment (Murcia 1995). The matrix quality might influence dispersal, resource availability, and the abiotic environment (Driscoll et al. 2013). Thus, the “hard contrast” between matrix and forest fragments has been shown to be one of the main causes of species loss (Fahrig 2001). The relevance of the matrix over habitat loss and fragmentation processes has been summarized in a recent review (Prevedello and Vieira 2010), which outlines that almost all the studies showed significant effects of the matrix type. Also, the authors point out that the quality of the remnant habitat and the matrix can be enhanced if the matrix vegetation physiognomy is similar to the fragment vegetation. However it

should be noted that all these studies deal with non-sessile organisms, which can move among fragments and could somehow use the matrix.

Lichens and bryophytes are suitable organisms to assess the forest loss and fragmentation because they are highly sensitive to small environmental changes (Kranner et al. 2008; Pinho et al. 2012), as their physiology is strongly coupled to the humidity, solar radiation, and temperature conditions (Green et al. 2008; Honegger 2009). They are important epiphytic organisms in Mediterranean forests (Coxson and Nadkarni 1995), where the diversity and composition of these communities depend on several environmental factors that operate at different scales (Ellis 2012).

Among the epiphytes, certain groups of shade species that require forest interior conditions (e.g., some cyanolichens) are more sensitive to environmental changes because they are highly dependent on water availability and they may experience photoinhibition with excessive radiation (Lange et al. 2004; Kranner et al. 2008). If the core area is reduced due to habitat loss and fragmentation processes, drastic changes in epiphytic composition associated to fragment size are expected. In addition, most previous studies agree that epiphytic communities are greatly influenced by the edge effect (Zartman and Nascimento 2006; Belinchón et al. 2007; Hauck et al. 2014); thus, we should expect higher diversity of epiphytes in fragments with a regular shape where the edge effect is lower.

Indeed, the consequences of the forest edge-effect on epiphytic lichens are well known (e.g., Hilmo and Holien 2002; Stewart and Mallik 2006; Belinchón et al. 2007; Brunialti et al. 2013; Aragón et al. 2015). By contrast, little is known about the effects on epiphytes of other attributes of the landscape structure related to the forest loss and fragmentation, such as the fragment size and the shape or type of the surrounding matrix, which are poorly documented and still unclear. For example, some studies have indicated that the matrix of coniferous forests may function as a filter for dispersing propagules, affecting negatively the populations of certain species linked to deciduous trees (Johansson and Ehrlén 2003; Belinchón et al. 2009). Conversely, a matrix that comprises scattered deciduous trees might facilitate dispersal of some epiphytes among fragments (Löhmus et al. 2006).

To the best of our knowledge, previous studies of forest loss and/or fragmentation have mainly focused

on the response of a single epiphytic species (Johansson and Ehrlén 2003; Snäll et al. 2003; Belinchón et al. 2009; Otálorra et al. 2011; Löbel et al. 2012), or on specific spatial attributes of fragmentation (the forest fragment size or edge effect) (Kivistö and Kuusinen 2000; Belinchón et al. 2007; Oliveira et al. 2011; Löbel et al. 2012). In addition, most studies focused on temperate or boreal forests where the humidity is not as limiting as that in Mediterranean forests (Valladares et al. 2004).

In a previous study of 306 Mediterranean oak forest fragments (Aragón et al. 2010b), the variables related to forest structure at the plot scale (management, canopy cover, and tree size) explained most of the variability in epiphytic communities, whereas the variables related to the habitat loss and fragmentation process (i.e., the size of fragments) did not have the expected importance (Aragón et al. 2010b). It is likely that the broad forest heterogeneity related to differences in management intensity and the forest structure minimized the effects of the fragment size. Thus, given these results, our main aim in the present study was to evaluate the impacts of forest loss and fragmentation on epiphytic communities (lichens and bryophytes) at plot and fragment scales after controlling the variation in forest structure.

We selected 40 fragments of dense oak forests with similar tree cover in a human-modified landscape. We quantified several landscape structure attributes (fragment size and shape, and the quality of the surrounding matrix) and forest stand structure, which are known to affect epiphytic diversity (Gignac and Dale 2005; Löbel et al. 2006; Coxson and Stevenson 2007). We hypothesized that reductions in the fragment size (i.e., loss of the core area and habitat heterogeneity), increases in irregularity (i.e., increased edge effect), and a high contrast between the matrix and forests would have negative effects on the richness and diversity of epiphytic bryophytes and lichens.

Methods

Study site

The study was performed in Montes de Toledo, central Spain (4°28'W, 39°32'N) (Fig. 1), where the climate is subhumid continental Mediterranean with a mean annual temperature of 13.2 °C and annual

precipitation of 716 mm. This area is characterized by an intense drought period during the summer (AEMET 2011). The landscape comprises Mediterranean forests fragments surrounded by different human-modified matrices, including pine plantations, shrublands (*Cistus ladanifer* and *Erica australis*), pastures, stony slopes, and crops (Perea and Perea 2008). Well-preserved forest fragments are located on unproductive stony slopes, whereas cultivated open woodlands are located in lowland areas. In the study area, forest loss and fragmentation is attributable mainly to logging activities related to charcoal production, cattle pastures, or farmlands (Perea and Perea 2008).

Experimental design and sampling

Orthophotos were taken in 2011 (provided by Centro Nacional de Información Geográfica) and used to select forest fragments with the following features: (1) fragments dominated by holm oak (*Quercus ilex* subsp. *ballota*), thereby avoiding possible changes in epiphytic communities related to different host tree species; and (2) fragments with tree cover >70 %, thereby ensuring their well preserved and mature status, as well as minimizing the effects of differences in forest structure. Finally, we selected 40 fragments with different sizes and shapes (Fig. 1), which were surrounded by a wide range of matrices.

We randomly established 10 × 10 m plots inside each fragment. A species-area curve was calculated using EstimateS 8.2 (Colwell 2009) based on data obtained in previous surveys (Aragón, unpublished data) to determine the effective number of plots per fragment that would reliably obtain at least 90 % of the species in each fragment. Consequently, the number of plots ranged from 4 to 8, proportionally to the fragment size. We selected four trees, always holm oaks, in each plot: two trees with the greatest and lowest diameter at breast height (dbh), and two trees with the closest dbh to the mean dbh in the plot, in order to capture all the variability in the epiphytic community at the plot level (Belinchón et al. 2007). The dbh of the selected trees ranged between 18 and 28 cm to avoid community changes associated with younger and older trees because the dbh is a very important factor for explaining the epiphytic community configuration (Aragón et al. 2010b). In total, 744 trees (holm oaks) were surveyed.

