

Edge type determines the intensity of forest edge effect on epiphytic communities

Gregorio Aragón · Laura Abuja · Rocío Belinchón · Isabel Martínez

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Abstract Edge effect involves microclimatic variations (light, temperature and humidity) in the forest edge that become unsuitable for organisms adapted to forest interior conditions. We speculate that under similar edge types (shrubland matrix), the pattern in the response to forest edge might be different and more hostile for epiphytes in south-oriented edges. Because different matrix types have different effects on microclimate, we hypothesized that the magnitude of the edge effects will depend on the contrast between the physiognomy of the matrix and the forest fragment. The study was carried out in central Spain and consisted of a beech fragment surrounded by different types of vegetation matrices: pine plantation (south orientation), semi-deciduous oak forest (south orientation) and shrubland (north and south orientations). For each type of edge, we established ten transects perpendicular to the edge, running 100 m into the forest patch. Data were collected from three plots placed at 5, 50 and 100 m from the beginning of each transect. The results revealed that variations in the epiphytic composition mainly showed a replacement of forest interior species with generalist light-demanding species at forest edge. Shrubs-bordered edges showed the strongest influence on epiphytic composition, with high species dissimilarity between edge and forest interior, whereas the edge effects were mitigated when the patch was surrounded by other

forests. Besides, in the case of shrub-bordered edge, the dissimilarity of species composition between edge interior was higher in the south than in the north-facing edge. We conclude that the magnitude of the edge effect on epiphytic communities is modulated by the physiognomy of the surrounding matrix and the orientation of the forest edge. In the case of a hard contrast matrix, at least 100 m of an edge buffer are required for the conservation of the species with high humidity requirements. Therefore, one of the main problems affecting the loss and even disappearance of shaded species is the decreasing of the amount of core conditions under the increasing forest fragmentation scenarios. This potentially exacerbates forest fragmentation effects linked to livestock use, due to the physiognomically different surrounding matrix compared to forest patches.

Keywords Edge-interior gradient · Surrounding matrix · Orientation · Fragmentation · *Fagus sylvatica* · Mediterranean climate · Bryophytes · Lichens

Introduction

The amount of forests edge habitat is currently increasing as a result of the ongoing world deforestation that are creating fragmented forests within a landscape with different land uses (Wade et al. 2003). Forest edges generate changes in the physical environment of forest fragments embedded in non-forest habitats, with direct consequences on biodiversity (Debinski and Holt 2000; Ries et al. 2004; Fisher and Lindenmayer 2007). Ecological conditions along the edge-interior gradient can be distinct in terms of light and moisture availability. First, edges experience higher wind speed, higher radiation and higher dust deposition than in the forest interior (Belinchón et al. 2007; Wuyts et al. 2009; Crockatt

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G. Aragón (✉) · L. Abuja · I. Martínez
Área de Biodiversidad y Conservación, ESCET,
Universidad Rey Juan Carlos, 28933 Móstoles, Madrid, Spain
e-mail: gregorio.aragon@urjc.es

R. Belinchón
Royal Botanic Garden Edinburgh, 20A Inverleith Row,
Edinburgh EH3 5LR, UK

2012). Second, the magnitude and intensity of the edge effect is highly modulated by spatial factors such as the edge orientation and the matrix habitat (Crockatt 2012). For example, the south-oriented edges become a more hostile environment in northern hemispheres than edge facing other directions (Matlack 1993; Chen et al. 1995; Kivistö and Kuusinen 2000). Moreover, the nature of the surrounding matrix exerts influence on the intensity of edge effects. Thus, microclimatic variations resulting of the “edge effect” may diminish if the nature of the surrounding matrix is physiognomically similar to the forest patch (Murcia 1995; Mesquita et al. 1999). Accordingly, this paper examines how forest edge effect on epiphytes is likely modulated by structural and spatial attributes of the landscape.