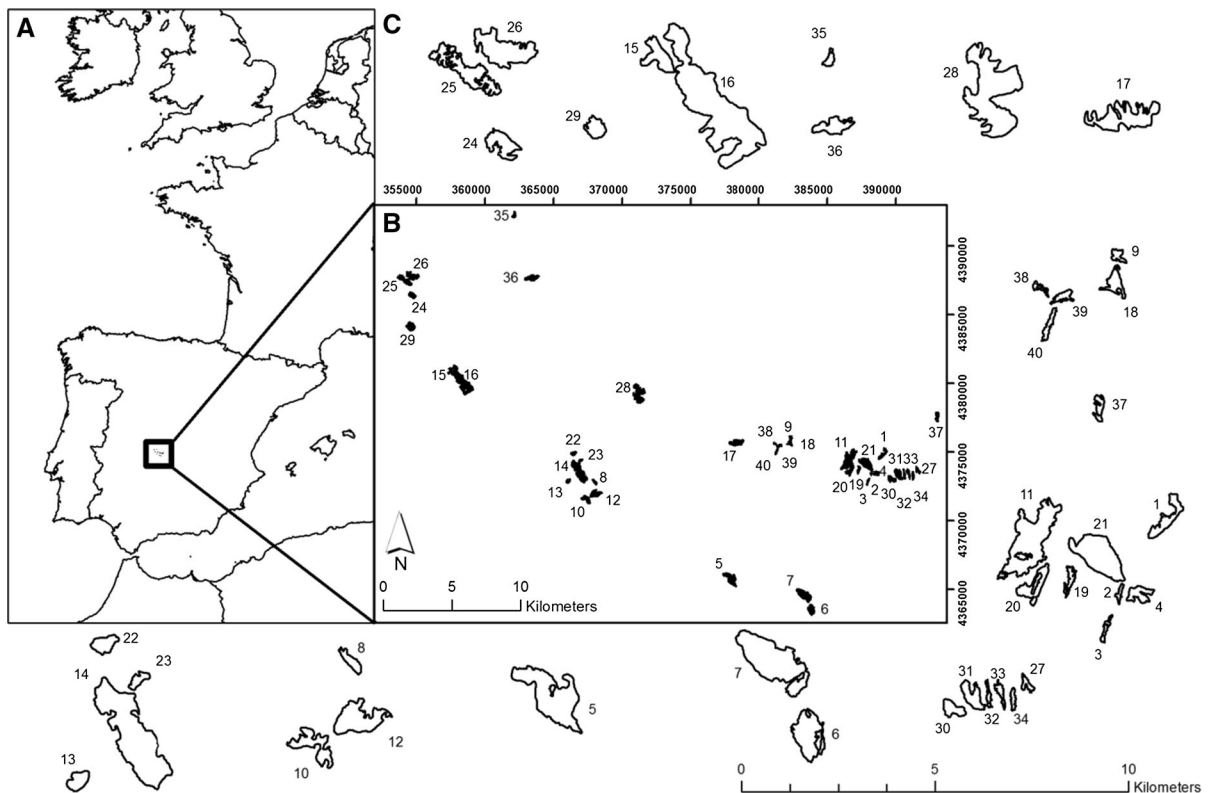


Fig. 1 Geographic location of the study site in southwest Europe. **a** The location of the fragmented landscape in southwest Europe. **b** Spatial relationships among the 40

fragments sampled. **c** Enlargements of the 40 fragments surround the figure (all at the same scale) to illustrate their sizes and shapes (their spatial relationships are not maintained)

In order to determine the occurrence of epiphytic lichens and bryophytes, we established four 20×30 cm grids on the bark of each selected tree: at breast height, at the tree base, and on the north and south aspects (2976 grids in total). We estimated the cover of each species (%) for every sample grid. For species identification we used mainly Aragón et al. (2001), Casas et al. (2006, 2009) and Smith et al. (2009). For the nomenclature of the species we followed mainly Casas et al. (2006, 2009) for bryophytes, and MycoBank, Ekman et al. (2014) and Otálora et al. (2014) for lichens. The total species richness was defined as the total number of species found at each level considered (plot and fragment). We also calculated the mean estimated cover for each species (% of the site area) in the four sites sampled on each tree, before determining the total species cover per tree (as the percentage of the grids). The same method was employed to determine the species cover at the plot and fragment levels. Simpson's diversity

index was used as a measure of species diversity for a given spatial unit (plot or fragment) using: $1/S = (\sum p_i^2)$, where p_i is the proportion of abundance for species (Feinsinger 2001). This index represents the number of species in a community if the species are equally distributed. The Bray–Curtis similarity index (Bray and Curtis 1957) was also calculated as an inverse measurement of the β -diversity, which is defined as the species turnover between the sample units in an upper sample unit, i.e., between trees within a plot or plots within a fragment in the present study.

Environmental variables

Environmental variables were considered at both the fragment and plot levels (Supplementary material Table S1).

At the fragment level, we quantified the fragment size (surface), shape, and surrounding matrix. All of the forest fragments were digitized and their sizes

were measured using the GIS package ArcMap 10.0 (ESRI Inc, USA). We used the shape index (SI), which was initially formulated by Patton (1975) and amended by Laurance and Yensen (1991). Higher SI values indicate greater irregularity in the fragments. We considered three different surrounding matrices: (1) pine plantations (PM), which could be unfavorable for dispersal of lichen propagules (Johansson and Ehrlén 2003; Belinchón et al. 2009); (2) a high-contrast matrix (HCM) that comprised crops, stony slopes, or shrubland, which is unfavorable for microclimatic forest conditions (Fahrig 2001); and (3) a low-contrast matrix (LCM) that consisted in open forests, such as dehesas (open woodlands with a very low tree density), which is less unfavorable for dispersal and microclimatic forest conditions (Murcia 1995; Boudreault et al. 2012). Next, we estimated the percentage of the perimeter around each fragment covered by PM, HCM, or LCM.

At the plot level, we measured the diameter of all trees to determine the mean plot dbh, the number of trees, altitude (m.a.s.l.), slope (°), aspect (cosine transformed), shrubland layer (%), and the canopy openness. Two hemispherical photographs were used to quantify the canopy openness with a horizontally leveled digital camera (Canon EOS 5D) aimed at the zenith, where we employed a fish-eye lens with a 180° field of view (SIGMA 8 mm F3.5 ex DG Fisheye). The photographs were analyzed with Gap Light Analyzer v2.0 (GLA v2) (<http://www.rem.sfu.ca/forestry/index.htm>), which estimates the canopy openness as a percentage. The value used comprised the average of the two values per plot.

Data analysis

We modeled the effects of environmental variables on the community traits (total species richness, lichen richness, bryophyte richness, inverse Simpson's diversity index, and Bray–Curtis similarity index) at the plot scale by fitting generalized linear mixed models (GLMMs) with the Laplace approximation (Bolker et al. 2009). We also tested the effects of the environmental variables on the abundance and presence of 40 species, which were selected based on their abundance and their representativeness in epiphytic forest communities (nitrophilous species were not considered). This modeling approach was selected because our data had an unbalanced and hierarchical structure where

plots were nested within fragments. A hierarchical data structure implies that there is a correlation between data points at different scales. This correlation inflates the degrees of freedom, thereby increasing the likelihood of a type I error. To overcome these problems, we analyzed the data using a multilevel approach that considered independent variables as explanatory (fixed factors) and fragments as random factors by applying mixed modeling (Verbeke and Molenberghs 1997). To avoid multicollinearity problems, the variable “number of trees per plot” was excluded from the data analysis because it was correlated with the “mean plot dbh” (Spearman's coefficient >0.7).

At the fragment level, we analyzed the environmental variables that might affect the richness, diversity, and species similarity at the landscape scale. We also analyzed the influence of these variables on the presence and abundance of each selected species. Thus, we fitted generalized linear models (GLMs) (McCullagh and Nelder 1989), where the predictive variables comprised the fragment size, shape, percentages of HCM and PM, and the interaction between the fragment size and HCM.

For each response variable, we assumed the most appropriate error distribution, i.e., Gaussian, Poisson, quasi-Poisson, or binomial, and applied different link functions, i.e., “identity”, “log”, “log”, and “logit”, respectively. The adequacy of the models was confirmed by examining the residuals and the predicted values, which were normally distributed, or approximately normally distributed in some cases, but without clear patterns (Zuur et al. 2009). The confidence levels (95 %) of the predictive environmental variables were obtained from the GLMs and GLMMs (Zuur et al. 2009). All the analyses were conducted with the statistical software R v.2.15.2 (R Core Team 2012) using the lme4 package (Bates et al. 2013) and the GLM function (`glm []`).

Results

Characterization of the forest fragments

The fragment size ranged between 1.5 and 97 ha, altitude varied between 680 and 1208 m.a.s.l., the tree density was 7–28 trees per plot, and the plot mean dbh was 13–22.4 cm (Supplementary material Table S1). The SI values were 1.16–4.07, which corresponded to

the highest values in the most irregular fragments. Both LCM and HCM were equally dominant in the region, whereas PM represented only 10 % of the overall area sampled.

Community response

In total, 117 species were identified: 93 lichens, 20 mosses, and four liverworts (Online Appendix 1). The total number of species per fragment varied from 17 to 73 (Supplementary material Table S1), with an average of 43.01 (SD = ± 10.75). The most common species were *Cladonia fimbriata*, *Parmelia tiliacea*, *Phlyctis argena*, *Physconia venusta*, *Homalothecium sericeum* and *Hypnum cupressiforme*, which were present in all of the fragments and in over 150 plots (Online Appendix 1). By contrast, 11 species were present in only one plot (e.g., *Micarea prasina*, *Mycobilimbia parvilobulosa* and *Hedwigia ciliata*).

The results obtained with the mixed models showed that fragment size and the HCM levels were the most important factors that contributed to the epiphytic communities (Table 1). The fragment size and the percentage of HCM had positive effects on the total and lichen richness and diversity, whereas the interaction between them had the opposite effect (Table 1). Species richness and diversity reached the highest values in the biggest fragments (Supplementary material Table S1), but relatively high values were also recorded in small fragments mainly surrounded by HCM (Figs. 2, 3). Conversely, the richness and diversity underwent a relatively intense decrease in the biggest fragments when these are surrounded by a high percentage of HCM (Figs. 2, 3). In the case of bryophyte richness, PM also had a positive effect, as well as the fragment size and HCM amount (Table 1). The species diversity also depended on the canopy openness and shrubland cover at the plot scale, with which it had a positive relationship, whereas it had a negative relationship with fragment shape at the fragment scale (Table 1). Furthermore, the similarity in the species composition was higher in small fragments but lower in those surrounded by higher percentages of HCM (Table 1).

Species response

Forest loss and fragmentation had negative effects on the presence and abundance of several species. In

general, the most demanding species (e.g., cyanolichens and squamulose species) were favored by large and regular fragments. In contrast to our hypothesis, HCM amount had positive effects on the abundance and presence of some lichens and bryophytes (e.g., *Lepraria incana*, *Nephroma laevigatum*, and *Fabronia pusilla*) (Tables 2, 3, 4). At the fragment level (Table 2), FS was the most relevant factor, exerting always a positive influence on the presence and abundance of a great number of species, especially on cyanolichens (7 out of 11 cyanolichens studied). Both kinds of matrices also had a remarkable influence over the species, but the HCM always in a positive way. Fragment shape also performed the community by determining the abundance and presence of 10 out of 40, negatively in most of the cases. At the plot level, it is noteworthy that the presence of species was mostly affected by fragment scale variables (fragment size, shape and matrix) (Table 3), whereas their abundances were largely modulated by variables at the plot scale (=microclimate) (Table 4). In this sense, lichen and bryophyte species were greatly affected in different ways by all the plot scale variables related to the forest structure (canopy cover or mean tree diameter), altitude, and aspect (Tables 3, 4). However, after evaluating the positive or negative effects of coverage and tree diameter, we found that the range of variation was very low (10–30 % for canopy openness and 13–22 cm for tree diameter) because we only considered mature forests with high coverage. In addition, some species (e.g., *H. cupressiforme*, *Ochrolechia balcanica*) were only affected by the plot level variables, whereas others (*L. incana* and *Pertusaria pertusa*) were influenced only by fragment scale variables (Tables 3, 4).