Lichens and bryophytes are well-suited organisms for assessment of forest edge because they are highly sensitive to small environmental changes (Kranter et al. 2008; Pinho et al. 2012) since their physiology is strongly coupled to humidity, solar radiation and temperature conditions (Green et al. 2008; Honegger 2009). Besides, eutrophication caused by dust particles in more exposed areas has been considered as a significant cause of change in epiphytic communities (Loppi and Dominici 1996; Pinho et al. 2009; Aragón et al. 2010). However, the generality of the “edge effect” theory has remained controversial due to contradictory results concerning the epiphytic richness. For example, some studies suggested that epiphytic richness may increase towards the forest interior (Baldwin and Bradfield 2005), with some studies indicating no richness variation associated with changes in species composition (Zartman and Nascimento 2006; Belinchón et al. 2007; Oliveira et al. 2011) and other studies have demonstrated decreasing richness into the canopy (Kivistö and Kuusinen 2000; Hauck et al. 2014). This is remarkable, because most of the authors agree that edge effect is a major driving force shaping epiphytic community composition. In fact, most nitrophytic and light-demanding species are located near the edge, whereas more shaded and hygrophytic species appeared only at the forest interior (i.e. over 50–100 metres from the forest edge) (Zartman and Nascimento 2006; Belinchón et al. 2007; Hauck et al. 2014). However, this effect can be mitigated or exacerbated depending on different reasons. First, the contrast between the landscape matrix and the forest fragment. The “hard contrast” between the edge and the forest interior has been assessed as the main cause of the disappearance of some epiphytic species (Jørgensen 1978; Sjöberg and Ericson 1992) or even the decline in their populations (Esseen and Renhorn 1998; Rheault et al. 2003). For example, the cover of a single hygrophytic species (*Lobaria pulmonaria*) diminished in *Quercus pyrenaica* forest patches surrounded by a heath matrix, likely hardening the microclimatic conditions

and the irradiation levels within the oak patches (Belinchón et al. 2009). On the other hand, the nature of the surrounding matrix may also have implications on the dispersion and colonization of epiphytes. Thus, a matrix of coniferous forests was shown to be a filter for dispersing propagules affecting the demography of certain species linked to deciduous trees (Johansson and Ehrlén 2003; Belinchón et al. 2009). Second, the microclimatic variation associated with different edge orientations. For example, more severe microclimatic conditions in south-exposed edges compared to north ones might modify the growth rates of epiphytic lichens, specially the more hygrophytic species (Hylander 2005; Löbel et al. 2012), thereby resulting in an impoverishment of the epiphytic communities (Kivistö and Kuusinen 2000).

Most studies on edge effects in epiphytes have been conducted on boreal forests (Esseen and Renhorn 1998; Kivistö and Kuusinen 2000; Rheault et al. 2003). The extent to which the results from these studies are also representative in Mediterranean forests is less clear, given the distinctive climatic features in the Mediterranean region (high temperatures and severe water deficit during the dry season). Mediterranean forest landscapes have been intensively fragmented during the last centuries, resulting in a mosaic of spatially heterogeneous landscapes, with scattered native forests remnants surrounded by shrubland, grassland and conifer plantations (Thirgood 1981; Scarascia-Mugnozza et al. 2000).

In this study, our main goal was to understand the response of epiphytic communities (lichen and bryophytes) to forest edge on a Mediterranean beech forest (*Fagus sylvatica* L.). First, we hypothesized that edge orientation is playing a significant role in determining the response of epiphytes to edge effect. For this, edge effect was evaluated on different aspects of the same surrounding matrix, e.g. shrubland. Second, we discuss the possible implications of the nature of the matrix (pine plantation, shrubland and semi-deciduous oak forest).

Materials and methods

Study area

The study was conducted in a well-preserved beech forest of ca. 300 ha, located in the easternmost tip of the Sistema Central Range in Spain. At this location, *F. sylvatica* reaches its southern and western limit (41°15N 3°23W) (Costa et al. 2001). The climate is Mediterranean with a mean annual temperature of 8.6 °C and annual rainfall of 1,253 mm (Climatic station Cerezo de Arriba, La Pinilla, 1,500 m a.s.l.), with a drought period from July to August. In this area, the presence of beech forests is determined by environmental conditions and topography, because closed

valleys favour the accumulation of moist winds and fogs in the summer months (Costa et al. 2001).

The study site consisted of one isolated patch of *F. sylvatica* embedded in a matrix as follows: (1) pine plantation (*Pinus sylvestris*) in south orientation, (2) shrubland (*Genista cinerea* ssp. *cinerascens*, *Cytisus oromediterraneus*, *Adenocarpus hispanicus* and *Erica australis*) in north and in south orientation and (3) semi-deciduous oak forests (*Q. pyrenaica*) in south orientation.

Experimental design and data collection

For each type of edge, we established ten transects perpendicular to the edge. Transects run 100 m into the forests patch (beech forest) and were distanced at least 15 metres apart. Data were collected from three plots (5 × 5 m) in each transect. Plots were placed at 5, 50 and 100 m from the beginning of each transect. A total of 120 plots were established, 30 for each type of forest edge.

Field sampling was based on the methods of Belinchón et al. (2007), and all epiphytic lichens and bryophytes were included in the study. Within each plot, occurrence of epiphytic lichens and bryophytes was estimated on two trees per plot (for a total of 240 trees). The tree with the greater diameter and the tree with a diameter at breast height (dbh) closed to the mean dbh of the plot were selected in order to get a good representation of the epiphytic community of the stand (Belinchón et al. 2007). 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. We used the means of four data sets (epiphytic composition, total species richness, lichen richness and bryophytes richness and Shannon index) for a given sample position. The species richness was defined as the total number of species found in the four grids per tree. For the lichen composition, we calculated the mean estimated cover of each species (% of the grid area) for the four sample grids. We calculated the total species cover per tree (as percentage of the grids) using the same methods.

Within each plot, we measured the dbh of all trees, the number of the trees, the distance to the edge and the canopy openness. Canopy openness was estimated from hemispherical photographs. Photographs were taken at breast height and at ground level in the centre of each plot, using an horizontally levelled digital camera (Canon EOS 5D) aimed at the zenith, using a fish-eye lens of 180° field of view (SIGMA 8 mm F3.5 ex DG Fisheye). Photographs were analysed using Gap Light Analyzer program version 2.0 (GLA v2) (<http://www.rem.sfu.ca/forestry/index.htm>) that estimates the canopy openness in percentage. The value used is the average of the two values in each plot.

Both air temperature and relative humidity were measured with twenty four sensors (HOBO pro V2) placed at 5,

50 and 100 m from the edge along two transect for each area. Sensors were read every hour. The microclimate station recorded temperature and relative humidity continuously (from October 2009 to November 2011).

Data analyses

We compared the effect of stand and tree scale variables among the four situations (types of forest edges) on the community traits of total richness, bryophytes richness and Shannon diversity index by fitting generalized mixed linear models (GLMMs) (McCullagh and Nelder 1989). Additionally, lichen species was grouped into three categories based on the sensitivity to solar radiation (see Nimis 1993; Nimis and Martellos 2008): light demanding, intermediate and shaded species. All data were analysed using a multilevel approach, considering plots and transects as random sources of the variation and predictors as explanatory variables (distance to the edge, canopy openness, number of trees and tree diameter). The significance of each predictor was estimated by means of an analysis of deviance. For total species richness and Shannon diversity index, we fitted the mixed models using a normal response, whereas for the rest of variables, we used the Poisson response. All GLMM computations were performed using SAS macro program GLIMMIX, which iteratively calls SAS procedure Mixed until convergence.

Epiphytic composition among the four situations was compared using version 6.1.11 of the PRIMER multivariate statistical analysis software (Anderson et al. 2008). In this analysis, the experimental design included two factors: distance to the edge (three levels, fixed factor) and plot (10 levels, random factor nested within distance) with two replicate trees for each plot. The cover data were $\log_{10}(x + 1)$ -transformed to account for contributions by both rare and abundant taxa. We used the Bray-Curtis distance measure.

To test whether the distance to the edge had significantly different compositions of epiphytic species and to detect the effects of plot variability, we performed a two-factor permutational multivariate analysis of variance (PERMANOVA) on the cover data for each situation (Anderson et al. 2008). To assess species similarity among the different distances, we performed additional pairwise PERMANOVA tests (Anderson et al. 2008). We also calculated the Bray-Curtis dissimilarity within distances. For all tests, we allowed 9,999 random permutations under the reduced model.