Discussion

Our results demonstrate the influence of Mediterranean forest loss and fragmentation on their epiphytic communities. The fragment size and shape, and the quality of the surrounding matrix were key factors that affected epiphytic richness and diversity in this fragmented landscape. Moreover, a high number of environmental factors influenced the responses of specific species. Previous studies have determined the importance of microhabitat characteristics for epiphytic communities (Gignac and Dale 2005; Hylander

Table 1 Summary of the generalized linear models at the fragment level and the generalized linear mixed models at the plot level, which examined the effects of the environmental factors on the community traits

Response variables (A–E) Explanatory variables	Plot level			Fragment level		
	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>
(A) Total richness						
FS	0.260	0.067	<0.001	0.545	0.099	<0.001
SI	−0.006	1.657	0.997	−0.650	2.243	0.772
HCM	0.109	0.039	0.005	0.162	0.054	0.003
PM	0.009	0.056	0.869	−0.045	0.078	0.565
FS × HCM	−0.004	0.002	0.029	−0.007	0.003	0.011
Altitude	−0.012	0.007	0.094			
Aspect	−0.609	0.859	0.478			
Shrubland cover	−0.010	0.018	0.558			
Canopy openness	−0.003	0.047	0.944			
dbh plot	−0.130	0.118	0.271			
(B) Lichen richness						
FS	0.204	0.055	<0.001	0.471	0.082	<0.001
SI	−0.032	1.368	0.982	−0.413	1.854	0.824
HCM	0.071	0.032	0.026	0.130	0.044	0.003
PM	−0.037	0.046	0.423	−0.084	0.065	0.192
FS × HCM	−0.003	0.002	0.041	−0.006	0.002	0.005
Altitude	−0.009	0.006	0.151			
Aspect	−0.340	0.758	0.654			
Shrubland cover	−0.005	0.016	0.740			
Canopy openness	0.009	0.042	0.828			
dbh plot	−0.122	0.105	0.247			
(C) Bryophyte richness						
FS	0.055	0.019	0.004	0.074	0.026	0.004
SI	0.022	0.477	0.963	−0.237	0.585	0.686
HCM	0.038	0.011	0.001	0.033	0.014	0.020
PM	0.047	0.016	0.003	0.039	0.020	0.054
FS × HCM	−0.001	0.001	0.078	−0.001	0.001	0.349
Altitude	−0.003	0.002	0.212			
Aspect	−0.147	0.333	0.659			
Shrubland cover	−0.011	0.007	0.136			
Canopy openness	−0.001	0.019	0.964			
dbh plot	−0.004	0.049	0.930			
(D) Inverse Simpson's index (diversity)						
FS	0.093	0.026	<0.001	0.140	0.031	<0.001
SI	−0.601	0.663	0.365	−1.720	0.709	0.015
HCM	0.044	0.016	0.005	0.059	0.017	<0.001
PM	0.028	0.022	0.204	0.026	0.025	0.301
FS × HCM	−0.002	0.001	0.006	−0.003	0.001	0.001
Altitude	−0.003	0.003	0.344			
Aspect	0.550	0.451	0.222			
Shrubland cover	0.023	0.010	0.018			
Canopy openness	0.064	0.026	0.013			
dbh plot	0.037	0.066	0.570			

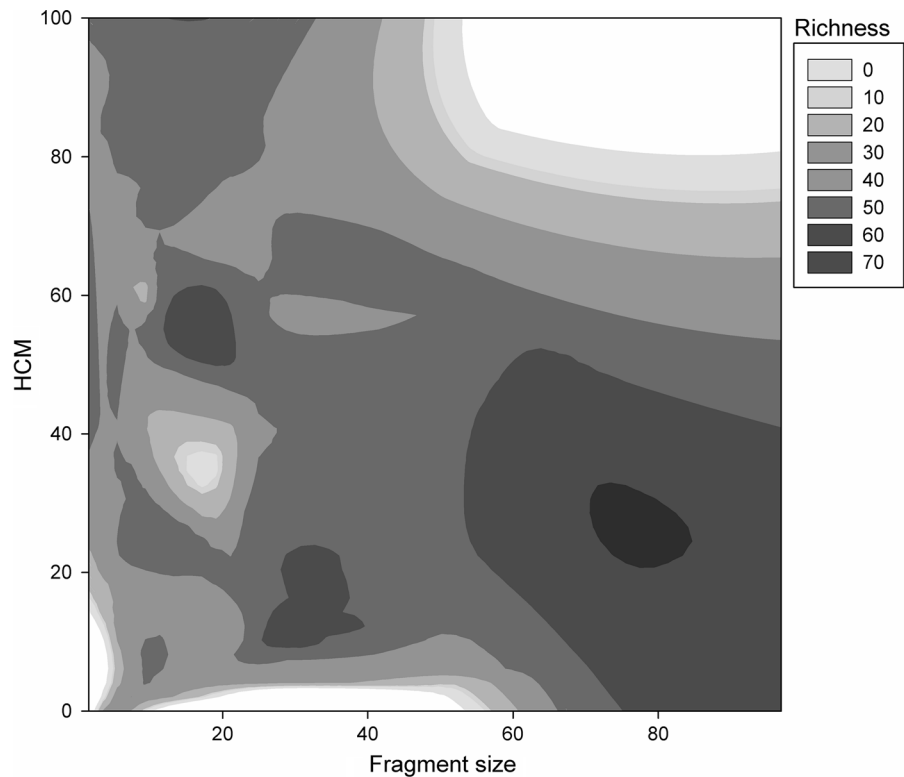
Table 1 continued

Response variables (A–E)	Plot level			Fragment level		
	Explanatory variables	Estimate	SE	<i>P</i>	Estimate	SE
(E) Bray–Curtis (similarity)						
FS	–0.211	0.067	0.002	–0.179	0.059	0.003
SI	0.062	1.681	0.970	–1.067	1.346	0.428
HCM	–0.079	0.039	0.045	–0.087	0.032	0.007
PM	–0.066	0.057	0.247	–0.058	0.047	0.217
FS × HCM	0.003	0.002	0.077	0.003	0.002	0.090
Altitude	–0.008	0.008	0.353			
Aspect	–0.024	1.243	0.984			
Shrubland cover	0.000	0.028	0.986			
Canopy openness	–0.039	0.073	0.590			
dbh plot	–0.013	0.185	0.943			

Values in bold are statistically significant ($P < 0.05$)

Estimate coefficient of the variable in the model, *SE* standard error, *FS* fragment size, *SI* shape index, *HCM* high-contrast matrix (%), *PM* pine matrix (%), *dbh* plot the mean diameter at breast height of all the trees in a plot