Results

Characterization of the patches

Environmental variables are summarized in Table 1. Number of trees per plot was significantly correlated with

Table 1 Mean \pm SD for the environmental variables grouped by the four types of forest edge

Structural features	South-pine	North-shrub	South-shrub	South-oak
Number of trees	6.7 \pm 1.51	6.23 \pm 1.98	5.73 \pm 1.97	4.83 \pm 1.23
Tree diameter (cm)	19.43 \pm 3.22	20.54 \pm 4.03	22.97 \pm 7.96	23.77 \pm 6.55
Canopy openness (%)	40.5 \pm 14.42	45.09 \pm 17.97	44.27 \pm 15.65	39.73 \pm 15.71

Table 2 Means for humidity and temperature at different distances of the forest edge (5, 50 and 100 m)

Distance (m)	South-pine			North-shrub			South-shrub			South-oak		
	5	50	100	5	50	100	5	50	100	5	50	100
Temperature (°C)	7.57	7.75	7.69	7.55	7.58	7.60	8.04	7.95	8.11	8.26	8.31	8.15
Humidity (%)	75.73	75.21	76.01	76.28	76.93	75.65	72.84	73.95	74.96	74.86	73.83	76.41
Canopy openness (%)	37.80	42.38	41.32	55.26	40.93	38.95	52.46	41.08	39.82	41.39	40.23	37.39

mean tree diameter per plot (Spearman rho -0.810 , $p < 0.001$). Tree density ranged between three and twelve trees per plot and canopy openness between 26.38 and 66.14 %. Higher canopy openness was at forest edges for shrubland matrices (Table 2). Significant differences in canopy openness were found in an edge-interior gradient in the cases of hard contrast matrices (*N*-shrubland, $p < 0.001$ and *S*-shrubland, $p = 0.001$), while no gradient was found when forested matrices (Pine forest, $p = 0.056$ and oak forest, $p = 0.153$).

Microclimatic variations along the distance gradient for temperature and moisture are shown in Table 2. Mean temperature and relative humidity were slight higher in the interior of the forest except for oak forests matrix and matrix of shrub in north orientation, respectively. However, differences only accounted for 0.2 °C from temperature and 2–3 % from relative humidity.

Species richness and diversity

A total of 49 epiphytic species (41 lichens and eight bryophytes) were identified on 240 trees (“Appendix”). Lichen species were grouped according to the solar radiation sensitivity as follows: nine light-demanding species, 16 intermediate and 16 shaded species (“Appendix”).

Results of the mixed models showed the influence of matrix type on epiphytic richness. Total species richness increased towards the forest interior when surrounding matrix is dominated by pines or shrubland-north orientation. However, no relationship was found in the case of shrubland-south orientation matrix. Finally, species richness was positively correlated to forest edge when considering oak forest matrix (Table 3). Similar trends were detected for the richness of bryophytes, whereas the Shannon diversity index showed non-significant differences in relation to distance to the edge.

In the case of epiphytic lichens, light-demanding species and shaded species had opposite patterns when surrounding matrix was dominated by shrubland, as light-demanding species preferred forest edge situations with shaded lichens mostly associated with forest interior (Table 3).

Epiphytic composition

Multivariate statistical analyses showed that large component of variation was associated with the forest edge-interior gradient (i.e. distance to the edge) (Table 4). However, the component of variation linked to distance to the forest edge was higher in the cases where there is no forest continuity as surrounding matrix (Table 4). The subsequent pairwise test revealed significant differences in epiphytic composition between all three distances, except when the contact edge was dominated by oaks (Table 5), and the dissimilarity between distances increased with an increase in length to the forest edge (Table 5).

Discussion

Our results revealed that the edge effect on our Mediterranean beech forest patch is highly modulated by the nature of the surrounding matrix. Although significant differences in microclimatic conditions along the edge-interior gradient were not found, epiphytic composition was affected by the edge type and edge orientation. Edge effect is a complex factor to interpret, because it co-varies with mixed of structural and spatial attributes (Murcia 1995). In addition, it is well documented that environmental heterogeneity within forested landscapes might mask the prevalence of edge-interior variation (Murcia 1995; Chen et al. 1999). For example, differences in the forest structure (e.g. number of trees per plot or mean tree diameter) can

Table 3 Results of the generalized mixed linear models (GLMMs) on some community traits (richness)