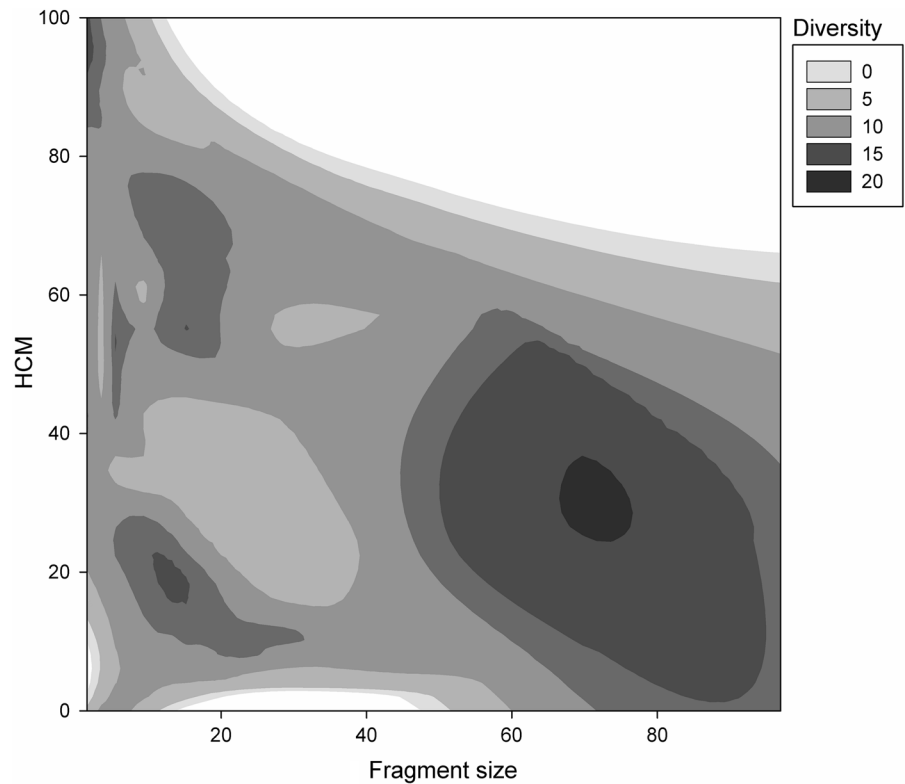
Fig. 2 Distribution of species richness along the interaction between the fragment size and the high-contrast matrix (HCM) percentage contacting each fragment



and Hedderson 2007; Aragón et al. 2010b; Oliveira et al. 2011), but after we minimized the variation in forest structure and management, the forest loss and fragmentation process still had clear effects on epiphytic communities.

Large forest fragments had the highest epiphytic richness and diversity (lichens and bryophytes), which might be related to the greater habitat availability and heterogeneity, as well as the presence of a “core area” with a greater surface (Jonsson and Jonsell 1999;

Fig. 3 Distribution of species diversity along the interaction between the fragment size and the high-contrast matrix (HCM) percentage contacting each fragment



Gignac and Dale 2005; Löhmus et al. 2007). Our results are consistent with those obtained in previous studies (Kruys and Jonsson 1997; Moen and Jonsson 2003; Zartman 2003; Pharo et al. 2004; Gignac and Dale 2005; Löbel et al. 2006; Alvarenga and Pôrto 2007; Alvarenga et al. 2009; Oliveira et al. 2011), but our study is the first to be conducted in Mediterranean climatic conditions. In a previous study of 306 Mediterranean oak forest fragments covering a greater area than in our study site, Aragón et al. (2010b) detected a non-significant relationship between fragment size and epiphyte communities, but only the variables related to forest quality and management had significant effects. However, this study included a high level of environmental heterogeneity, and thus the effect of forest loss and fragmentation was probably obscured.

Moreover, some previous studies have shown that greater habitat availability is associated with a higher number of species, simply by pure chance (Coleman 1981; Coleman et al. 1982; Carnicer et al. 2007, 2008; Honkanen et al. 2010; Alexander et al. 2011; Kraft et al. 2011). Random chance implies that more

elements will be found in a larger area than a smaller area, so randomness might play an important role when considering habitat size.

Higher species richness is also related to the presence of forest specialist species in larger fragments, presumably due to their high water demands, sensitivity to direct sunlight, and limited dispersal (Söderström 1988; Sillett et al. 2000). Thus, the surface of the “core area” might play an important role due to the lifestyles of these organisms (poikilohydric and poikilothermic). Inside the core area, the environmental conditions are optimal for the development of shaded species, which are highly sensitive to excessive irradiation and they are also highly dependent on water availability (Lange et al. 1986; Gauslaa and Solhaug 1996; Gauslaa and Coxson 2011). In general, a reduction of the core area in small fragments is associated with a loss of habitat for species that require forest interior conditions (Baldwin and Bradfield 2005; Crouzeilles et al. 2014). In the present study, the abundance of species with higher water demands and greater sensitivity to direct solar radiation (e.g., *Collema subflaccidum*, *Pectenia plumbea*,

Table 2 continued

	Fragment level									
	Presence					Abundance				
	FS	SI	HCM	PM	FS × HCM	FS	SI	HCM	PM	FS × HCM
<i>Waynea stoechaditana</i>	-	-	-	-	-	-	-	-	-	-
Bryophytes										
<i>Antitrichia californica</i>	-	-	0.055**	-	-	-	-	-	-	-
<i>Fabronia pusilla</i>	0.362*	-	0.062*	-	-	-	0.030**	-	0.052***	-
<i>Frullania dilatata</i>	-	-	-	-	-	-	-	-	-	-
<i>Hypnum cupressiforme</i>	-	-	-	-	-	-	-	-	-	-
<i>Leucodon sciuroides</i>	-	-	-	-	-	0.035*	-	-	-	-
<i>Orthotrichum affine</i>	-	-	-	-	-	-	-	-	-	-
<i>Orthotrichum diaphanum</i>	-	-	-	-	-	-	-	-	-	-
<i>Orthotrichum lyellii</i>	-	-	-	-	-	-	0.752**	-	0.020*	-
<i>Pterygandrium filiforme</i>	-	-	-	-	-	-	-	0.023*	-	-
<i>Ulota crispa</i>	-	-	-	-	-	-	-	-	-	-

Only significant estimates are shown

FS fragment size, SI shape index, HCM high-contrast matrix (%), PM pine matrix (%), + cyanolichens, · liverworts

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 3 Summary of the generalized linear mixed models at the plot level based on the presence of 40 species