	Total richness	Shannon diversity	Bryophyte richness	Shaded species	Sunny shaded	Light-demanding species
South-pine forest matrix						
Distance	(+)16.94***	(+)4.40*	(+)6.23*	(+)25.02***	(+)0.12	(-)0.27
Canopy openness	(-)12.45**	(-)4.78*	(-)1.04	(-)0.11	(-)11.63**	(+)0.33
Number of trees	(-)0.17	(-)2.12	(-)2.40	(-)2.29	(+)1.19	(+)0.01
Tree diameter	(+)0.06	(-)0.06	(+)1.53	(-)0.24	(+)0.63	(-)6.93*
North-shrubland matrix						
Distance	(+)12.33**	(+)0.87	(+)7.73*	(+)29.20***	(+)0.23	(-)9.28**
Canopy openness	(+)2.72	(+)1.61	(-)1.43	(-)0.21	(+)1.57	(+)1.16
Number of trees	(+)2.54	(+)5.93	(+)0.26	(-)0.97	(+)0.08	(+)1.67
Tree diameter	(+)8.36**	(+)11.13**	(+)7.80**	(+)14.14***	(+)0.57	(-)6.30*
South-Shrubland matrix						
Distance	(+)0.05	(-)0.30	(+)1.27	(+)35.37***	(-)0.96	(-)51.56***
Canopy openness	(-)0.07	(-)0.60	(-)1.50	(+)0.47	(+)0.01	(-)0.92
Number of trees	(-)0.15	(+)0.01	(-)0.03	(-)0.01	(-)0.43	(+)1.14
Tree diameter	(+)1.42	(+)4.17*	(-)0.01	(+)15.07***	(-)6.81*	(-)8.53**
South-Oak forest matrix						
Distance	(-)13.50**	(-)4.16	(-)8.36**	(-)0.30	(-)1-03	(-)3.56
Canopy openness	(-)9.70**	(-)9.40**	(-)5.53*	(-)0.81	(-)0.01	(-)1.40
Number of trees	(+)1.24	(+)2.47	(+)0.59	(+)0.98	(-)0.01	(-)0.94
Tree diameter	(+)0.15	(+)11.14**	(+)10.67**	(+)10.89**	(-)19.45***	(-)20.70***

Sign of trend, F value and level of significance are included

* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. The random variable plot was only significant for the richness of shaded species (Z value = 1.71, Prob. $Z = 0.043$) and bryophytes (Z value = 2.60, Prob. $Z = 0.005$) in the case of south-pine forest matrix

modulate the canopy openness and, consequently, influence the light and humidity patterns. Therefore, in agreement with other studies (Murcia 1995; Esseen and Renhorn 1998), our results suggest that edge dynamics are complex and a portion of variability is associated with forest structure (plot and tree levels).

Edge orientation determines the strength of edge effect

As we a priori expected, edge aspect (e.g. north vs. south facing) was extremely important for the magnitude of the edge effect. We observed that the magnitude of edge effect on epiphytic communities was higher in the south than in the north-facing edges in the case of shrub-bordered edge. Dissimilarity of species composition between edge interior was higher in the case of south-exposed edge. However, contrary to Kivistö and Kuusinen (2000), differences in community composition were not associated with changes in richness or diversity. At south-facing edge, the canopy openness was the main factor explaining the presence of light-demanding species at the edge; besides, high species replacement between the edge and forest interior was found. However, in the case of the north-facing edge, the severe conditions of the edge were mitigated by the

orientation, being light-demanding species absent at the edge. Thus, the similarity in species composition along the edge-interior gradient was higher with increasing total richness at forests interior. Our results are in agreement with Hylander (2005), who found a significant reduction in growth of two bryophytes as a result of changes in microclimate linked to the edge orientation. Hylander addresses that the magnitude of the edge effect was mitigated in north-facing edge in relation to the low irradiance levels compare to the south-facing edge.

Edge types determine edge effect

Shrubs-bordered showed the strongest influence on epiphytic composition, while the direct consequences of edge effects decreased when edges are surrounded by forests (natural oak forest and pine plantation). The results support the idea that the magnitude of the edge effect is driven by the patch contrast between the surrounding matrix and the natural habitat (Cadenasso et al. 2003; Harper et al. 2005; Gieselman et al. 2013). Certainly, our results also showed that the harshness of the edge (i.e. greater insolation exposure and more intense desiccation) is more abrupt in open clear-cut boundaries, triggering photoinhibition stress

Table 4 Results of the two-factor PERMANOVA by distance from edge and plot

Type of edge	Source	df	MS	Pseudo-F	<i>P</i>	CV (%)
South-pine	Distance	2	5,181.2	9.315	0.0001	15.21
	Plot (Distance)	27	556.2	1.695	0.0002	10.68
	Residual	30	328.1			18.11
	Total	59				
North-shrub	Distance	2	9,364.3	12.354	0.0001	20.74
	Plot (Distance)	27	758	1.792	0.0001	12.94
	Residual	30	423.1			20.57
	Total	59				
South-shrub	Distance	2	13,612	14.762	0.0001	25.19
	Plot (Distance)	27	922.1	1.461	0.0021	12.06
	Residual	30	631.3			25.13
	Total	59				
South-oak	Distance	2	4,234	3.830	0.0002	12.51
	Plot (Distance)	27	1,105.4	1.437	0.0084	12.96
	Residual	30	769.5			27.74
	Total	59				

Table 5 Results of pairwise PERMANOVA test between distances (5, 50 and 100 m)

Zonas de estudio	Distances (m)	Dissimilarity	<i>P</i>
South-pine	5–50	35.67	0.0002
	5–100	40.27	0.0001
	50–100	30.15	0.0054
North-shrub	5–50	41.92	0.0001
	5–100	51.19	0.0001
	50–100	38.53	0.0005
South-shrub	5–50	48.25	0.0001
	5–100	62.01	0.0001
	50–100	43.12	0.0006
South-oak	5–50	43.96	0.0009
	5–100	49.19	0.0001
	50–100	43.52	0.7347

Dissimilarity (%) (Bray-Curtis index) and level of significance

that impairs lichen growth (Coxson and Stevenson 2007). In addition, the particular composition of the epiphytic communities may be partially predicted based on the type of edge associated with the over imposed physical changes in the microclimatic conditions (Baldwin and Bradfield 2005; Belinchón et al. 2007; Brunialti et al. 2013). Thus, the most light-demanding and disturbance-tolerant species were related to shrub-bordered edges.

Although air humidity and temperature not showed differences along the edge-interior forest gradients, we consider that irradiance levels may be strongly modulating epiphytic responses. For instance, some authors showed that light variability in forest understory was the main factor influencing epiphytic communities rather than the

atmospheric humidity and temperature (Renhorn et al. 1997; Belinchón et al. 2007; Brunialti et al. 2013). In this sense, we detected a high species replacement (as a measure of Bray-Curtis dissimilarity) between edge and forests interior, but not necessarily changes in the epiphytes richness as previously showed by several authors (e.g. Belinchón et al. 2007; Oliveira et al. 2011). In the case of abrupt contrast matrix, light-demanding species were linked to forest edge and replaced towards the forests interior by shaded species. In general, lichens and bryophytes occurring in sheltered habitats are more sensitive to environmental changes, because they are strongly dependent on atmospheric moisture and they suffer photoinhibition when are exposed to greater sunlight than their normal environment (Green et al. 2008; Kranner et al. 2008). This is the case of some cyanolichens without cortical pigments, or drought-sensitive mosses, that are usually associated with old-growth forests growing under low-light environments of forests interior (Burgaz et al. 1994; Sillett and Antoine 2004; Green et al. 2008; Király et al. 2013).

When considering a matrix type that is physiognomically similar to forests patch, the abiotic edge effect is mitigated (Driscoll et al. 2013). However, in the case of the matrix of pine plantation, although there is a forest continuity with the forest patch at landscape level, total epiphytic richness species increased at forests interior mainly caused by an increasing of shaded species. Three reasons might be explaining this fact: (A) Some authors suggested that bark features of *P. sylvestris* (i.e. roughness, hardness, pH) could be a filter for dispersion and colonization of propagules (Johansson and Ehrlén 2003; Belinchón et al. 2009). However, this study was not conducted for this

forest, and it is much easy to assume that most lichen propagules came from the forest itself. (B) Management of the pine matrix (clearing and logging) for timber extraction may affect forest edge, causing the disappearance of the most sensitive species, due to gap formation and increased eutrophication (Aragón et al. 2010; Nascimbene et al. 2013). (C) The span of 40 years of recovery by pine plantation (Fernández 2002) was not enough to regenerate the diversity of shaded species in the forests edge lacking for a long time when forest patch was contacting with a shrubland matrix. However, when considering a forestry matrix of *Q. pyrenaica*, shaded species are also present in forests edge. Bark features of *Q. pyrenaica* (pH, roughness, etc.) provide resources that support a wide range of species also growing on *F. sylvatica*, facilitating the dispersion and colonization in the forest edge.