	Plot level presence									
	Fragment level predictors					Plot level predictors				
	FS	SI	HCM	PM	FS × HCM	Altitude	Aspect	Shrubland	Canopy op	dbh plot
Lichens										
<i>Anapychia ciliaris</i>	–	–	0.034*	–	–0.002*	–	–1.455*	–	0.164***	0.287**
<i>Bacidia rubella</i>	0.161**	–	–	–	–	–	–	–	–	–
<i>Cladonia contocraea</i>	–	–	–	–	–	–	–	–	–	–
<i>Cladonia fimbriata</i>	–	–	–	–	–	–	1.301*	–	–	–
+ <i>Collema furfuraceum</i>	–	–	–	–	–	–	–	–0.028	–	–
+ <i>Collema subflaccidum</i>	0.099***	–	–	–	–	–	–1.950**	–	–	0.225*
+ <i>Collema subnigrescens</i>	–	–	–	0.044**	–	–	–1.036*	–	–	0.129*
+ <i>D. umhausense</i>	–	–	–	–	–	–	–	–	–	–
+ <i>Fuscopannaria ignobilis</i>	0.089*	–	–	–	–	–	–	–	–	–
+ <i>Fuscopannaria mediterranea</i>	0.087**	–	0.050**	–	–0.002*	–0.008*	–1.186*	–	–	–
+ <i>Fuscopannaria olivacea</i>	0.075*	–	–	–	–	–	–	–	–	–
<i>Lepraria incana</i>	0.039*	–	–	–	–	–	–	–	–	–
+ <i>Leptogium furfuraceum</i>	–	–	–	–	–	–	–	–	–	–
+ <i>Nephroma laevigatum</i>	0.147*	–	0.054*	–	–	–	–	–	–	–
<i>Normandina pulchella</i>	0.073*	–	–	–	–	–	–	–	–	–
<i>Ochrolechia balcanica</i>	–	–	–	–	–	–	–	–	–	–
<i>Ochrolechia pallescens</i>	–	–	–	–	–	–	–	–	–	–
<i>Parmelia sulcata</i>	–	–	–	–0.048**	–	–0.005*	–	–	–	–
<i>Parmotrema chinense</i>	–	–	–	–	–	–	–	–	–	–
+ <i>Pectenia plumbea</i>	0.168*	–	–	–	–	–	–	–	–	–
<i>Pertusaria albescens</i>	–	–	–	–	–	–	–	–	–	–
<i>Pertusaria amara</i>	–	–	–	–	–	–	–	–	–	–
<i>Pertusaria flavida</i>	–	–	–	–	–	–0.008*	–	–	–	–
<i>Pertusaria hemisphaerica</i>	–	–	–	–	–	–	–	–	–	–
<i>Pertusaria pertusa</i>	0.108***	–	0.032*	–0.121*	–0.003**	–	–	–	–	–
<i>Phlyctis argena</i>	–	–	–	–	–	–	–	–	–	–
<i>Physconia venusta</i>	–	–	–	–	–	–	–	0.026*	–	–
+ <i>Scytinium lichenoides</i>	–	–	–	0.093***	–	–	–	–	–	–
<i>Waynea adscendens</i>	0.193**	–	0.119**	–	–	–	–	–	–	–

Table 3 continued

	Plot level presence										
	Fragment level predictors					Plot level predictors					
	FS	SI	HCM	PM	FS × HCM	Altitude	Aspect	Shrubland	Canopy op	dbh plot	
<i>Waynea stoechaditana</i>	0.101*	-	-	-	-	-	-	-	-	0.438**	
Bryophytes											
<i>Antitrichia californica</i>	0.051*	-	-	-	-0.001*	-	-	-	-	-	
<i>Fabronia pusilla</i>	-	-	0.062***	0.099***	-	-	-	-	-	-	
<i>Frullania dilatata</i>	-	-	-	-	-	-	-	-	-	-	
<i>Hypnum cupressiforme</i>	-	-	-	-	-	-	-	-	-	-	
<i>Leucodon sciuroides</i>	0.050*	-	-	-	-	-	-	-	-	-	
<i>Orthotrichum affine</i>	-	-	-	-	-	-	-	-	-	-	
<i>Orthotrichum diaphanum</i>	-	-	-	0.050*	-	-	-	-	-	-	
<i>Orthotrichum lyellii</i>	-	-	-	-	-	-	-	-	-	-	
<i>Pterygandrium filiforme</i>	-	-	0.043***	-	-	-0.008**	-	-	-	-	
<i>Ulota crispa</i>	-	-	-	-	-	-	-	-	-	-	

Only significant estimates are shown

FS fragment size, SI shape index, HCM high-contrast matrix (%), PM pine matrix (%), canopy op canopy openness, dbh plot the mean diameter at breast height of all the trees in a plot, + cyanolichens, - liverworts

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 4 Summary of the generalized linear mixed models at the plot level based on the abundance of 40 species

	Plot level abundance									
	Fragment level predictors					Plot level predictors				
	FS	SI	HCM	PM	FS × HCM	Altitude	Aspect	Shrubland	Canopy op	dbh plot
Lichens										
<i>Anaptychia ciliaris</i>	-	-	-	-	-	-	-1.748***	-	0.247***	-
<i>Bacidia rubella</i>	-	-	-	-	-	-	-	-	0.033*	0.179***
<i>Cladonia contocraea</i>	-	-	-	-	-	-	-	-	-0.132**	-0.641**
<i>Cladonia fimbriata</i>	-	-	-	-	-0.001*	-	0.576***	0.006***	-	-
+ <i>Collema furfuraceum</i>	0.050*	-	0.030*	-	-	-0.006***	-	-0.007**	-0.024***	-
+ <i>Collema subflaccidum</i>	-	-	-	-	-	-0.006*	-0.434**	-	-0.046***	0.033*
+ <i>Collema subnigrescens</i>	-	-2.457*	-	-	-	-	-0.685***	-	0.058***	0.061***
+ <i>D. umhausense</i>	-	-	-	-	-	0.008**	-1.645***	-	-0.083***	-
+ <i>Fuscopannaria ignobilis</i>	-	-	-	-	-	-	-	-	-	0.058***
+ <i>Fuscopannaria mediterranea</i>	-	-	-	-	-	-	0.425***	-0.003*	-0.024*	-
+ <i>Fuscopannaria olivacea</i>	-	-	-	-	-	0.030***	-1.880***	-	-0.224***	0.192***
<i>Lepraria incana</i>	0.064*	-	-	0.046*	-	-	-	-	-	-
+ <i>Leptogium furfuraceum</i>	-	-	-	-	-	-	-2.111*	-	0.179***	0.280***
+ <i>Nephrona laevigatum</i>	0.072*	-	-	-	-	-0.0017*	0.241***	-	-0.003*	-0.026***
<i>Normandina pulchella</i>	-	-	-	-	-	-	1.028**	0.043**	-	-0.210*
<i>Ochrolechia balcanica</i>	-	-	-	-	-	-	-1.541***	-0.022***	-	0.195***
<i>Ochrolechia pallescens</i>	-	-	-	-	-	-	-1.196*	-0.039*	0.053**	-
<i>Parmelia sulcata</i>	-	-	-	-0.060***	-	-	0.380***	0.009***	0.048***	-0.067***
<i>Parmotrema chinense</i>	-	-	-	-	-	-0.021*	-	-	-	-0.715***
+ <i>Pectenia plumbea</i>	-	-	-	-	-	0.010***	-	-	-	-
<i>Pertusaria albescens</i>	-	-	-	-0.033*	-	0.002**	-0.111*	0.004***	-	-
<i>Pertusaria amara</i>	-	-	-	-	-	-	-	-0.058***	0.056***	-0.049**
<i>Pertusaria flavida</i>	-	-	-	-	-	-	1.265***	-	-	-0.108***
<i>Pertusaria hemisphaerica</i>	0.060***	-	0.038***	-	-0.001*	-0.008***	-0.936***	-	-	-0.058***
<i>Pertusaria pertusa</i>	0.180**	-	0.069*	-	-0.005*	-	-	-	-	-
<i>Phlyctis argena</i>	-	-	-	-	-	-0.003***	-0.130***	-0.003***	-	-0.019***
<i>Physconia venusta</i>	-	-	-	-	-	-	0.068**	0.003***	-0.007***	0.007*
+ <i>Scytinium lichenoides</i>	-	-	-	0.098*	-	-	-0.933***	-	-	0.158***
<i>Waynea adscendens</i>	0.119**	-	0.086***	0.079**	-0.002*	-	-	-0.014***	-0.012**	-