This pattern of severe shifts in the composition of epiphytic communities could be extrapolated to the Mediterranean landscape with similar management and climatic conditions, and consequences of the increase in forest fragmentation could be predicted. In central Spain, several forests have been transformed into pasture and heathlands due to the intensive livestock during the sixteenth–twentieth centuries (Hernández and Sainz 1978), and currently, the small isolated remnant forests are included within the human-modified landscape (Belinchón et al. 2009). Under increasing forests fragmentation (i.e. reduction in the patch size and increase in the high contrast matrix), the amount of core conditions will be decreased, and therefore shade-

adapted species linked to forests interior conditions could become rarer or even disappear.

Conclusions

Variations in epiphytic communities along the forests edge-interior gradient were modulated by the nature of the surrounding matrix. Abrupt edges (i.e. non-forested surrounding matrix) caused shifts in epiphytes at forest edge mainly due to the replacement of shaded species with generalist light-demanding species, and the magnitude of these changes was strongly dependent on edge orientation. In a context of increasing forest fragmentation due to agriculture or livestock land use, the fragment size will be reduced (i.e. loss of core area) and the amount of high contrast matrices (shrubland, grassland or bare soil) will be increased. This might affect the occurrence of the species that require forests interior conditions, more sensitive to the more extreme conditions of the forests edge.

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Appendix

See Table 6.

Table 6 Lichen and bryophyte species and number of trees on which each species appears in the four types of edges, at different distances

Species	Pine-S			Shrub-N			Shrub-S			Oak-S		
	5	50	100	5	50	100	5	50	100	5	50	100
Lichens												
<i>Anaptychia ciliaris</i> (L.) Kórb.*	0	0	3	0	2	3	0	1	5	3	1	2
<i>Buellia disciformis</i> (Fr.) Mud	20	20	20	20	17	8	19	16	11	13	11	7
<i>Caloplaca holocarpa</i> (Hoffm.) Wade [#]	0	0	0	0	0	0	7	0	0	0	0	0
<i>Candelariella vitellina</i> (Hoffm.) Müll. Arg. [#]	0	0	0	9	0	0	14	0	0	0	0	0
<i>Chromatochlamys muscorum</i> (Fr.) H. Mayrh. & Poelt*	0	0	0	0	0	0	0	0	0	0	1	1
<i>Cladonia coniocraea</i> (Flórke) Sprengel*	0	0	0	0	0	0	0	8	1	0	0	0
<i>Cladonia fimbriata</i> (L.) Fr.*	0	2	3	1	7	12	0	4	10	9	6	5
<i>Evernia prunastri</i> (L.) Ach	1	2	2	0	0	0	0	0	0	0	0	0
<i>Flavoparmelia soredians</i> (Nyl.) Hale [#]	0	0	0	1	0	0	0	0	0	0	0	0
<i>Hypogymnia tubulosa</i> (Schaer.) Hav.	1	0	0	4	0	0	0	0	0	0	0	0
<i>Lecanora argentata</i> (Ach.) Malme	20	20	17	20	17	17	17	15	11	11	8	7
<i>Lecanora carpinea</i> (L.) Vainio	3	6	0	1	9	12	8	9	2	4	0	1
<i>Lecanora chlarotera</i> Nyl. [#]	20	20	20	20	18	16	17	12	7	12	8	7
<i>Lecanora intumescens</i> (Rebent.) Rabenh.	12	5	6	1	7	2	2	9	4	2	4	0
<i>Lepraria incana</i> (L.) Ach.*	0	0	1	0	4	4	5	7	10	7	4	3
<i>Leptogium lichenoides</i> (L.) Zahlbr.*	0	0	0	0	0	0	0	0	0	0	1	1

Table 6 continued

Species	Pine-S			Shrub-N			Shrub-S			Oak-S		
	5	50	100	5	50	100	5	50	100	5	50	100
<i>Lobaria pulmonaria</i> (L.) Hoffm.*	0	0	1	0	0	0	0	0	4	0	2	3
<i>Melanohalea exasperata</i> (De Not.) O. Blanco et al.#	12	11	8	12	10	2	14	12	2	12	4	1
<i>Melanelixia glabra</i> (Schaer.) O. Blanco et al.	8	17	20	0	14	16	7	20	19	20	20	19
<i>Melanelixia fuliginosa</i> (Fr. ex Duby) O. Blanco et al.	1	2	9	6	3	0	10	5	5	6	5	6
<i>Nephroma resupinatum</i> (L.) Ach.*	0	7	10	0	3	13	0	7	15	7	9	7
<i>Ochrolechia pallescens</i> (L.) A. Massal.	0	0	5	1	0	2	1	3	2	2	1	3
<i>Ochrolechia turneri</i> (Sm.) Hasselrot*	0	0	0	0	0	0	0	2	1	2	0	1
<i>Parmelia saxatilis</i> (L.) Ach.	0	0	0	7	0	0	4	0	0	0	0	0
<i>Parmelia sulcata</i> Taylor	20	20	20	20	20	20	20	20	20	20	20	20
<i>Parmelina tiliacea</i> (Hoffm.) Hale	4	6	10	11	5	13	18	16	6	17	11	5
<i>Peltigera collina</i> (Ach.) Schrader*	0	0	0	0	0	2	1	3	7	5	2	9
<i>Pertusaria amara</i> (Ach.) Nyl.*	1	4	4	0	3	11	0	0	4	0	2	6
<i>Pertusaria albescens</i> (Huds.) M.Choisy & Werner*	0	0	0	0	0	0	0	1	10	5	3	1
<i>Pertusaria coronata</i> (Ach.) Th.Fr.*	0	0	0	0	0	0	0	0	3	2	2	2
<i>Pertusaria hemisphaerica</i> (Flörke) Erichsen*	0	0	0	0	0	0	0	1	5	0	15	14
<i>Phlyctis argena</i> (Sprengel) Flotow*	0	0	1	0	0	3	0	0	0	2	2	4
<i>Physcia tenella</i> (Scop.) DC.#	0	0	0	12	0	0	0	0	0	0	0	0
<i>Physconia distorta</i> (With.) J.R. Laundon#	0	0	0	0	0	0	11	1	0	0	0	0
<i>Physconia enteroxantha</i> (Nyl.) Poelt#	0	0	0	0	0	0	5	0	0	0	0	0
<i>Physconia venusta</i> (Ach.) Poelt*	0	2	8	0	7	15	0	10	15	11	9	7
<i>Platismatia glauca</i> (L.) Culb. & C. Culb.	12	0	0	1	0	0	0	0	0	0	0	0
<i>Pseudevernia furfuracea</i> (L.) Zopf	13	0	0	7	0	0	0	0	0	0	0	0
<i>Ramalina farinacea</i> (L.) Ach.	0	3	1	0	0	0	2	0	0	0	0	0
<i>Ramalina fraxinea</i> (L.) Ach.	16	17	18	7	12	11	9	17	18	15	12	11
<i>Xanthoria parietina</i> (L.) Th. Fr.#	0	0	0	0	0	0	5	0	0	0	0	0
Bryophytes												
<i>Antitrichia curtipendula</i> Hedw. Brid.	0	0	0	0	3	4	0	0	0	2	13	14
<i>Homalothecium sericeum</i> (Hedw.) Schimp.	0	0	0	0	0	0	0	0	0	2	2	0
<i>Orthotrichum lyellii</i> Hook. & Tayl.	14	18	17	16	20	20	14	14	12	18	11	9
<i>Orthotrichum affine</i> Brid.	0	0	0	0	0	0	0	0	1	0	0	1
<i>Leucodon sciuroides</i> Schwägr.	0	2	3	0	5	10	0	11	6	4	1	0
<i>Frullania dilatata</i> (L.) Dum.	0	6	1	0	8	8	1	1	5	13	11	11
<i>Porella platyphylla</i> (L.) Pfeiff.	0	2	1	0	6	7	1	0	4	8	4	4
<i>Pterigymnandrum filiforme</i> Hedwig	15	18	20	17	19	20	11	20	19	19	20	20

Lichens are classified according to their sensitivity to solar radiation in the Mediterranean region (Nimis 1993; Nimis and Martellos 2008)

* Shaded species; # light-demanding species; no-symbol, intermediate sunny-shaded species

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