Table 4 continued

	Plot level abundance									
	Fragment level predictors					Plot level predictors				
	FS	SI	HCM	PM	FS × HCM	Altitude	Aspect	Shrubland	Canopy op	dbh plot
<i>Waynea stoechaditana</i>	-	-	-	-	-	0.030***	-	-	-	0.176***
Bryophytes										
<i>Antitrichia californica</i>	0.033*	-	-	-	-0.001**	-0.003***	-0.232***	-0.007***	-0.008***	0.021***
<i>Fabronia pusilla</i>	-	-	0.080**	0.084*	-	-	-0.489***	0.021***	-0.018***	0.024*
<i>Frullania dilatata</i>	-	-	-	-	-	-0.003***	-0.111**	-	-0.022***	-0.047***
<i>Hypnum cupressiforme</i>	-	-	-	-	-	0.004***	0.060*	-0.003***	-0.013***	-
<i>Leucodon sciuroides</i>	-	-	0.038*	-	-	-0.004***	0.305**	-	-	-
<i>Orthotrichum affine</i>	-	-	-	0.046*	-	-0.006***	0.293**	-	0.027***	-0.032*
<i>Orthotrichum diaphanum</i>	-	1.433*	-	0.056*	-	-0.012***	-	-	-	-
<i>Orthotrichum lyellii</i>	-	1.051**	0.015*	0.031**	-	-0.002***	-	-	-	-
<i>Pterygandrium filiforme</i>	-	-	0.040**	-	-	-0.004**	0.288**	-	-	-
<i>Ulota crispa</i>	-	-	-	-	-	-	-	-	-0.089**	-

Only significant estimates are shown

FS fragment size, SI shape index, HCM high-contrast matrix (%), PM pine matrix (%), canopy op canopy openness, dbh plot the mean diameter at breast height of all the trees in a plot, + cyanolichens; - liverworts

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Fuscopannaria ignobilis, *F. olivacea* and *Leucodon sciuroides*) was much lower in smaller fragments that lacked a core area. Therefore, the loss of higher humidity conditions and shade, which are linked to losses of the forest “core area”, lead to the disappearance of Mediterranean forest specialists, as well as an increase in the similarity of taxa that can be found in the different environments within each fragment.

The species richness and similarity were not affected significantly by the forest shape, but the epiphytic diversity was lower in more irregular fragments (Table 1). The fragment shape determines the perimeter/area relationship, and thus it can be interpreted as the incidence of the edge effect (Didham and Ewers 2012). Previous studies have demonstrated the relationships between more irregular fragments and different groups of organisms. For example, more irregular fragments are associated with lower amphibian and reptile richness (Cabrera-Guzmán and Reynoso 2012), as well as changes in the community composition of web-producing spiders (Baldissera et al. 2012), while several studies have demonstrated an association with the increased richness of understory herbs (Honnay et al. 1999; De Sanctis et al. 2010; Lomba et al. 2011). However, the larger fragments in our landscape had higher irregularity values, and thus although there was an edge effect, the large fragments facilitated the existence of the core area. Thus, the negative effect of irregularity (forest edge) on epiphytic communities could be mitigated by the fragment size due to the presence of more shade and a more humid interior environment.

The negative effect of fragment irregularity on the species diversity appears to act via the edge effect according to previous analyses of forest species (Yamaura et al. 2008). This was also the case for some interior forest lichens in the present study (Tables 2, 3, 4; e.g., *Collema subnigrescens*, *L. incana*, *Leptogium furfuraceum*, and *Pertusaria amara*), which were negatively affected by the higher edge effect in the more irregular fragments. Thus, the replacement of these typical forest species by generalist species is to be expected in more irregular fragments. Few studies have analyzed the relationship between epiphyte communities and forest fragment shape but, in agreement with our results, previous studies of the edge effect in Mediterranean epiphyte communities have highlighted the major influence of microclimatic gradients perpendicular to the edge,

which modify the diversity and community composition, but not the richness (Belinchón et al. 2007; Brunialti et al. 2013). Conversely, at the plot level, the diversity was not affected by the fragment shape, but was additionally determined by two contrasting factors: the shrubland cover, which breaks the wind flow and provides shady and humid conditions (Aragón et al. 2010a), and a higher canopy openness, which allows that more solar radiation reaches the trunks and generates a higher water evaporation (Machado and Reich 1999). Regarding the wide heterogeneity of requirements of the whole community (see Results section), the creation of different microhabitats by antagonistic conditions inside the fragments could be a key factor for the increase of diversity at the plot level (Jonsson and Jonsell 1999; Gignac and Dale 2005).

The amount of HCM surrounding the fragments clearly had a positive effect on the total species richness, and on the richness of lichens and bryophytes separately (Table 1). Similarly, the diversity and community similarity were also higher. In contrast to our expectation and to the “matrix structural similarity” hypothesis (Prevedello and Vieira 2010), the HCM appeared to have some beneficial effects on the biodiversity parameters, but only in certain cases, because its interaction with fragment size had the opposite effects on lichen richness and diversity.

The quality and spatial configuration of the matrix can enhance or mitigate the effects of forest loss and fragmentation in a pre-existing community, as reported previously (Murphy and Lovett-Doust 2004; Kupfer et al. 2006). The matrix can influence the inhabitants of a forest fragment in three ways: resource availability, allowing or preventing dispersal of organisms, and modifying the microclimatic forest conditions (Driscoll et al. 2013). A HCM does not improve the resource availability for epiphytic species because most are not capable of living there. In addition, this type of matrix does not mitigate the harshness of the edge conditions because of its structural configuration. Its structure lacks trees or even woody vegetation in most cases, thereby modifying the characteristic temperature, humidity, and light conditions in the forest core (Murcia 1995; Bergès et al. 2013; Driscoll et al. 2013). However, HCM that comprises crops, stone slopes, or shrubland can have a positive effect on dispersal because these land types do not present a barrier that prevents the arrival of new propagules. Previous studies by

Johansson and Ehrlén (2003) and Belinchón et al. (2009) showed that pine plantations surrounding forest fragments act as filters for lichen species, thereby hindering the establishment of new individuals. Finally, the interaction between fragment size and HCM can be interpreted as a beneficial effect of matrix, which is more important when the fragment size is small because the core area is also much smaller, where this allows the arrival of new propagules, thereby significantly enhancing the richness and diversity of these small forest fragments (darkest areas in the upper left part of Figs. 2 and 3). However, when the forest fragments are larger, the core area size seems to play a more important role than dispersal processes for lichens, whereas higher percentages of HCM has the opposite effect by reducing the core area and negatively affecting the richness and diversity of epiphytic communities (upper right area in Figs. 2, 3).

This result strongly contrasts with the previous findings on the effect of matrix on biodiversity patterns (Prevedello and Vieira 2010). This study showed general acceptance of the “structural similarity hypothesis” for the majority of groups of organisms, which means the more the structural contrast between the matrix and the habitat fragments, the less the richness and diversity of the communities inhabiting the fragment. But it has to be noted that this fact has been verified mostly in animals, which are able to move by themselves along the landscape and choose the “less unfavorable” matrix, while the forest epiphytes depend mostly on wind, and on the structures present along the matrix, which modulate the wind flow, to reach new localities. In the case of plants, a contrasting matrix has in general a negative effect over forest species (Murphy and Lovett-Doust 2004), but the effect of different types of matrix and its quality has been poorly explored (Jules and Shahani 2003; Prevedello and Vieira 2010). In the few cases it was tested (Mesquita et al. 1999; Nascimento et al. 2006), the structural similarity hypothesis was confirmed. For all those reasons, this positive effect of a greater amount of HCM can be considered as very new and can change the thinking about the matrix. It puts the dispersal process as a key factor controlling the species richness and diversity in Mediterranean fragmented forests, being modulated by the configuration of the matrix. Further studies are needed to go more deeply in the knowledge of the process, in two ways: first, the same hypothesis can be tested in other regions

or with other groups of wind-dispersed organisms (e.g., fungi or pteridophytes), and second, future studies should take into account dispersal at landscape scale considering variables like fragment connectivity or total remnant habitat amount around the fragments.

Moreover, the bryophyte richness increased in those forest fragments surrounded by PM and HCM. The positive influence of PM could be related to two different causes: firstly, PM could allow the establishment of propagules therein, enlarging the effective size of the fragment; secondly, PM might increase the structural forest complexity, providing any microclimatic advantage for bryophyte species. It has been documented that, at least more than a half of the bryophyte species recorded in this study, are able to grow on pine bark (Puche et al. 2006). Similarly, Pharo et al. (2004) and Pharo and Lindenmayer (2009) revealed how an exotic pine plantation surrounding non-pine native forest fragments can host a high percentage of native bryophyte flora. Moreover, the HCM increased the richness of bryophytes. The contrasting environmental conditions at the edge of the fragment compared to those inside the forest, likely increase the habitat heterogeneity inside the fragments, leading to an increase of bryophyte species differing in ecological requirements (Baldwin and Bradfield 2005; Gignac and Dale 2005).

In relation to the species response, we found that, at the plot level, the species presence is mainly determined by the fragment scale variables, and the fragment size was the most important factor. While the determination of the species abundance relied mostly on the plot scale variables, which are directly linked to the microclimatic conditions inside the fragments. Then, the structure of the landscape seems to be acting in first instance as a filter for the identity of the species inhabiting each fragment. The structure of the landscape and the fragmentation pattern have already been shown to be crucial for the composition of a wide range of species in the ecosystems (Wright et al. 1998; Echeverría et al. 2007), which emphasizes again the great consequences of the alteration of the landscape over the biodiversity. Subsequently, the abundance is mostly defined by the microclimate, highlighting the importance of the small scale climatic conditions for epiphytes (Gignac and Dale 2005, Belinchón et al. 2007; Brunialti et al. 2013), even though we searched to minimize the range of variation of the forest structure variables (mainly canopy

openness and mean tree diameter). Thus, we can conclude that the epiphytes are able to detect very small changes in their close environment, responding rapidly to the anthropogenic activity.

Implications for conservation

Our results demonstrate that the structure of the current landscape, resulting from the loss and fragmentation of Mediterranean forests, provide powerful explanations of the observed losses of epiphytic species richness and diversity. At present, studies are required to facilitate the maintenance of the highest epiphyte diversity in natural communities, thereby ensuring that the role of lichens and bryophytes in the ecosystem functionality will be retained when faced with human-related environmental change. The retention of the function of epiphytes demands the maintenance of rich and diverse communities. This objective is only possible if management strategies consider the quality of forest fragments as well as an adequate forest landscape composition, thereby allowing the existence of large and regular forest fragments. The matrix quality has been shown to be very important, and also have to be taken into account when planning forest management. Our results show that, if the conservation efforts are focused on epiphyte communities, the smallest fragments should be surrounded by a HCM, which would prevent the lack of core area by favoring the arrival of propagules, but taking into account that the empirical evidence found this measure detrimental for the habitat suitability of the overall biodiversity. Its application will depend on the local conservation goals. Future studies must try to disentangle the causes behind this unexpected effect of a HCM. Further analysis should also consider the isolation of fragments and the dispersal traits of species, to be able to give more clear and specific answers, e.g., how the degree of isolation modulates the threshold fragment size above which the sign of the impact of the HCM changes.

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